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Avoiding lodging in irrigated spring wheat. II. Genetic variation of stem and root structural properties

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ABSTRACT

Lodging-related traits were evaluated on the CIMMYT Core spring wheat Germplasm Panel (CIMCOG) in the Yaqui Valley of North-West Mexico during three seasons (2010–2013). Genetic variation was significant for all the lodging-related traits in the cross-year analysis, however, significant G × E interaction due to rank changes or changes in the absolute differences between cultivars were identified. The inconsistences on cultivar performances across seasons particularly reduced the heritability of key characters related to root lodging resistance (anchorage strength). Target characters related to stem lodging resistance (stem strength) showed good heritability values equal or above 0.70. Positive correlations between stem strength and stem diameter and between root plate spread and root strength were found. Selecting for greater stem diameter and wall width, greater root plate spread and shorter plant height could enable breeders to increase lodging resistance by increasing stem strength, root strength and decreasing plant leverage, respectively. Achieving a lodging-proof crop will depend on finding a wider root plate spread and implementing new management strategies. Genetic linkages between lodging traits will not constrain the combination of the key lodging-trait dimensions to achieve a lodging-proof ideotype. However, strong association between stem strength and stem wall width will increase the total biomass cost needed for lodging resistance.

1. Introduction

The prediction of world population growth for the next decades entails an urgent need to adapt food crops to ensure global food supply demands in the future (Foulkes et al., 2011). Raising wheat productivity will be a fundamental strategy to achieve this (Reynolds et al., 2012). In the last years, breeding efforts have been focussed on increasing wheat production by raising yield potential (Acreche et al., 2008; Fischer and Edmeades, 2010; Slafer and Araus, 2007). Substantial yield increases will require a two-pronged approach composed by: i) increasing photosynthetic capacity and above-ground biomass (Parry et al., 2011) and ii) optimizing dry matter partitioning to grain yield while maintaining lodging resistance (Foulkes et al., 2011). Lodging, the permanent displacement of stems from the vertical position, may limit yield improvement by two routes: i) directly by reducing photosynthetic capacity due to changes in canopy architecture (Berry and Spink, 2012) and ii) indirectly through breeding by increasing the amount of dry matter that must be partitioned into support structures at the expense of spike dry matter growth and yield when lodging resistance is increased (Berry et al., 2007). An improved lodging resistance achieved through careful optimisation of biomass partitioning will be required if genetic gains in yield potential are to be realized (Reynolds et al., 2011).

Lodging is a complex phenomenon influenced by many factors including wind, rain, topography, soil type, previous crop, husbandry and disease. There are two main types of lodging; root lodging caused by failure of the anchorage system, and stem lodging caused by buckling of the stem. Conditions promoting prolific growth, such as an abundant supply of nutrients and high seed rate, are also frequently associated with lodging (Berry et al., 2004). Irrigation of wheat (e.g. in Mexico, India, and Australia) can cause significant lodging as the application of water reduces the soil strength, weakening plant anchorage. In North-West Mexico (NWM) concurrence of irrigation events and windy conditions soon after or during flowering and in early grain filling often occurs.

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Avoiding this situation is very difficult due to the unpredictable nature of weather (climate change included) or simply because some irrigation events are difficult to avoid. Lodging can reduce grain yield from 7 to 80% (Acreche and Slafer, 2011; Berry and Spink, 2012; Easson et al., 1993; Fischer and Stapper, 1987; Stapper and Fischer, 1990; Tripathi et al., 2005; Weibel and Pendleton, 1964), and may result in reduced grain quality, greater drying costs, and slower harvest (Berry, 1998; Berry et al., 2004). Lodging losses are greatest when lodging occurs soon after flowering and when the angle of stem displacement from the vertical is high (Berry and Spink, 2012; Fischer and Stapper, 1987) and can be as great as those caused by pest and disease (Pinthus, 1974). For instance, it has been reported that lodging with an angle of 45° would cause a grain yield loss of 18% (Berry and Spink, 2012). Meanwhile, an angle of 80° from the vertical at anthesis would cause a grain yield loss in the range of 7–35% (Fischer and Stapper, 1987), 43–61% (Acreche and Slafer, 2011), and 54% (Berry and Spink, 2012). Considering the lodging problem in the context of the 76 000 ha of wheat harvested in the Yaqui Valley in NWM every year alone (SIAP, 2016) the economic loss in a severe lodging year would be around US$29 million. This is assuming 40% of the area affected with yield losses around 50% and US$215 per tonne of wheat grain (Lantican et al., 2016). Such a percentage of wheat area affected with lodging has been observed by CIMMYT researchers in NWM (Tripathi et al., 2005). The percentage of yield loss would be the average of the upper values reported by the aforementioned researchers when lodging angle is around 80°.

The introduction of dwarfing genes during the Green Revolution reduced the lodging susceptibility (Conway, 1997) by decreasing the leverage exerted on the stem base and anchorage system via reducing plant height, which allowed greater rates of fertilisation and this leverage was further reduced with the use of plant growth regulators (Berry et al., 2004; Crook and Ennos, 1995; Pinthus, 1974; Tripathi et al., 2004; Webster and Jackson, 1993). However, there is substantial evidence that indicates a minimum plant height requirement of 0.7 m compatible with high yields (Allan, 1986; Balyan and Singh, 1994; Berry et al., 2015; Flintham et al., 1997; Kertesz et al., 1991; Miralles and Slafer, 1995; Richards, 1992). On the other hand, important wheat breeding programs such as the one developed by CIMMYT have increased plant height of spring wheat cultivars by year for release from 1966 (introduction of semi-dwarf cultivars) to 2009 from 0.9 to 1.0 m (Aisawi et al., 2015). These observations indicate that exploiting plant height to reduce lodging risk should not be the main strategy in breeding programs.

If there is limited scope for plant breeders to counter the greater lodging risk caused by heavier yielding varieties by further shortening plants in some countries, then it follows that the biophysical components that support the plant (stem and anchorage system) must be strengthened. The properties of the biophysical support structures have been quantified for winter wheat (Berry et al., 2007) and spring wheat (Piñera-Chavez et al., 2016) using a validated model of wheat lodging which evaluates the interaction of plant, soil (moisture) and wind characteristics (Berry et al., 2003b). Genetic variation of lodging-related traits, including stem and anchorage strength (stem and anchorage failure moment) found for winter wheat crops growing in UK conditions (Berry and Berry, 2015; Berry et al., 2007, 2003a), has demonstrated that breeding for these characters is feasible and will help towards the achievement of a lodging proof plant at least for a period of 25 years. More recently, Piñera-Chavez et al. (2016), have quantified the biophysical structure dimensions required for a crop lodging return period of 25 years in spring wheat grown in NWM. These requirements include a root plate spread of 51 mm and for the lowest basal internode, a stem strength of 268 N mm, diameter of 4.12–4.76 mm, material strength of 35–50 Mpa and wall width of 0.65 mm for a crop yielding 6 t ha^{-1}, with 500 shoots m^{-2}, 200 plants m^{-2} and crop height of 0.7 m. However, the potential for plant breeders to achieve these targets and whether this would incur any trade-offs with other traits affecting yield is unknown. Previous studies have reported genetic variation for length, diameter, wall width (Kelbert et al., 2004; Tripathi et al., 2003) and stem strength (Wiersma et al., 2011) of internodes and shoot height at centre of gravity (Tripathi et al., 2003) of spring wheat. However, these efforts have not been enough to fully understand the lodging issue in spring wheat. For instance, Tripathi et al. (2003) and Kelbert et al. (2004) evaluated length, diameter and wall width of internodes in NW Mexico and Western Canada, respectively, but stem strength was not assessed; and Wiersma et al. (2011) evaluated stem strength in a single cultivar. Dimensions for anchorage strength characters were only reported for a single cultivar growing under greenhouse conditions (Ennos, 1991a,b). From the above it can be concluded that more research should be done on the full set of lodging-related traits on spring wheat.

The aim of this paper was to investigate the potential for plant breeders to improve lodging resistance in spring wheat grown in NWM under high yield potential conditions by: a) evaluating the genetic variation and heritability of the lodging-related traits, particularly, those strongly related to the stem and anchorage strength; b) assessing the associations of stem and anchorage strength traits and other key physiological characters; and, c) evaluating the potential of achieving a lodging-proof ideotype able to resist lodging during 25 years defined for spring wheat grown in NWM.

2. Experimental methods

2.1. Plant material and experimental conditions

The CIMMYT Mexico Core Germplasm Panel (CIMCOG), consisting of 58 *Triticum aestivum* and two *Triticum durum* cultivars, was evaluated during 2010–11, and subsets of 30 cultivars during 2011–12 and 2012–13 and five cultivars during 2013–14 (Table S1) in four field experiments (referred to hereafter as 2011, 2012, 2013 and 2014 respectively) established at CENEB (Campo Experimental Norman E. Borlaug) in the Valle del Yaqui, Sonora, Mexico (27° 24′ N, 109° 56′ W, 38 masl). The soil type at the experimental station is a coarse, sandy clay, mixed montmorillonitic typic caliciorthid, low in organic matter and slightly alkaline (pH 7.7) in nature (Sayre et al., 1997). For experiments 2011, 2012 and 2013 a typical raised bed planting system was used to arrange the cultivars (treatments) in a resolvable incomplete block design (Alpha Design). During 2011, each treatment was replicated twice in plots measuring 5 m × 3.2 m (each plot consisted of four raised beds each separated by a 0.56 m irrigation furrow and each bed had two rows with a row width of 0.24 m). Each replicate block contained 10 sub-blocks and each sub-block contained six treatment plots. During 2012 and 2013, each treatment was replicated three times in plots measuring 8.5 m × 2.4 m (3 raised beds each separated by a 0.8 m irrigation furrow, each bed had two rows with a 0.24 m row width). Each replicated block contained six sub-blocks and each sub-block contained five genotype treatment plots. 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. A split plot design using the typical raised bed planting system was used. The seed rates were randomised on main plots and the five cultivars were randomised on sub-plots. Sub-plots were 8.5 m × 2.4 m (3 raised beds each separated by a 0.8 m irrigation furrow, each bed had two rows with a 0.24 m row width). Further plant population treatments were imposed after plant emergence on the lowest seed rate (75 seeds m^{-2}) treatment to increase the contrast between plant densities as: 1) six plants which were completely isolated in each plot within a 1.5 m × 2.4 m area of the plot; 2) plant population on the rest of the plot was thinned to 25 plant m^{-2}. For all the experiments a conventional agricultural management was used to ensure the crop was not deficient in water and nutrients or affected by weeds, pests or diseases. 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.

2.2. *Weather conditions*

Long term mean weather conditions were obtained from two weather stations, the first was located at CENEB (1–2 km from the field trials) which collected all key weather parameters, but only spanned an 18-year period from 1997 to 2014, the second weather station was located 8–9 km from the field trials and collected only temperature data, but spanned a 40-year period from 1973 to 2014. Data were used to calculate the long-term mean and compared with data per experimental year (weather station at CENEB) for the two major growth periods: pre-anthesis (December–February) and grain filling (March–April) (Table 1). Mean temperatures during the pre-anthesis period for 2011, 2012 and 2013 were 2 °C colder than the LTM at Obregon airport (1973–2014) and similar to LTM from CENEB. The mean temperature during 2014 was in between the LTMs at Obregon airport and CENEB. Solar radiation was similar in all cases for both growth periods. Accumulated rainfall was absent or very low during the whole 2011 growing season. Whilst rainfall was similar across 2012, 2013 and 2014 and LTM at CENEB for the pre-anthesis period. Rainfall for the grain filling period of the 2014 season was higher and significantly greater than the other seasons and the LTM at CENEB.

2.3. *Lodging traits measurements*

Plant measurements were made 20 days after anthesis (GS65 + 20 days) (Zadoks et al., 1974) on 15 plants per plot during 2011 and 10 plants per plot during 2012 and 2013. These plants were randomly selected and extracted from each plot, avoiding the outer two rows in the plot and plot border. Plant extraction was achieved by pulling up the plants after excavating the surrounding soil with a hand fork to recover roots to a depth of 10 cm. After, the soil was removed from the roots by pressure washing. Measurements associated with lodging resistance included the root plate spread (mm) and structural rooting depth (mm) of the plant root system and fertile shoot number per plant. The remaining measurements were made on the main stem and included the height to the ear tip (mm), height at centre of gravity (mm) (with ears attached during 2012 and 2013 and without ears during 2011), natural frequency (Hz) for the whole shoot and, the diameter (mm), length (mm), wall width (mm), breaking strength (Newtons) and dry weight for internodes 1 and 2 (stem base) without leaf-sheath. Internode 1 was determined as the first internode of more than 10 mm originated just or below the soil surface (superior internodes in the stem were numbered in ascending order and identifying the uppermost as the peduncle). The detailed methods for these measurements are described by Berry et al. (2000) and have been added in this paper as supplementary material (Table S2). Internode dry weight (g) was determined by drying the internodes until no further weight loss occurred at 75 °C. Root dry weight (g) was determined by trimming the roots at the stem base, washing off any remaining soil and drying at 75 °C until no further weight loss occurred. Measurements taken on the 2014 experiment used in this paper included only root plate spread at GS65 + 20. Natural lodging for each cultivar was evaluated in terms of the angle of displacement of plants from the vertical position (0–90°), and the percentage of the plot area lodged (0–100%). These measurements were recorded once or twice a week during the lodging period (between the first occurrence at early grain filling and harvest) and used to generate a lodging score:

$$\text{Lodging score} = (\%\text{ of plot area lodged}) \times (\text{angle of lodging from the vertical})/90 (\text{Fischer and Stapper, 1987})$$

2.4. *Agronomic and physiological traits*

Agronomic and physiological traits measured for this study included grain yield (t ha^{-1}), harvest index, thousand grain weight (g), straw yield (t ha^{-1}), chaff weight (t ha^{-1}), ears per square meter and heading and anthesis dates (GS55 and 65 in the Zadoks scale, respectively) (Zadoks et al., 1974). The methods used to collect the data for these traits were obtained from Pask et al. (2012). Measurements taken on the 2014 experiment included only grain yield. Heading and anthesis date were recorded when more than 50% of the plot was at the respective growth stages. Grain yield was estimated from the harvested area which was determined avoiding border effects. The rest of the traits were estimated from a subsample of 100 ear-bearing shoots taken from the harvest area.

2.5. *Calculated lodging parameters*

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), stem material strength, anchorage failure moment (anchorage strength), the wind-induced base bending moment (leverage) of the shoot and plant, and overall risk to stem and root lodging on spring wheat (stem and root failure wind speed). Details for these calculations are given in a companion paper by Piñera-Chavez et al. (2016).

2.6. *Statistical analysis*

Individual analysis for each experiment was done using REML and performed with the MIXED procedure from SAS Institute Inc. (2004) considering the cultivar as fixed effect and the replicate and blocks within replications as random effects. Combined analysis across experiments (cross-year) was also performed using REML considering the effects of experiments, replicates within experiments and genotype by environment (experiment) interaction (G × E) as random and genotype as fixed. Individual analysis was done according to the experimental design while cross-year analysis was done on 27 cultivars (consistent cultivars in each experiment, see Table S1) under a randomised complete block design. Adjusted means were estimated for each trait by experiment from individual analyses and combining data from 2011, 2012 and 2013 experiments (cross-year mean). Average standard error of difference (SED) between cultivar means by experiment and cross year mean was calculated. Broad sense heritability (H^2) was calculated using Eq. (1) for analyses for individual experiments and 2 for analyses combined across experiments (Cooper et al., 1996).

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2/n_r} \tag{1}$$

Table 1
Summary of weather conditions during pre-anthesis and grain filling periods for experiments 2011, 2012 and 2013 at the Yaqui Valley.

Parameter	Growth period	2011	2012	2013	2014	LTM[a]	LTM[b]
Minimum temperature (°C)	Pre-anthesis	6.4	6.4	7.4	9.3	10.6	7.3
	Grain filling	10.2	10.1	9.8	11.4	13.7	9.7
Maximum temperature (°C)	Pre-anthesis	25.0	25.6	24.1	26.4	25.0	25.1
	Grain filling	30.0	29.4	29.0	30.5	28.9	29.1
Mean temperature (°C)	Pre-anthesis	14.8	15.0	14.9	16.7	17.6	15.3
	Grain filling	19.7	19.1	18.7	20.2	21.0	18.9
Mean solar radiation (MJ m^{-2})	Pre-anthesis	18.0	17.0	14.5	14.8	–	15.9
	Grain filling	26.9	24.9	21.6	21.4	–	24.1
Mean accumulated rainfall (mm)	Pre-anthesis	0.4	14.0	12.9	20.9	–	22.2
	Grain filling	0.0	0.3	2.5	15.4	–	2.4

LTM[a], long term mean for 1973–2014 at Obregon Airport; LTM[b], long term mean for 1997–2014 at CENEB.

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{n_e} + \frac{\sigma_e^2}{n_e n_r}} \qquad (2)$$

where $\sigma_g{}^2$ and $\sigma_e{}^2$ are the genotypic (cultivar) and error variance, $\sigma_{ge}{}^2$ is the G × E interaction. The number of environments and number of replicates are represented by n_e and n_r, respectively. Phenotypic correlations (r_p) between traits were simple Pearson correlations. Genetic correlations among traits (r_g) were calculated for cross-year means using the equation from Cooper et al. (1996).

$$r_g = \frac{\overline{\sigma_{g(jj')}}}{\overline{\sigma_{g(j)}\sigma_{g(j')}}} \qquad (3)$$

where $\overline{\sigma_{g(jj')}}$ is the arithmetic mean of all pairwise genotypic covariances between trait j and j' and $\overline{\sigma_{g(j)}\sigma_{g(j')}}$ is the arithmetic average of all pairwise geometric means among the genotypic variance components of the traits. All the analyses, except for genetic correlations, were done using the suite META (Multi Environment Trial Analysis) which includes 33 SAS programs to analyse multi- environment trials (Vargas et al., 2013). Genetic correlations were done using a suite of R codes (META-R) for analysing multi-environment trials (Alvarado et al., 2015). SAS version 9.0 and R 3.2.1 were used to run the suites. Experiment 2014 was analysed separately using a PROC MIXED from SAS for a split plot design.

3. Results

3.1. Variation of lodging related traits due to genetic and environmental effects

Analysis of variance showed consistent differences ($P < 0.01$–0.001) between cultivars for most of the traits across all three experiments. Anchorage strength and root plate spread during 2011 and plant leverage during 2012 were the only cases were no statistically significant cultivar differences were detected. Reducing the number of cultivars from 60 in the 2011 experiment to 30 in 2012 and 2013 did not affect the statistical significance of the cultivar effects. The height at centre of gravity of the shoot measured in 2011 was less than in 2012 and 2013 because the ear was removed in the 2011 experiment before measuring this trait. This trait was, on average, 60% of the plant height in 2012 and 2013, while it was 44% of plant height in 2011. The cultivar range, expressed as the difference between the proportion of the grand mean of the smallest and largest cultivar, was greatest for anchorage strength, for which the values ranged from 1.39 in 2011 to 2.93 in 2012. For material strength this proportion ranged from 0.93 in 2012 to 1.29 in 2013 and for plant leverage from 0.93 in 2013 to 1.25 in 2011. The lowest proportion was found for internode diameter, root plate spread, structural rooting depth and plant height. These proportions ranged from 0.30 in 2011 to 0.35 in 2013 for internode diameter, 0.28 in 2011 to 0.47 in 2012 for root plate spread, 0.34 in 2011 to 0.45 in 2012 for structural rooting depth and 0.50 in 2012 to 0.39 in 2011 for plant height (Table 2).

Cross-year analysis of data from the 27 cultivars common across the experiments in 2011, 2012 and 2013 indicated large differences between the cultivars (G) ($P < 0.001$) (Table 3) consistent with the analyses of the individual experiments (Table 2). Environmental effects (E) were found ($P < 0.05$–0.001) for most of the traits, except for shoot and plant leverage and ear number per plant. A G × E interaction ($P < 0.05$–0.001) was observed for all traits (Table 3).

3.2. Broad sense heritability of lodging related traits

Broad sense heritability for plant/shoot leverage and stem/root strength characters are illustrated in Table 4. Heritability values estimated for traits associated with stem strength in each experiment ranged 0.60–0.86 for 2011, 0.69–0.90 for 2012 and 0.74–0.94 for 2013. Despite the G × E interactions observed for all stem strength traits (Table 3) high values of heritability ranging from 0.70 to 0.94 were determined for the cross-year analysis, except for dry weight per unit length ($H^2 = 0.38$) which in turn caused a low heritability for dry weight per unit length per unit strength ($H^2 = 0.33$). Stem diameter was the most consistent trait and showed the highest heritability (0.93). Root characters related to the anchorage strength had the lowest heritability values when compared with the rest of the characters (range 0.19–0.61 for 2011, 0.66–0.82 for 2012 and 0.62–0.82 for 2013) and for the cross-year values (range 0.11–0.48). Plant height had the highest and most consistent heritability ranging from 0.95 to 0.96 for the individual and cross year analysis. Similarly, traits strongly related to plant height such as natural frequency (0.78–0.91) and height at centre of gravity (0.88–0.94) showed high consistent heritability values for the individual and cross year analysis. Heritability for the area of the main shoot ear ranged from 0.85–0.93 between experiments and for the cross-year analysis. Ear number per plant had the lowest heritability ranging from 0.43 to 0.56. Shoot leverage heritability was consistent across years and for the combined analysis ($H^2 = 0.72$–0.92); plant leverage had lower heritability (0.36–0.74) which probably resulted from the low heritability of component trait ear number per plant.

3.3. Agronomic and physiological traits

Cross-year analysis of variance has shown differences ($P < 0.001$) between cultivars for all the agronomic and physiological traits measured. Differences between environments ($P < 0.05$–0.01) were also found for all traits, except for, ears m^{-2}. Genotype by environment interaction ($P < 0.05$–0.001) affected all traits, except for thousand grain weight and chaff weight. High broad sense heritability was found for grain yield, yield components (TGW, ear m^{-2}), harvest index, non-grain biomass traits (straw yield, chaff)

Table 2
Summary of the individual analysis for stem (bottom internode 1), root and leverage characters associated to lodging resistance for spring wheat cultivars grown at NWM during 2011, 2012 and 2013.

Trait	2011[a]			2012[b]			2013[c]		
Stem	Mean	Range	SED	Mean	Range	SED	Mean	Range	SED
Diameter (mm)	4.21	3.60–4.87	0.157^{***}	3.94	3.31–4.65	0.165^{***}	3.74	3.07–4.37	0.150^{***}
Wall width (mm)	0.80	0.67–1.25	0.059^{***}	0.86	0.74–1.04	0.051^{***}	0.72	0.53–0.96	0.065^{***}
Strength (N mm)	134	97.9–189	20.3^{**}	207	147–289	26.0^{***}	206	137–295	20.5^{***}
Material strength (MPa)	25.1	17.3–40.8	3.82^{***}	39.0	28.9–65.2	3.77^{***}	49.0	27.2–90.3	6.38^{***}
Dry weight per length (mg mm^{-1})	2.17	1.54–2.91	0.208^{***}	2.88	2.38–3.56	0.244^{**}	3.21	1.89–6.08	0.373^{***}
Dry weight per length per unit strength (mg mm^{-1}/N mm)	0.015	0.010–0.021	0.0021^{***}	0.014	0.012–0.020	0.0015^{***}	0.016	0.010–0.034	0.002^{***}
Stem failure wind speed (m s^{-1})	11.0	9.06–16.1	0.981^{***}	13.7	11.6–17.9	0.879^{***}	14.0	11.1–17.6	0.675^{***}
Root strength									
Root plate spread (mm)	33.0	27.9–37.2	2.51^{ns}	37.0	28.5–45.8	3.77^{**}	44.3	40.0–54.7	2.67^{**}
Structural rooting depth (mm)	36.8	31.0–43.4	2.21^{***}	38.6	32.6–50.0	2.55^{***}	38.9	31.3–45.8	1.97^{***}
Root dry weight (mg $plant^{-1}$)	372	215–550	78.3^{**}	327	169–566	74.8^{***}	244	151–366	42.0^{**}
Anchorage strength (N mm)	232	78.0–400	80^{ns}	262	66.6–835	116^{***}	397	177–1133	130^{***}
Anchorage failure wind speed (m s^{-1})	8.67	4.63–12.6	1.47^{**}	8.59	5.14–14.5	1.75^{***}	11.5	7.98–19.6	1.39^{***}
Leverage									
Plant height (mm)	1002	727–1120	25.0^{***}	924	730–1049	21.5^{***}	921	716–1047	19.5^{***}
Height at centre of gravity (mm)	383	303–450	11.4^{***}	565	483–640	12.2^{***}	542	446–602	16.5^{***}
Natural frequency (Hz)	1.28	0.97–2.21	0.115^{***}	1.48	1.14–2.12	0.095^{***}	1.68	1.28–2.45	0.130^{***}
Ear area of main shoot (cm^2)	20.4	10.8–27.4	1.60^{***}	19.3	12.8–25.3	1.24^{***}	16.3	10.6–22.1	0.91^{***}
Ear number per plant	2.73	1.60–3.50	0.360^{*}	2.69	2.13–3.39	0.290^{**}	2.63	1.97–3.07	0.250^{***}
Shoot leverage (N mm)	192	66.0–283	20.8^{***}	189	122–296	28.6^{***}	179	89.1–279	13.4^{***}
Plant leverage (N mm)	524	165–820	89.7^{***}	506	359–845	113^{ns}	469	242–677	63.3^{***}

[a] 60 cultivars.
[b] 30 cultivars.
[c] 30 cultivars. ns not significant.
[*] $P < 0.05$.
[**] $P < 0.01$.
[***] $P < 0.001$.

Table 3
Summary of the cross-year analysis for stem (bottom internode), root and leverage characters associated to lodging resistance for 27 spring wheat cultivars (G) grown at NWM during 2011, 2012 and 2013 (E).

Trait	Mean	Range	SED (G)	*P* value (E)	*P* value (G × E)
Stem					
Diameter (mm)	3.96	3.35–4.47	0.120***	<0.01	<0.05
Wall width (mm)	0.80	0.64–0.92	0.054***	<0.01	<0.01
Strength (N mm)	184	134–252	20.5***	<0.01	<0.01
Material strength (MPa)	37.5	27.4–59.4	6.13***	<0.001	<0.001
Dry weight per length (mg mm^{-1})	2.78	1.95–3.85	0.525***	<0.01	<0.001
DW/L/SS (mg mm^{-1}/N mm)	0.016	0.013–0.023	0.0025***	<0.05	<0.001
Stem failure wind speed (m s^{-1})	13.1	10.8–15.7	0.792***	<0.01	<0.001
Root					
Root plate spread (mm)	38.3	34.4–42.2	2.74***	<0.01	<0.01
Structural rooting depth (mm)	38.1	34.4–44.0	2.37***	<0.05	<0.001
Root dry weight (mg $plant^{-1}$)	315	213–437	55.9***	<0.05	<0.01
Anchorage strength (N mm)	302	169–585	0.120***	<0.05	<0.001
Anchorage failure wind speed (m s^{-1})	9.84	7.12–12.8	1.68***	<0.01	<0.001
Leverage					
Plant height (mm)	938	726–1067	20.3***	<0.01	<0.01
Height at centre of gravity (mm)	492	410–543	10.9***	<0.001	<0.01
Natural frequency (Hz)	1.50	1.22–2.25	0.093***	<0.01	<0.01
Ear area of main shoot (cm^2)	18.4	11.5–24.8	1.05***	<0.01	<0.01
Ear number per plant	2.65	2.06–3.07	0.227***	ns	<0.01
Shoot leverage (N mm)	183	103–283	17.8***	ns	<0.05
Plan leverage (N mm)	483	263–643	69.1***	ns	<0.05

DW/L/SS, dry weight per unit length per unit strength; ***, $P < 0.001$; ns, not significant.

and key developmental stages (heading and anthesis date) (range 0.72–0.98) (Table 5).

3.4. Association among traits

Associations between important agronomic, physiological and lodging traits for the 27 common cultivars in 2011–2013 are described in Table 6. The correlations caused by both genetic and environmental factors combined are given by Pearson correlation coefficients (upper diagonal) (r_p) for the cross-year cultivar means and correlations caused by genetic factors alone are described by genetic correlation coefficients (lower diagonal) (r_g) obtained using the same cross-year cultivar means. Stem strength was positively correlated to stem diameter ($r_p = 0.44$, $r_g = 0.46$; $P < 0.05$), stem wall width ($r_p = 0.84$, $r_g = 0.97$; $P < 0.001$) and stem dry weight per unit length ($r_p = 0.61$, $r_g = 0.78$; $P < 0.001$). Stem dry weight per unit length per unit strength was negatively correlated to the stem strength ($r_p = -0.41$, $P < 0.05$; $r_g = -0.71$; $P < 0.001$). Material strength was not correlated with stem strength. Stem diameter, stem wall width and stem material strength are considered the major components of the stem strength. Within the stem strength components, the only significant negative association was found between stem diameter and stem material strength ($r_p = -0.75$, $r_g = -0.86$; $P < 0.001$). Positive associations between

Table 4
Broad sense heritability (H^2) for stem (bottom internode), root and leverage characters associated to lodging resistance for spring wheat cultivars grown at NWM during 2011, 2012 and 2013.

Trait	2011[a]	2012[b]	2013[c]	Cross-year[d]
Stem				
Diameter	0.86	0.87	0.91	0.93
Wall width	0.84	0.82	0.74	0.76
Strength	0.60	0.71	0.88	0.78
Material strength	0.72	0.90	0.90	0.72
Dry weight per length	0.72	0.63	0.94	0.38
Dry weight per length per unit strength	0.68	0.69	0.92	0.33
Stem failure wind speed	0.71	0.80	0.91	0.82
Root				
Root plate spread	0.19	0.66	0.62	0.11
Structural rooting depth	0.61	0.82	0.74	0.40
Root dry weight	0.54	0.72	0.63	0.48
Anchorage strength	0.25	0.81	0.76	0.17
Anchorage failure wind speed	0.56	0.78	0.82	0.38
Plant and shoot				
Plant height	0.95	0.96	0.96	0.96
Height at centre of gravity	0.92	0.94	0.88	0.94
Natural frequency	0.78	0.89	0.88	0.91
Ear area of main shoot	0.85	0.89	0.93	0.92
Ear number per plant	0.43	0.53	0.56	0.46
Shoot leverage	0.85	0.72	0.92	0.87
Plant leverage	0.70	0.36	0.74	0.58

[a] 60 cultivars.
[b] 30 cultivars.
[c] 30 cultivars.
[d] 27 cultivars.

Table 5
Summary of cross-year analysis of variance for agronomic and physiological traits of spring wheat cultivars (G) grown at NWM during 2011, 2012 and 2013 experiments (E).

Trait	Mean	Range	SED (G)	P value (E)	P value (G × E)	H^2
Grain yield ($\mathrm{t\,ha^{-1}}$)	6.68	5.48–7.69	0.254***	<0.05	<0.01	0.82
Harvest index	0.47	0.43–0.53	0.0088***	<0.01	ns	0.89
Thousand grain weight (g)	42.8	31.2–51.6	1.12***	<0.05	ns	0.98
Straw yield ($\mathrm{t\,ha^{-1}}$)	5.58	4.77–6.32	0.263***	<0.01	<0.05	0.86
Chaff ($\mathrm{t\,ha^{-1}}$)	1.88	1.52–2.24	0.111***	<0.01	ns	0.72
Heading date (DAE)	83	73–93	1.61***	<0.01	<0.001	0.92
Athesis date (DAE)	88	78–97	1.76***	<0.01	<0.001	0.91
Ear $\mathrm{m^{-2}}$	303	224–375	15.5***	ns	< 0.05	0.93
Lodging score	2.28	0–15.7	–	–	–	–

H^2, broad sense heritability; DAE, days after emergence; ***, $P < 0.001$. ns, not significant.

stem dry weight per unit length with stem diameter ($r_p = 0.27$, not significant; $r_g = 0.48$; $P < 0.05$) and stem wall width ($r_p = 0.59$, $r_g = 0.90$; $P < 0.001$) were also found. Stem strength and its components were also associated to grain yield and yield components and other physiological traits. For instance, stem wall width, stem diameter and stem strength were consistently and negatively associated with thousand grain weight and ears per meter squared ($r_p = -0.49$ to -0.79, $r_g = -0.53$ to -0.78; $P < 0.01$–0.001). The strongest association with grain yield was found for stem diameter ($r_p = 0.37$, $P = 0.06$; $r_g = 0.41$, $P < 0.05$). There were no negative correlations between stem strength traits and grain yield. Material strength was correlated to the date at growth stages heading ($r_p = -0.53$, $r_g = -0.57$; $P < 0.01$) and anthesis ($r_p = -0.49$, $r_g = -0.52$; $P < 0.01$). This indicated that cultivars with later heading and anthesis developed smaller material strength.

Anchorage strength was strongly and positively correlated to its two components namely root plate spread ($r_p = 0.88$, $r_g = 0.88$; $P < 0.001$) and structural rooting depth ($r_p = 0.89$, $r_g = 0.95$; $P < 0.001$), as expected given nature of the formula relating anchorage strength to its components. Surface root dry weight was strongly and positively related to anchorage strength ($r_p = 0.71$, $r_g = 0.91$; $P < 0.001$). Strong positive associations were also found within the anchorage strength components and root dry weight ($r_p = 0.70$–0.75, $r_g = 0.77$–0.94; $P < 0.001$). Root dry weight was positively correlated to internode diameter ($r_p = 0.48$, $P < 0.01$; $r_g = 0.71$, $P < 0.001$), stem strength ($r_p = 0.33$, ns; $r_g = 0.44$, $P < 0.05$) and dry weight per length ($r_p = 0.35$, ns; $r_g = 0.70$, $P < 0.001$) and negatively correlated to internode material strength ($r_p = -0.36$, ns; $r_g = -0.58$, $P < 0.001$). Additionally, a negative correlation between root plate spread and stem wall width ($r_g = -0.44$, $P < 0.01$) and positive association between and anchorage strength with stem dry weight per unit length were found ($r_p = 0.22$, ns; $r_g = 0.93$, $P < 0.001$). Genetic correlation coefficients also indicated a significant and positive association between root dry weight and grain yield, thousand grain weight and harvest index ($r_g = 0.44$ to -0.50; $P < 0.05$–0.01). In some cases involving root traits, genetic correlation coefficients were not calculated or simply no association was identified due to genetic variance component values equal or close to zero.

Plant height as a main component of the plant leverage was negatively correlated with the natural frequency ($r_p = -0.65$, $r_g = -0.70$; $P < 0.001$) and positively to the height at centre of gravity ($r_p = 0.85$, $r_g = 0.87$; $P < 0.001$). Plant height was also negatively correlated to stem dry weight per unit length per unit strength ($r_p = -0.48$, $P < 0.05$; $r_g = -0.85$, $P < 0.001$). Other agronomic traits related to plant height were thousand grain weight ($r_p = 0.56$, $r_g = 0.58$; $P < 0.01$), harvest index ($r_p = -0.41$, $r_g = -0.44$; $P < 0.05$) and lodging score ($r_p = 0.30$, not significant; $r_g = 0.85$; $P < 0.001$).

Grain yield was positively correlated with natural frequency ($r_p = 0.41$, $P < 0.05$; $r_g = 0.50$; $P < 0.01$) and harvest index ($r_p = 0.58$, $P < 0.01$ $r_g = 0.62$; $P < 0.001$). Also, a genetic correlation coefficient

Table 6

Phenotypic (upper diagonal) and genetic (lower diagonal) correlations between cross-year means of lodging, agronomic and physiological traits of 27 spring wheat cultivars growing at NWM during 2011, 2012 and 2013.

Traits	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. Grain yield		**0.41**	−0.12	0.15	−0.25	0.04	−0.09	−0.10	0.19	−0.19	0.37	0.24	0.18	0.11	−0.32	0.14	−0.22	0.02	0.05	0.33	**0.58**	0.01
2. Natural frequency	**0.50**		**−0.65**	0.23	**−0.81**	**−0.40**	−0.12	−0.17	0.14	−0.31	0.18	−0.06	0.20	**0.42**	−0.37	−0.11	−0.16	0.20	0.25	−0.07	0.36	0.27
3. Plant height	−0.16	**−0.70**		0.08	**0.85**	0.27	−0.06	−0.05	−0.09	0.30	0.33	0.12	−0.09	**−0.48**	0.00	0.33	−0.04	−0.29	−0.25	**0.56**	**−0.41**	−0.34
4. Ear per plant	0.21	**0.43**	0.11		−0.25	−0.35	−0.32	**−0.58**	**−0.39**	0.11	−0.09	−0.23	−0.25	−0.16	0.04	−0.16	**−0.46**	**−0.50**	**−0.45**	0.23	0.23	**0.40**
5. Centre of gravity	−0.31	**−0.87**	**0.87**	**−0.42**		**0.40**	0.17	0.28	0.08	0.27	0.10	0.17	−0.06	**−0.38**	0.20	0.27	0.28	−0.09	−0.10	0.34	**−0.44**	**−0.42**
6. Ear area	0.02	**−0.42**	0.27	**−0.57**	**0.42**		**0.53**	**0.48**	**0.51**	0.04	0.37	**0.61**	0.28	−0.35	−0.07	**0.56**	**0.56**	0.01	−0.02	**0.54**	0.07	**−0.82**
7. Root plate spread	0.04	−0.11	−0.12	na	**0.61**	na		**0.79**	**0.70**	−0.14	0.23	0.09	0.23	0.08	−0.20	0.14	**0.88**	0.23	0.19	0.07	0.15	**−0.49**
8. Structural root depth	−0.06	−0.24	0.00	na	**0.55**	**0.76**	**0.90**		**0.75**	0.03	0.13	0.07	0.28	0.25	−0.14	0.09	**0.89**	0.36	0.32	0.00	0.07	**−0.48**
9. Root dry weight	**0.50**	0.29	−0.07	na	0.13	**0.77**	**0.94**	**0.77**		−0.04	**0.48**	0.30	0.35	0.08	−0.36	0.33	**0.71**	0.32	0.31	0.31	0.28	**−0.65**
10. Lodging score	0.00	**−0.79**	**0.85**	**0.41**	**0.90**	0.05	na	−0.09	−0.22		0.06	−0.08	−0.05	−0.13	0.04	0.07	−0.04	0.02	0.05	0.14	−0.15	−0.10
11. Stem diameter	**0.41**	0.21	0.34	−0.20	0.12	0.35	0.35	0.09	**0.71**	0.08		0.31	0.27	−0.14	**−0.75**	**0.44**	0.15	0.20	0.26	**0.59**	0.10	**−0.51**
12. Stem wall width	0.37	−0.02	0.16	**−0.56**	0.21	**0.69**	**−0.44**	−0.21	0.23	**−0.43**	0.32		**0.59**	−0.28	0.19	**0.84**	0.14	−0.08	−0.08	**0.49**	−0.02	**−0.64**
13. SDWL	**0.54**	**0.51**	−0.17	**−0.48**	−0.12	**0.38**	Na	Na	**0.70**	**−0.54**	**0.48**	**0.90**		**0.45**	0.13	**0.61**	0.22	−0.21	−0.20	0.28	0.19	**−0.43**
14. SDWLSS	0.30	**0.89**	**−0.85**	−0.37	**−0.65**	**−0.65**	**0.89**	**0.95**	0.18	**−0.39**	−0.15	**−0.67**	−0.18		−0.13	**−0.41**	0.07	0.16	0.14	**−0.41**	0.26	0.32
15. Stem material strength	−0.36	**−0.38**	−0.01	0.30	0.22	−0.08	−0.33	0.04	**−0.58**	0.11	**−0.86**	0.30	−0.11	−0.34		0.21	−0.12	**−0.49**	**−0.53**	−0.16	−0.16	0.08
16. Stem strength	0.24	−0.10	0.37	−0.26	0.30	**0.59**	0.07	0.11	**0.44**	−0.21	**0.46**	**0.97**	**0.78**	**−0.71**	0.12		0.16	−0.29	−0.25	**0.65**	−0.04	**−0.72**
17. Anchorage strength	−0.34	−0.18	−0.01	na	**0.72**	na	**0.88**	**0.95**	**0.91**	**−0.72**	0.09	−0.19	**0.93**	**0.55**	0.04	0.22		0.38	0.33	0.02	−0.03	**−0.52**
18. Anthesis date	0.00	0.20	−0.32	**−0.87**	−0.10	0.02	**0.69**	**0.56**	**0.56**	0.19	0.22	−0.09	−0.27	0.24	**−0.52**	−0.25	**0.80**		**0.99**	**−0.43**	−0.26	0.08
19. Heading date	0.02	0.25	−0.29	**−0.77**	−0.11	−0.02	**0.60**	**0.48**	**0.56**	0.22	0.28	−0.06	−0.25	0.20	**−0.57**	−0.22	**0.71**	**1.00**		**−0.38**	−0.28	0.08
20. Thousand grain weight	0.37	−0.05	**0.58**	**0.39**	0.36	**0.57**	0.21	0.02	**0.48**	**0.40**	**0.62**	**0.56**	**0.49**	**−0.72**	−0.20	**0.76**	0.10	**−0.43**	**−0.39**		0.18	**−0.67**
21. Harvest index	**0.62**	**0.42**	**−0.44**	0.35	**−0.47**	0.05	0.35	0.07	**0.44**	**−0.48**	0.08	−0.03	0.30	**0.38**	−0.10	−0.01	−0.19	−0.32	−0.33	0.19		−0.10
22. Ear m^{-2}	−0.06	0.31	−0.36	**0.57**	**−0.46**	**−0.88**	na	**−0.70**	**−0.97**	0.01	**−0.53**	**−0.73**	**−0.74**	**0.46**	0.14	**−0.79**	na	0.05	0.06	**−0.70**	−0.12	

Coefficients in bold indicate significant correlations ($P < 0.05–0.001$); na, not available; SDWL, stem dry weight per unit length; SDWLSS, stem dry weight per unit length per unit strength.

Table 7
Analysis of variance for root plate spread and grain yield under different seed rates (SD) for a subset of five cultivars (G) from CIMCOG panel grown at NWM during 2014.

Seed rate	Root plate spread (mm)	Grain yield (t ha^{-1})
Isolated plants	102.3	–
25 seed m^{-2}	68.7	6.33
125 seed m^{-2}	48.4	6.21
175 seed m^{-2}	49.2	6.40
SED (SD)	2.65***	0.173 ns
SED (G)	2.20***	0.135***
SED (interaction)	4.74***	0.297 ns

ns, not significant.
*** $P < 0.001$.

of 0.54 ($P < 0.01$) between grain yield and stem dry weight per unit length was found. No significant association was found for grain yield and lodging score. Harvest index was correlated positively to natural frequency ($r_p = 0.36$; $P = 0.07$, $r_g = 0.42$; $P < 0.05$), and negatively correlated to the height at centre of gravity ($r_p = -0.44$, $r_g = -0.47$; $P < 0.05$) and lodging score ($r_p = -0.15$, not significant; $r_g = 0.48$; $P < 0.05$).

In summary, it can be confirmed that stem strength was associated positively with its main components (stem diameter and stem wall width), except for stem material strength were no association was found. Also was confirmed that the stem strength it is tightly associated with the specific weight of the true stem (stem dry weight per unit length). On the other hand, anchorage strength, root plate spread, structural rooting depth and root dry weight were positively interrelated. Plant height correlated negatively with natural frequency and positively with centre of gravity and grain yield was associated positively with stem diameter, natural frequency and root dry weight.

3.5. *Seed rate effect on root plate spread and grain yield*

A summary of the statistical analysis performed on root plate spread and grain yield data from 2014 experiment indicated genetic differences for both traits. Also root plate spread differed between seed rates and there was an interaction between seed rate and cultivar ($P < 0.001$). These results showed that root plate spread could be increased from 49.2 mm to 68.7 mm by reducing seed rate from 175 to 25 m^{-2} without reducing grain yield (Table 7). Interestingly there was no interaction between seed rate and grain yield.

4. Discussion

4.1. *Breeding a lodging-proof plant*

Piñera-Chavez et al. (2016) estimated that for spring wheat yielding 6 t ha^{-1} with 500 shoot m^{-2} and 200 plants m^{-2} grown in the NWM environment a lodging return period of 25 years will require a maximum height of 0.7 m, a minimum root plate spread of 51 mm and a minimum stem strength for the bottom internode of 268 N mm. The target stem strength could be achieved with a diameter of 4.76 mm diameter, and a material strength of 35 MPa, or with a diameter of 4.12 mm and a material strength of 50 MPa, each with a maximum wall width of 0.65 mm. The rationale for having a thin internode wall width was to minimise biomass cost to increase stem strength based on engineering principles. The cross-year cultivar analysis demonstrated that not all of the target traits could presently be achieved by a single cultivar. Individual target traits that could be achieved included stem diameter and material strength. Minimum wall width observed in spring wheat was 0.64 mm which was below of the maximum requirement of 0.65 mm. Maximum stem strength found in CIMCOG panel (252 N mm) was 6% below the target requirement (268 N mm). Root plate spread was not achieved by any of the CIMCOG panel cultivars investigated, with a maximum value observed of 42 mm which was 17% less than the requirement of 51 mm. A minimum plant height of 0.73 m was observed in the CIMCOG panel which was 4% above the requirement (0.70 m) (Table 8). Coincidentally, the best values observed in winter wheat cultivars were also lower than the target stem strength and root plate spread and with greater plant height than the estimated lodging proof winter wheat in a UK environment (Berry et al., 2007).

It is important to highlight that the genetic range for key lodging traits found in this study has important implications for lodging risk. If the cultivar mean values of key crop properties estimated are used to calculate lodging risk (in terms of failure wind speed), an average wheat crop for NWM will have a stem failure wind speed of 12.8 m s^{-1} and anchorage failure wind speed of 8.5 m s^{-1}. This is far below of the ideotype requirement of 22 m s^{-1} and 18 m s^{-1} to resist stem and root lodging for a period of 25 years, respectively. In this context, if we decrease plant height to the minimum which was 0.7 m, stem and anchorage failure wind speeds will be increased about 1 m s^{-1}. On the other hand, if stem strength is increased to the maximum which was 252 N mm, stem failure wind speeds will be increased about 2 m s^{-1}. Greater effect of about 6 m s^{-1} can be obtained if anchorage strength is increased to the maximum which was 585 N mm. This reinforce the idea that genetic ranges for several key lodging traits can substantially affect lodging risk (Berry and Berry, 2015). Moreover, a combination of these traits in a single cultivar can give greater positive effects for lodging resistance.

Correlations between lodging and agronomic traits are relevant to inform breeders on strategies to improve resistance to both stem and root lodging, whilst also increasing grain yield. For instance, spring wheat has showed significant associations between stem strength and stem wall width and diameter and a positive weak but not significant association between diameter and wall width (Table 6). No significant relationship was found for stem strength and stem material strength. Maximising stem diameter and minimizing stem wall width will result in less investment of biomass to increase stem strength (Berry et al., 2007). However, our results have demonstrated a strong linkage between stem wall width and stem strength which will be difficult to break. It appears then that thicker walled stems should be considered for spring wheat. For example, to obtain the targeted stem strength (268 N mm) with the maximum stem wall dimension observed in spring wheat of 0.92 mm, a stem diameter of 3.89 mm with a material strength of 50 MPa will be required. A thicker stem wall will increase the biomass per unit strength (Berry et al., 2007) which in turn will demand more biomass investment for support structures. This additional biomass investment in the stem may compete for resources with spike dry matter growth and yield determination. However, this maybe an acceptable compromise if it makes breeding for strong stems easier and quicker.

This study has indicated that genetic linkages between stem strength and its components, root strength and its components, plant height and yield and its components do not represent a significant limitation to achieve the dimensions of a desired lodging resistant ideotype. Similar investigations on winter wheat reached the same conclusions (Berry et al., 2007, 2003b) and in fact several of these inter-relationships can help breeders to improve stem and root strength (Berry and Berry, 2015). Additionally, traits with positive effects on stem and root strength such as natural frequency, stem diameter, stem dry weight per unit length and root dry weight showed positive associations with grain yield.

Table 8
Ideotype targets, genetic range and best cultivar for the key lodging traits of spring wheat (CIMCOG panel). Values represent the means of 27 cultivars from 2011 to 2013.

Trait	Ideotype target*	Genetic range	Best observed value
Stem diameter (mm)	4.12–6.03	3.35 – 4.47	4.47 (cv. 60)
Stem wall width (mm)	0.65	0.64 – 0.92	0.64 (cv. 37)
Stem strength (N mm)	268	134 – 252	252 (cv. 23)
Stem material strength (MPa)	20 – 50	27.4 – 59.4	59.4 (cv. 45)
Root plate spread (mm)	51	34 – 42	42 (cv. 16)
Height (m)	0.70	0.73 – 1.07	0.73 (cv. 9)

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

4.2. Heritability

This study has observed large genetic variation in spring wheat for the majority of the traits involved in the stem strength, anchorage strength, leverage of the stem base and structural biomass for plant support. Apart from root plate spread, anchorage strength and plant leverage this variation has been consistent for the individual and cross-experiment analysis of variance. Experimental means differed in all cases, except for ear number per plant and shoot and plant leverage. Lodging-traits have been reported to show G × E interactions in winter wheat (Berry and Berry, 2015; Berry et al., 2003a) and our study has confirmed the same finding for spring wheat. Breeding for these traits may therefore need selection in multiple environments. Additionally, repeatability of cultivar performance across experiments will be an interesting parameter to check since G × E decreases both heritability and response to selection (Cooper et al., 1996). The key traits for stem strength (stem diameter, wall width and material strength) and plant leverage (plant height) have heritability values equal or above 0.70, which make them useful for breeding selection. However, for anchorage strength characters such as root plate spread and structural rooting depth cross-year heritability values were 0.11 and 0.40, respectively. Thus, response to selection will be more difficult for anchorage characters. In the literature it is reported that lodging characters are highly heritable with values in the range of 0.73–0.93 (Berry et al., 2007). Nevertheless, Berry and Berry, (2015) indicated a lower range from 0.17–0.90 with the lowest values for root lodging characters. (Keller et al., 1999) indicated heritability values in the range of 0.51–0.93 for traits such as stem dry weight per length, stem diameter, stem wall width and natural frequency, although, except for stem dry weight per length, their trait assessment was using score numbers rather than actually measuring the traits.

4.3. Implications for selection of improved lodging resistant cultivars

The investment of additional structural biomass in roots and stems required for greater lodging resistance has been fully explained by Berry et al. (2007) and Piñera-Chavez et al. (2016) and is one of the challenges of improved lodging resistance in wheat. The strong positive correlations between stem dry weight per unit length and stem strength, and root plate spread with root surface biomass indicated in Table 6 supports this premise. However, even with greater biomass, careful optimization of yield and lodging traits will be required to minimize the inevitable trade-offs between grain yield-formation traits and lodging-related traits that develop at the same time. The strong genetic linkage found between stem strength and stem wall width is likely to compromise the strategy of minimising the biomass invested in the stem by breeding for wide thin walled stems, as was done by Berry et al. (2007). A comparison between thin walled stems with a dimension of 0.65 mm and thick walled stems with 0.92 mm (maximum dimension observed in the cross-year genetic range) has indicated that stem biomass investment in support structures would increase by approximately 1.0 t ha^{-1} with thicker walled stems.

Reducing plant height to a 0.7 m might decrease overall stem biomass and the storage capacity of stems. This will represent a trade-off for yield if lodging-resistant ideotype is achieved. Nevertheless, to counteract this situation other traits such as fruiting efficiency (i.e. the number of grains set per unit of spike dry weight at anthesis) can be improved. Improving fruiting efficiency has been proposed as one of the strategies to raise grain yield through increasing grain number per unit area in cultivars that already reached the optimum height (0.7–1.0 m) (Slafer et al., 2015).

Finding germplasm with the root plate spread target dimension will be difficult based on the known genetic ranges of winter and spring wheat. Low repeatability will limit the response for selection of improved lodging resistance of this trait. Root dry weight may play an important role for anchorage strength improvements and it was found to be more heritable. Possible strategies to find material with the target dimension will include screening new germplasm or even wild relatives and improving this trait by management. For instance, reducing the plant population increases root lodging resistance (Berry et al., 2007, 2004) by increasing anchorage strength (Berry et al., 2000). Present results from the 2014 experiment have also indicated that root plate spread dimensions identified at 213–292 seeds m^{-2} (experiments 2011, 2012 and 2013) could be enhanced by reducing seed rate while maintaining high grain yields (Table 7). Additionally, plants arranged equidistantly or with variations in the plant arrangement under the same seed rate could be further investigated for effects on root anchorage. Easson et al. (1993) indicated that plots with seed rates in the range of 50–100 seeds m^{-2} yielded 10 t ha^{-1} in Northern Ireland which is a high yield performance. Similarly, our results have indicated that with low seed rates, high yields can be obtained in NWM. Tillering could explain this grain yield since all cultivars used for 2014 experiment responded by compensating for the low plant population with more fertile tillers. Fertile shoots per plant at harvest ranged from 9.5 to 12.5 and 2.9 to 4.1 for 25 and 175 seeds m^{-2}, respectively. This response of tillering to low plant population from all 2014 cultivars can also explain the lack of G × E interaction between seed rate and grain yield. Whaley et al. (2000) stated that crops grown at low densities increased green area per plant with a longer tillering period and concluded that grain yield is maintained even with large reductions in plant density. More recently, Aisawi (2011) indicated no differences in grain yield for seed rates at 50, 150 and 450 seeds m^{-2} for experiments under NWM growing conditions. This demonstrates the great potential for improving anchorage strength by establishing lower plant populations without affecting grain yield, assuming a relatively uniform stand establishment can be achieved on farm. However, using lower seed rates does run the risk of establishing a sub-optimal plant population for yield when plant establishment conditions are poor and may increase weed growth between more widely spaced plants.

Optimisation of sample size and number of traits to evaluate lodging can reduce the time-consuming nature of the methodologies used in this paper. However, precision and power to detect genetic differences among cultivars must be maintained. The time-consuming nature of measuring these traits represents a disadvantage and restricts the capacity to evaluate a large number of cultivars. A subsequent paper using data from this study will estimate the minimum plant sample size while maintaining reliability in identifying genetic differences and a reduced number of traits that enables the lodging model to estimate cultivar lodging susceptibility performances.

The absence of rapid lodging screening methodologies could also be counteracted by the implementation of molecular tools to improve lodging resistance of wheat. QTLs (quantitative trait loci) or other trait-marker associations related to lodging resistance traits must be identified to develop genetic markers for marker-assisted selection that can accelerate breeding for these characters. Several studies have identified QTLs linked to stem diameter (Berry and Berry, 2015; Hai et al., 2005; Keller et al., 1999), stem wall width (Berry and Berry, 2015; Hai et al., 2005), stem strength, stem material strength, root plate spread and root plate depth (Berry and Berry, 2015). Gene *TaCM*, involved in the biosynthesis of lignin, was associated to the stem strength and lodging index (Ma, 2009). Moreover, it has been found that several QTL in the wheat genome are linked to both yield and straw biomass (Berry et al., 2008; Li et al., 2014) which might be useful on increasing yield and lodging resistance simultaneously.

5. Conclusion

The present study has identified genetic variation in spring wheat elite germplasm for lodging related traits. However, significant G × E interactions have also been found affecting consistency across experiments and resulting in low heritability for several characters. Target stem strength traits had good heritability values equal or above 0.70. The major anchorage strength trait (root plate spread) was strongly affected by G × E interaction and this had a low heritability of 0.11. This study has indicated that lodging-proof ideotyope targets for diameter, material strength and wall width of the stems can be achieved in spring wheat, but not yet in the same cultivar. Stem strength and plant height were 6 and 4 percent below the required dimensions and do not represent a difficult challenge. However, new germplasm and management strategies should be implemented to achieve the target root plate spread since this was significantly below the ideotype target. Linkages between lodging traits do not represent a significant challenge to achieve the lodging-proof ideotype through breeding, although strong association between stem strength and stem wall width will increase the biomass cost for stronger stems. These results will help breeders to (i) select potential parents for strategic crosses, (ii) focus on the most important traits that determine genetic variation in lodging risk and (iii) indirectly select for stem lodging related traits during the early segregating generations when yield tests are not yet being conducted.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.06.007.

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