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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 $G \times E$ interaction due to rank changes or changes in the absolute differences between cultivars were identified. The inconsistencies 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.

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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% (Acrcche 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% (Acrcche 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 typical caliciorrhithid, 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

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