

Spatial and temporal patterns of lodging in grain sorghum (*Sorghum bicolor*) in Australia

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Abstract. Grown in water-limited environments, sorghum (*Sorghum bicolor* (L.) Moench) is often exposed to water deficits of varying extent and timing. One of the impacts of water stress on sorghum production is lodging; however, there has been no published study quantifying the temporal and spatial frequency and severity of lodging in grain sorghum in Australia. In this study, we investigated the frequency and severity of lodging, using a dataset of 83 advanced yield-testing trials of the sorghum pre-breeding program grown in the seven major sorghum-production environments in Australia over 14 summer growing seasons. Lodging occurred in most production regions but with varying frequency and severity. Lodging was significantly greater in regions that were more prone to water stress (e.g. Central Highlands in Queensland) and significantly lower in regions that were less likely to suffer from water stress (e.g. Liverpool Plains in northern New South Wales) compared with the overall average across regions. The severity of lodging also varied across regions, with the most severe lodging (>20%) occurring in Central Highlands and Western Downs in Queensland. In addition, seasonal patterns of lodging frequency and severity were also observed. Over the 14 growing seasons, the frequency of lodging varied from 0% to 100%, with the most severe lodging (>20%) observed in 2005, 2016 and 2017. The Southern Oscillation Index explained 29% of the seasonal variation in lodging frequency. The findings of this study clearly support a link between lodging incidence and water stress across regions and seasons. Our data also showed that although there was a substantial turnover of commercial hybrids during the period of this study, the level of resistance to lodging appeared not to have improved. It is possible that this is due to plant breeders trading off improvements in lodging resistance to increase grain yield.

Additional keywords: commercial hybrids, drought, geographical variation in lodging, lodging resistance, seasonal variation in lodging.

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Introduction

In Australia, sorghum (*Sorghum bicolor* (L.) Moench) is the major summer grain crop. It plays a crucial role in providing feed grains to the livestock industries (Hammer 2006) and is an important source of grains for bio-ethanol fermentation in Australia (Puri *et al.* 2012; GAIN Report 2018). Sorghum production in Australia is relatively evenly distributed among central Queensland (CQ), southern Queensland (SQ) and northern New South Wales (NNSW) (Henzell *et al.* 1984; Hammer *et al.* 2014), with significant fluctuation largely due to the timing and quantity of rainfall over the planting window and the expected returns from growing cotton (Agbenyegah *et al.* 2017) and other crops. There is very limited production in Victoria, South Australia, Western Australia, and the Northern Territory.

Sowing of sorghum in Australia generally occurs from September to January, depending on location, timing of planting rains, and stored soil-water during fallow in the previous season (Hammer *et al.* 2014). The earlier sowings tend to occur in southern regions such as NNSW, with later sowings tending to occur in northern regions such as CQ. In NNSW, wide sowing windows occur for most areas, from early September to early January (Moore *et al.* 2014). Planting at the start of these windows is often more successful in minimising moisture stress during and after flowering. The planting window for sorghum in Queensland is wide, from October to mid-January in SQ and from early November to January in CQ to avoid the heat in December (Chapman *et al.* 2002) or even until February in CQ (Cameron *et al.* 2018).

Grown in dryland conditions, sorghum production relies on in-crop precipitation and the soil moisture stored during a previous fallow (Passioura and Angus 2010; Jordan *et al.* 2012). Soils vary in depth and water-holding capacity from region to region (Dang *et al.* 2006). Only a small proportion of the precipitation received during the fallow period (e.g. 25–30% in Australia, Passioura and Angus 2010) can be saved, which rarely meets the crop's water demand throughout the entire growth period without some additional rainfall during the growing season (Jordan *et al.* 2012). This often results in the crop being exposed to various types of water stresses throughout the entire crop cycle, with post-anthesis drought being common (Chapman *et al.* 2000; Hammer *et al.* 2014).

One of the consequences for the crop growing in water-deficit conditions during grain filling is lodging. Lodging is the permanent displacement of plant stems from the erect position (Pinthus 1974). Three types of lodging have been reported in sorghum: stem, root, and panicle (weak neck) lodging (Esechie *et al.* 1977; Henzell *et al.* 1984; Rosenow 1984). Stem lodging induced by water deficit during grain filling is the most prevalent type of lodging in Australia (Henzell *et al.* 1984) and causes the greatest loss of grain worldwide, especially in regions where grains are harvested mechanically (Johnson *et al.* 1997). Stem lodging happens when the lower culm internodes are weakened, bend or break, whereas root lodging results from the failure of root anchorage and results in straight, unbroken culms leaning from the crown (Pinthus 1974). Lodging in grain sorghum in Australia is greatly affected by carbohydrate remobilisation during grain filling and may be accelerated by stalk rots (Henzell *et al.* 1984).

To date, there has been no published study quantifying the temporal and spatial frequency and severity of lodging in grain sorghum in Australia. In this study, we conducted a retrospective analysis of a dataset of the advanced yield-testing trials across the major sorghum-growing regions in Australia over 14 seasons to unravel the geographical and temporal patterns of lodging.

Materials and methods

Breeding trials

This study was a retrospective analysis from 146 advanced yield-testing (AYT) trials for male (AYTM) and female (AYTF) lines grown from the sorghum core pre-breeding program of the University of Queensland/Department of Agriculture and Fisheries/Grains Research and Development Corporation. The trials were grown across the major sorghum-growing regions in CQ, SQ and NNSW in Australia over 14 summer growing seasons from 2004 to 2017. The trials covered a wide range of environments (from 22.295°S to 31.633°S, and from 147.517°E to 152.331°E; see Supplementary material table S1 available at the journal's website), and had 88 different sowing dates extending from 21 September to 16 March. As well as experimental hybrids being grown by the sorghum pre-breeding program, each trial contained the majority of commercial sorghum hybrids on the market in that year: in total, 37 commercial hybrids across all 14 seasons. In order to investigate the frequency and severity

of lodging under production environments across years and locations, we examined the performance of the 37 commercial hybrids. From the confidential annual reports received from commercial sorghum-breeding companies, we found that the 37 commercial hybrids provided an excellent representation of the genetic diversity of commercial sorghum hybrids sold on the market during this period. Hybrids that were not included were those with very low sales volumes and commercial lives. Details of the trials are listed in table S1. Trials were arranged in partially replicated designs, with 20–30% of entries replicated at least twice. Trials were managed according to local commercial agronomic practices. AYTM and AYTF trials grown at the same location were sown end-to-end generally on the same day or 1 day apart, therefore experiencing the same environment. Hence, each pair of AYTM and AYTF trials grown at the same location in the same year was considered a single trial.

The trials were grouped into seven regions based on their locations (table S1). CQ was divided into two regions, Capricornia and Central Highlands, based on longitude. Capricornia is in the east of CQ, and Central Highlands in the west. NNSW was divided into two regions, Liverpool Plains and North West Slopes, based on latitude. Trials grown in SQ were grouped into three regions, Western Downs, Southern Downs and Lockyer Valley, depending on their administration district.

Lodging severity was visually rated as the percentage of plants that lodged in a plot once lodging occurred in a trial. Rating of lodging visually is an accepted and widely used practice in breeding trials. It provided a good and reliable estimate of the actual percentage of lodged plants in sorghum-breeding trials with thousands of plots per trial. Visual rating has been demonstrated to show high correlations with counts of lodged plants and image-based counts of lodged plants (D. Jordan, unpubl. data, 24 January 2020). One of our previous studies used the same method to scale lodging severity of sorghum trials of the same pre-breeding program and observed high heritability of lodging (Wang *et al.* 2019), which demonstrated the reliability of the method of rating lodging visually. In addition, we grew common check hybrids in each trial to enable comparison across trials. Lodging scores of all commercial hybrids in individual trials were averaged to represent lodging severity of each trial.

Southern Oscillation Index

The Southern Oscillation Index (SOI) indicates the development and intensity of El Niño or La Niña events in the Pacific Ocean. The SOI used by the Australian Bureau of Meteorology (BoM) is the Troup SOI (www.bom.gov.au/climate/glossary/soi.shtml), which is the standardised anomaly of the mean sea-level pressure difference between Tahiti and Darwin for each calendar month (McBride and Nicholls 1983). Sustained negative values of the SOI below –7 often indicate El Niño episodes, which are usually accompanied by a reduction in winter and spring rainfall over much of eastern and northern Australia. Sustained positive values of the SOI above +7 are typical of La Niña episodes, which are associated with a higher than normal

rainfall in eastern and northern Australia (www.bom.gov.au/climate/glossary/soi.shtml).

The SOI data of the growing months in all seasons were retrieved from the Australian BoM (www.bom.gov.au/climate/current/soi2.shtml). The period of the growing months in each season was considered from the month when the earliest trial was sown to the month when the latest trial was harvested in that season. Mean SOI of each season was averaged over all growing months in that season.

Statistical analyses

The association between lodging occurrence and region was tested by separating the trials grown in each region across the seasons into two categories according to the presence of lodging in the commercial hybrids. The expected numbers of trials in which lodging occurred was calculated based on the overall frequency of lodging across all regions and seasons. A χ^2 test was used to determine whether the number of trials with observed lodging in each region deviated significantly from the expectation.

The relationship between lodging and SOI was investigated by calculating the Pearson's correlation between mean SOI over all growing months and the proportion of trials in which lodging was observed. The number of trials with varying average lodging severity of commercial hybrids was compared with the SOI of the third month after sowing to investigate the relationship between lodging severity and SOI. In order to investigate the relationship between lodging severity and region, we classified lodging severity into four categories based on the average lodging ratings across all commercial hybrids within a trial: category 1, no lodging in commercial hybrids; category 2, average lodging score across all commercial hybrids $>0\%$ and $\leq 10\%$; category 3, average lodging score across all commercial hybrids $>10\%$ and $\leq 20\%$; and category 4, average lodging score across all commercial hybrids $>20\%$. These categories reflected farmers' views of lodging severity.

Three commercial hybrids were grown in all 83 trials across all 14 seasons, whereas the other 34 commercial hybrids were grown in only subsets of the 14 seasons. We previously

showed that lodging generally had a high heritability (Wang *et al.* 2019), which indicates that the relative ranking of lodging of sorghum hybrids is quite consistent across years and environments and there is relatively little crossover genotype \times environment variation in lodging. Therefore, we used average lodging scores across the three consistent commercial hybrids as a baseline in each season to estimate the change in lodging resistance of commercial hybrids over time. The average visual rating of lodging across all hybrids grown in each season was first calculated; then relative lodging of the 34 hybrids compared with the three reference hybrids was calculated by dividing the average lodging rating across all hybrids grown in each season by the average lodging ratings of the three reference hybrids in the same season. Mean relative lodging of the first five (2004–08) and last five (2013–17) seasons was averaged across all commercial hybrids in the corresponding seasons. A two-sided *t*-test was conducted to determine whether there was significant difference between the average relative lodging of the first and last five seasons.

Results

Summary of the AYT trials

The number of trials grown over seasons varied across the regions depending on seasonal conditions and planting opportunities. The lowest numbers of trials overall were grown in Lockyer Valley (three trials) and North West Slopes (four trials), whereas the highest numbers of trials were grown in the Central Highlands (20 trials overall) and Western Downs (27 trials) (Table 1). The total numbers of trials grown in Capricornia, Liverpool Plains and Southern Downs, respectively, across all seasons were eight, 10, and 11. Trials were grown in Capricornia only before the 2012 season. In the Liverpool Plains, trials were grown in eight seasons after 2006, whereas in the Southern Downs, a single trial was grown in all seasons except in 2010, 2013 and 2017.

Regional variation in the frequency and severity of lodging

The proportion of trials in which lodging occurred varied across regions (Table 2). The Central Highlands and

Table 1. Number of trials grown in each region across the 14 seasons included in the study

Region	Capricornia	Central Highlands	Liverpool Plains	Lockyer Valley	North West Slopes	Southern Downs	Western Downs	Total
2004	2	2	0	0	1	1	3	9
2005	1	1	0	0	0	1	3	6
2006	1	0	0	0	1	1	2	5
2007	1	2	1	1	0	1	0	6
2008	1	2	1	0	0	1	3	8
2009	1	1	0	0	1	1	1	5
2010	0	1	0	0	0	0	1	2
2011	1	0	1	0	0	1	1	4
2012	0	1	1	0	0	1	2	5
2013	0	1	1	0	0	0	4	6
2014	0	3	0	1	0	1	0	5
2015	0	2	1	1	0	1	2	7
2016	0	3	2	0	1	1	3	10
2017	0	1	2	0	0	0	2	5
Total	8	20	10	3	4	11	27	83

Table 2. Chi-square test on lodging occurrence in individual regions

Region	Observation		Expectation		P-value
	No. of trials with lodging	No. of trials without lodging	No. of trials with lodging expected	No. of trials with lodging not expected	
Capricornia	4	4	3.3	4.7	0.603
Central Highlands	14	6	8.2	11.8	0.008
Liverpool Plains	1	9	4.1	5.9	0.046
Lockyer Valley	0	3	1.2	1.8	0.149
North West Slopes	1	3	1.6	2.4	0.516
Southern Downs	7	4	4.5	6.5	0.126
Western Downs	7	20	11.1	15.9	0.112
Total	34	49			

Southern Downs were the only two regions in which the number of trials lodged was greater than the number not lodged, with lodging occurring in 14 of 20 trials in the Central Highlands and seven of 11 trials in the Southern Downs. In Capricornia, lodging was observed in 50% of trials. In the other four regions, the number of trials that did not lodge was higher than of trials that lodged, with the Lockyer Valley being the only region where no lodging was observed.

A χ^2 test revealed that trials showed significantly more lodging than expected in the Central Highlands ($P = 0.008$), but significantly less in the Liverpool Plains ($P = 0.046$) (Table 2). The other five regions displayed no significant difference in lodging occurrence compared with the overall average frequency (41%) across all regions.

Lodging severity varied across regions. The most severe lodging rating (category 4, >20%) was observed in one trial in the Central Highlands and two trials in the Western Downs (Fig. 1). The second most severe lodging rating (category 3, 10–20% lodging) was observed in the North West Slopes (one trial) and the Southern Downs (three trials). For two regions, the highest lodging rating observed was category 2 (1–10%); these were Capricornia (four trials) and Liverpool Plains (one trial). No lodging was observed in any of the three trials in the Lockyer Valley.

Seasonal variation in the frequency and severity of lodging

The frequency of lodging varied across seasons. Lodging was not observed in any trial in four seasons (2006, 2010, 2011 and 2013), whereas it was observed in all trials in the 2005 season (Fig. 2). In the other nine seasons, the proportion of trials that lodged varied from 20% to 86%.

Lodging severity also varied across growing seasons. Most of the trials over the seasons did not lodge (59%), whereas lodging rating category 2 (1–10%) occurred in 27 of the 83 trials. The most severe lodging rating (category 4, >20%) was observed in three trials, with one each in 2005, 2016 and 2017. The second most severe lodging rating (category 3, 10–20%) occurred in four trials, with one each in 2014 and 2015 and two in 2016.

Relationships of lodging to SOI and soil characteristics

A general trend was observed whereby the proportion of trials lodged was associated with the mean SOI over the

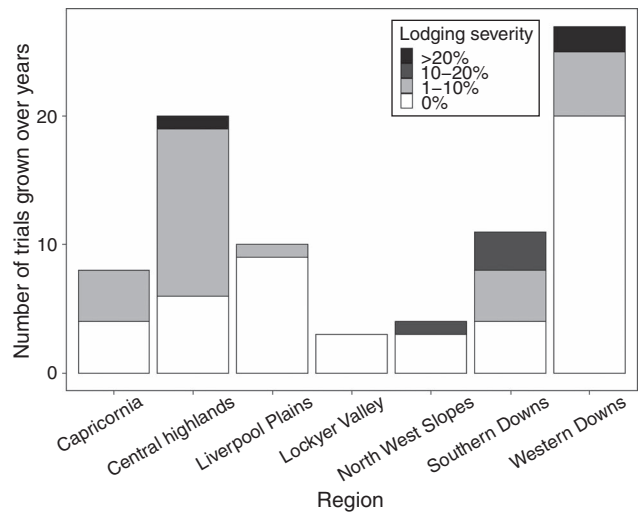


Fig. 1. Number of trials with one of the four lodging-severity ratings (0%, 1–10%, 10–20%, >20%) in each region.

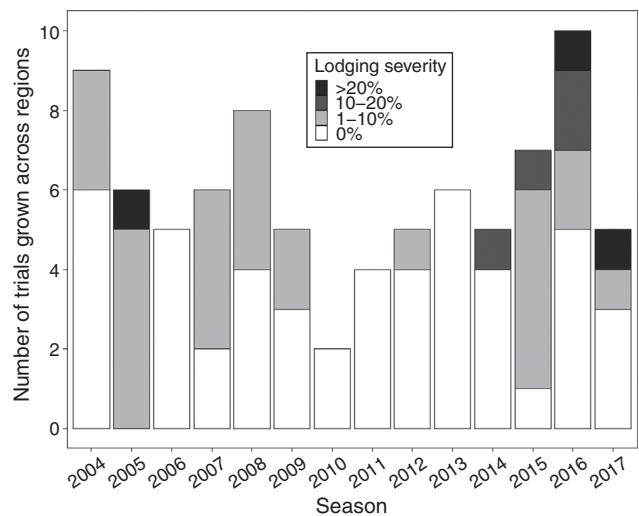


Fig. 2. Number of trials with one of the four lodging-severity ratings (0%, 1–10%, 10–20%, >20%) in each season.

growing months in individual seasons (Fig. 3). Specifically, the proportion of trials in which lodging occurred was significantly negatively correlated with mean SOI over the

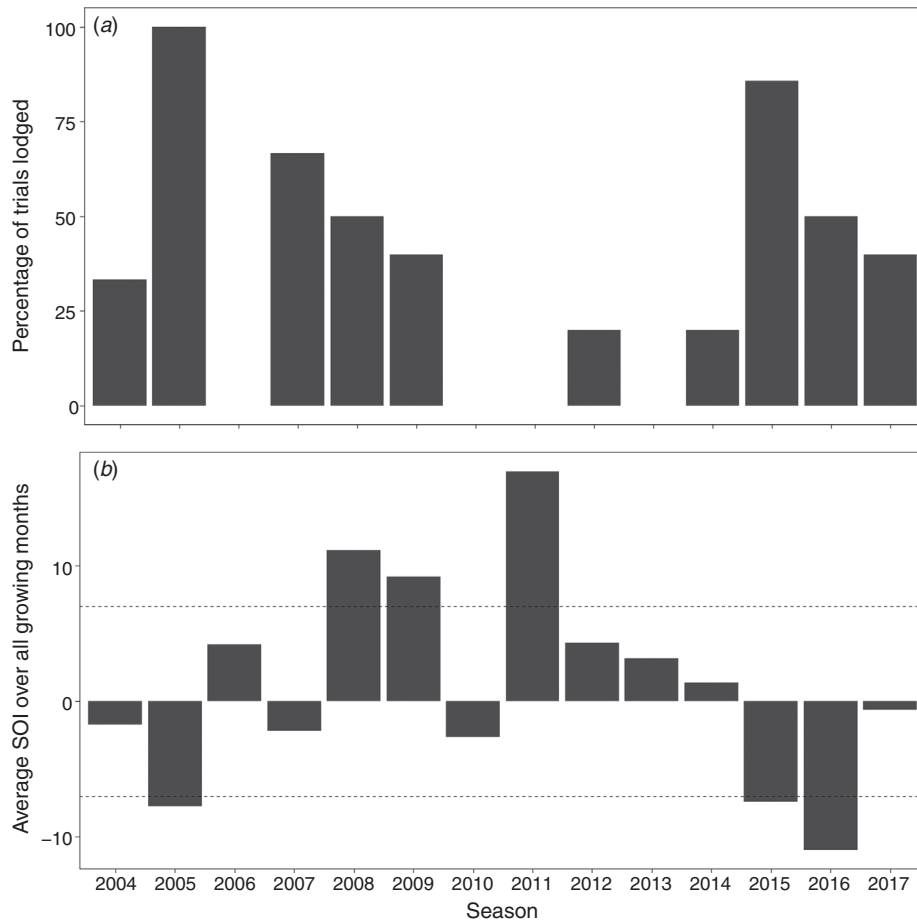


Fig. 3. (a) Percentage of trials lodged and (b) the average Southern Oscillation Index (SOI) over the growing months in individual seasons. The two dashed lines indicate SOI = 7 and SOI = -7 respectively.

growing months of individual seasons ($r = -0.54$, $P = 0.045$; Fig. 4). Mean SOI over the growing months explained 29% of variation in the proportion of trials lodged. Of the three seasons with mean SOI < -7 , two seasons (2005 and 2015) had $>80\%$ of trials with lodging observed and the third season (2016) had 50% of trials with lodging observed (Fig. 3). By comparison, of the three seasons with mean SOI >7 , one season (2011) had no trials with lodging observed and the other two seasons (2008 and 2009) had $\leq 50\%$ of trials with lodging observed.

Soil characteristics such as soil depth and the water-storage capacity of the soil (PAWC, plant-available water capacity) are important factors affecting water availability to the crop, and can thus affect lodging. PAWC is defined by the soil drained upper limit, crop lower limit, saturation and total porosity, and is the maximum amount of stored soil-water that can be accessed by the crop (Dalglish and Foale 1998). We investigated whether lodging was related to soil depth and PAWC. We were able to identify the GPS coordinates for 69 of the 83 trials. Ten of the 14 trials where exact locations could not be identified were grown in the Central Highlands and Capricornia in Queensland, and two were grown in each of the Liverpool Plains in NSW and Western Downs in Queensland (table S1). Results showed that average lodging score across commercial hybrids was negatively associated with both soil depth (Fig. 5a) and PAWC (Fig. 5b). However, the associations were non-significant. Because soils of

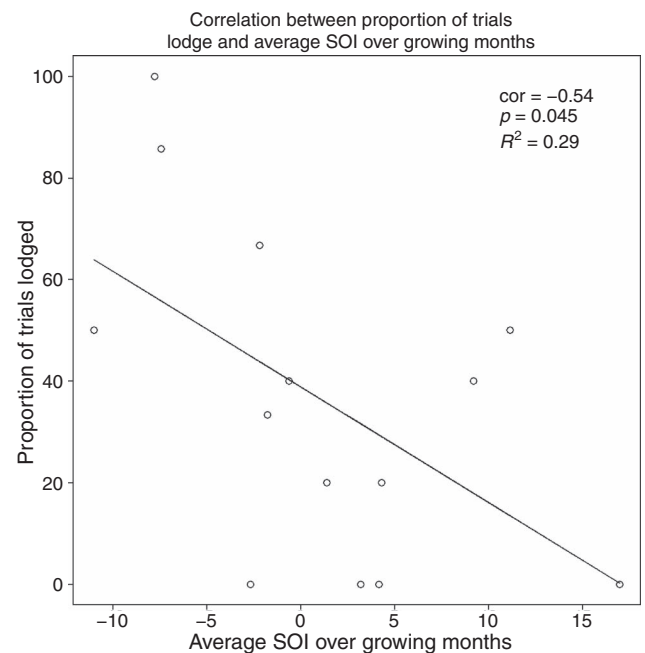


Fig. 4. Relation of the proportion of trials lodged to the average Southern Oscillation Index (SOI) over the growing months of the 14 seasons.

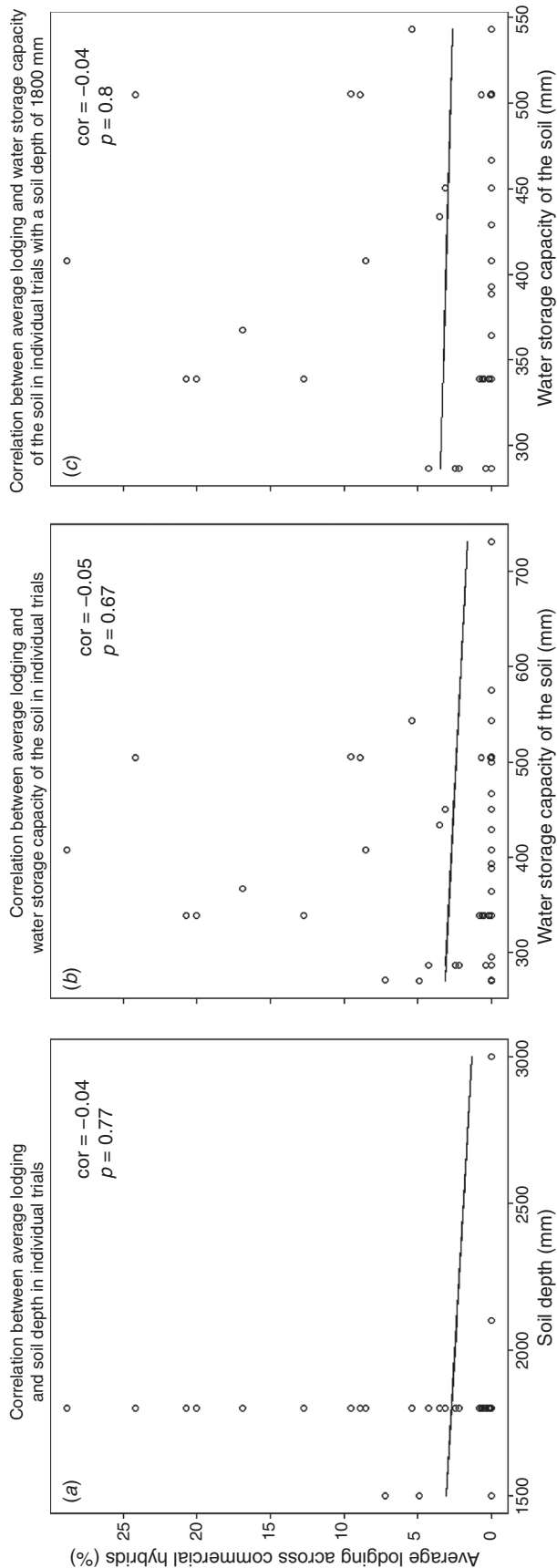


Fig. 5. Relation of the average lodging (% of plants lodged) across commercial hybrids to (a) soil depth, (b) water-storage capacity (PAWC) of the soil of individual trials, and (c) PAWC of the soil of trials with a soil depth of 1800 mm.

the majority of the trials had a depth of 1800 mm, we further investigated the association between average lodging across commercial hybrids and PAWC for trials that had a soil depth of 1800 mm, and found that the association was negative but also non-significant (Fig. 5c).

Average lodging resistance of commercial hybrids across seasons

Typically, commercial hybrids are marketed for a period of years then replaced by new hybrids with improved performance. Over the period of these trials, hybrids entered or left the market according to commercial factors. There was a significant turnover of commercial hybrids across the seasons. Thirteen commercial hybrids were grown in the 2004 trials. The proportion of commercial hybrids grown in the other seasons that were in common with those grown in 2004 decreased steadily, reducing from 77% (i.e. 10) in 2005 to 23% (i.e. three) in 2017 (Fig. 6). Only three commercial hybrids were grown in all 14 seasons and their overall average lodging score in each season was used as a reference to show the trend in the levels of lodging for the other 34 commercial hybrids over the seasons. Another three commercial hybrids were grown in both the first five (2004–08) and last five (2013–17) seasons, accounting for only 12.5% of the commercial hybrids grown in the 2013–17 seasons.

Average lodging severity of the three reference commercial hybrids varied from 0% to 10.68% over the seasons. Most of the relative average lodging-severity values of the other commercial hybrids (i.e. relative to that of the three reference hybrids grown in all seasons) were within the range 0–1. A two-sided *t*-test indicated no significant difference ($P = 0.67$) between the average relative lodging of commercial hybrids in the first five seasons (2004–08) and the last five seasons (2013–17).

Discussion

Sorghum in Australia is grown in water-limited environments of varying intensity, with post-anthesis drought stress being common in most environments (Hammer *et al.* 2014). One of the consequences of post-anthesis drought conditions is lodging (Henzell *et al.* 1984). Hybrids with high yield potential tend to be more susceptible to lodging (Wang *et al.* 2019) and farmers discriminate against hybrids where lodging is severe and/or frequent, owing to the risk of financial loss. As a result, lodging is one of the major constraints limiting genetic improvement of yield in Australian grain sorghum, and sorghum breeders place strong selection pressure for lodging resistance (Henzell and Hare 1996). Despite its importance, very little is known about the severity and frequency of lodging both temporally and geographically. In this study, we conducted a retrospective analysis of a dataset of 83 yield trials grown in the major sorghum-production regions in Australia over 14 consecutive seasons in order to understand temporal and geographical patterns of lodging. The results provide insights into the patterns of the occurrence and severity of lodging of grain sorghum in Australian environments.

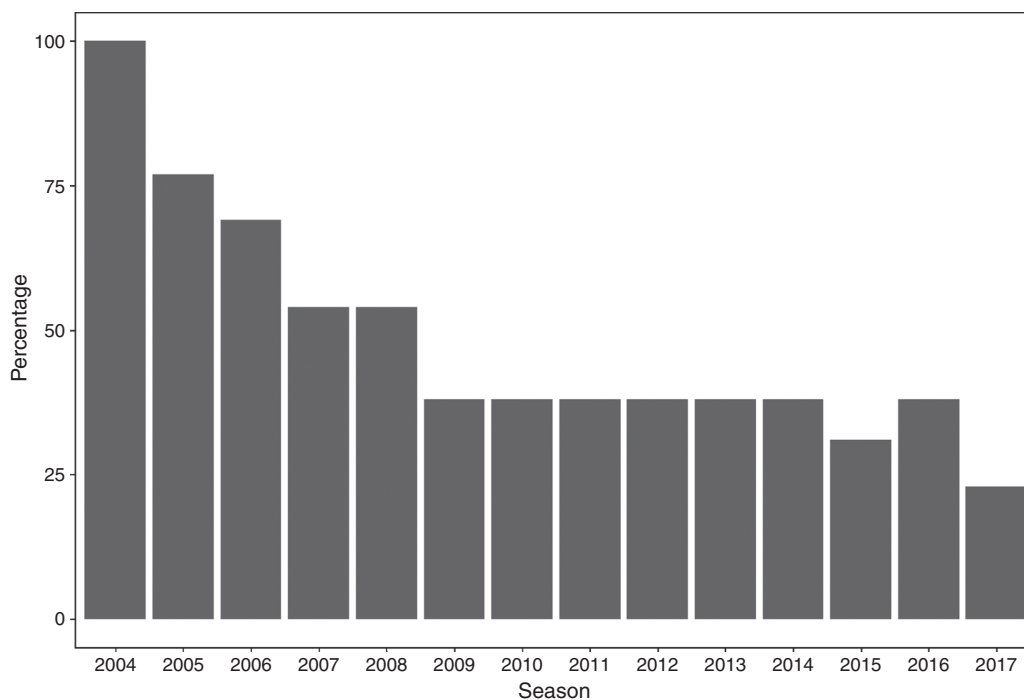


Fig. 6. Percentages of commercial hybrids grown across all seasons in common with the commercial hybrids grown in 2004.

Lodging frequency and severity varied geographically and temporally

The occurrence of lodging varied across regions. Different locations varied in the frequencies of environment types, with different locations having varying levels of soil-water supply and varying demands by crop growth within the crop growth window. Water stress is more common in Central Highlands and Capricornia locations such as Emerald, Capella and Biloela and less common in Western Downs locations such as Dalby and in Southern Downs locations such as Warwick (Chapman *et al.* 2000; Hammer *et al.* 2014; Clarke *et al.* 2019). Soil characteristics such as depth and PAWC are important factors affecting the supply of water during the growth season, and thus the types of environments that the crop experiences. As a result, differences in the frequency and severity of lodging may be related to geographical factors such as soil characteristics. However, average lodging across commercial hybrids within a trial was not significantly associated with either soil depth or PAWC of the soil (Fig. 5), although their relationships were negative. The lack of significant association might be due to lack of soil information in over one-third (i.e. 10/28) of the trials in the Central Highlands and Capricornia in Queensland. It may also be confounded by farming practices such as fallow and cropping history that could affect water availability to the crop. Therefore, the significantly high incidence (70%) and severity (up to >20%) of lodging in the Central Highlands (Table 2; Fig. 1) was likely a result of low in-season rainfall and possibly other environmental factors. These conditions likely result in the sorghum crop being frequently exposed to water stresses

during grain filling and consequently to lodging as reported previously (Henzell *et al.* 1984). Because this is a post-hoc study, we do not have enough data (e.g. on-site weather information) to prove this claim directly.

By comparison, among the regions examined in this study, the Liverpool Plains and Southern Downs are characterised by higher mean rainfalls and deeper soils with higher PAWC (Jordan *et al.* 2012). Trials in these two regions are therefore less likely to experience water stress during grain filling, as found by Hammer *et al.* (2014). Similarly, the Lockyer Valley is also a region characterised by deep soils and high rainfall; for example, more-than-adequate in-season rainfall was reported for three seasons (2007, 2014 and 2015) in Lockyer Valley locations (136.6–370.8 mm, <http://www.bom.gov.au/climate/data/>, station number 040082). This is in line with a previous simulation study (Clarke *et al.* 2019), which showed that trials grown in 2014 and 2015 in the Lockyer Valley (Gatton) experienced either no or very limited water stress. Hence, lodging was expected to occur both at a low frequency and with a low severity rating in these three regions. The observation met these expectations for the trials in both the Liverpool Plains and Lockyer Valley. Only one trial had mild (1–10%) lodging in the Liverpool Plains and none of the trials in the Lockyer Valley lodged (Table 2, Fig. 1), although it should be noted that only three trials were grown in the Lockyer Valley, and a greater sample size would provide more confidence. However, there was a non-significant, but higher number of trials lodged (i.e. seven of 11 trials) in the Southern Downs region (Table 2), of which three trials had 10–20% lodging and four trials had 1–10% lodging (Fig. 1). The higher than

expected levels of lodging occurrence and severity in the Southern Downs region could be related to high grain-yield potential in this region, with the trials in the Southern Downs producing the highest grain yield among all seven regions (data not shown). Previous studies have shown that, within the same trial, hybrids with higher grain-yield potential also tend to be more susceptible to lodging (Wang *et al.* 2019).

Long-term simulations have shown that trials in the North West Slopes region are often exposed to water stresses of varying extents, with water stress occurring in ~90% of the simulations (Hammer *et al.* 2014). Lodging in grain sorghum often occurs under drought during grain filling (Henzell *et al.* 1984), which suggests that trials grown in the North West Slopes region may be more likely to suffer from lodging. However, lodging was observed in only one trial (of four trials in total) grown in this region, with a severity rating of 10–20% (Fig. 1). This may be explained by the fact that, overall, the North West Slopes is low yielding (Hammer *et al.* 2014) and genotypes with low grain yield tend to be less susceptible to lodging (Henzell *et al.* 1984). In the Western Downs, the high frequency (observed in two of the three trials in this region) of the most severe lodging rating (>20%) might be explained by the high frequency of water stress together with high grain yield produced in this region (Hammer *et al.* 2014). Finally, in Capricornia, although only at mild levels (1–10% lodging), lodging occurred in 50% of the region's trials (Fig. 1). Overall, although it is difficult to isolate individual causal factors, these results indicate that geographical location plays an important role in both lodging occurrence and severity.

Lodging also varied across seasons in all regions except in the Lockyer Valley, and varied significantly from the overall pattern in two regions (Central Highlands and Liverpool Plains). In the Central Highlands, lodging occurred at a significantly higher frequency than expected, in eight of the 12 seasons ($P < 0.008$). By contrast, in the Liverpool Plains, lodging occurred at a significantly lower frequency than expected (in one of the 10 seasons; $P < 0.046$). This suggested that seasonal variations in the amount and timing of rainfall are likely to play an important role in occurrence of lodging.

Seasonal variation in SOI is an important factor in driving lodging

Variations in patterns of lodging between seasons are likely to be associated with seasonal patterns of rainfall. Rainfall in and before the sorghum growing season is related to the SOI (Nicholls 1986). In this study, the average SOI over the crop-growing months was significantly associated with lodging, explaining 29% of the variation in lodging (Fig. 4). Previous studies have suggested that lodging in grain sorghum is closely related to water deficit (Henzell *et al.* 1984). In order to reduce the risk of crop failure, sorghum growers in Australia normally sow a crop when the soil moisture exceeds a threshold. Although this practice reduces the incidence of pre-flowering water stress, varying levels of water stress after flowering are likely to occur depending on the timing and amount of in-season rainfall (Jordan *et al.* 2012; Hammer *et al.* 2014). Rainfall varied

across regions during the period of the 14 seasons included in this study. Generally, the seasons that had high lodging received a low amount of in-season rainfall, whereas the seasons that had limited or no lodging received high in-season rainfall (Bureau of Meteorology 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2015, 2016, 2017, 2018, 2019). It is likely that limited in-season rainfall resulted in post-anthesis drought stress, and hence lodging.

The relationship between in-season rainfall and lodging could be further explored if rainfall data were available. However, onsite weather data were not available for most of the 83 trials. We could use the data for the closest weather stations of the Australian BoM; however, the nature of rainfall in Australia can be highly variable over relatively small distances, and so we are doubtful of the value of these data to the interpretation of the results. In addition, further complexity is introduced to water availability by farming practices such as fallowing and previous cropping history (Passioura and Angus 2010), which influence plant-available water and the timing and intensity of water stress. Because this is a post-hoc study, we cannot conduct strict statistical analysis to prove the relationship between lodging and in-season rainfall.

The observation that 29% of the variation in lodging is accounted for by the average SOI over the growing months suggests that a large proportion of lodging occurrence cannot be explained by seasonal rainfall. Other variables such as genotypic factors and management practices can also affect lodging. Genotypic factors and management practices can possibly affect lodging through their influence on the extent and timing of water use (van Oosterom *et al.* 2011). Management practices such as row configuration, planting density, selection of hybrids, and sowing time can affect spatial and temporal soil moisture (Muchow *et al.* 1994; Whish *et al.* 2005; Hammer *et al.* 2016; Clarke *et al.* 2019), which will affect water availability to the crop, and thus the occurrence of lodging. Therefore, it is possible that differences in management practices across and within the regions can explain a large proportion of the variation in lodging.

Genetic resistance to lodging in commercial hybrids has not improved over the period of the study

There was a substantial turnover of commercial hybrids in the market (as shown in Fig. 6). Only three commercial hybrids were grown in all 14 years targeted by this study, whereas the other commercial hybrids were grown in only some of the years and represented new releases into the market and replacements for older varieties. We were therefore able to use the three commercial varieties as standard varieties to compare the levels of resistance of the other commercial hybrids over the period of the seasons in this study. Resistance to lodging is a major target of selection in sorghum breeding programs (Henzell and Hare 1996), so progress to improve resistance is expected. However, we observed that the lodging resistance of varieties grown in the last five seasons was not significantly different from that of varieties grown in the first five seasons (two-sided t -test, $P = 0.82$), indicating that lodging resistance

has not changed over the years. This might be due to the positive association between lodging susceptibility and grain yield (Wang *et al.* 2019). Significant genetic yield gain in grain sorghum has been achieved in Australia over the last three decades (Potgieter *et al.* 2016); hence, recently released varieties have higher yield than older varieties (Clarke *et al.* 2019). Therefore, although grain yield has increased, it is likely that lodging resistance has been maintained at a level that farmers can accept. This was possibly due to the strategy that sorghum breeders implemented of selecting for hybrids with high yield potential and simultaneously selecting against lodging susceptibility rather than selecting for improved resistance to lodging (Wang *et al.* 2019).

Conclusions

This study is the first to document the frequency and severity of lodging in the major sorghum-production environments in Australia across seasons. Results showed that lodging was prevalent over most regions. However, within the materials used and the environments sampled in this study, lodging in sorghum varied across regions. Lodging occurred significantly more often in the Central Highlands in Queensland but significantly less frequently in the Liverpool Plains in NSW, whereas the occurrence of lodging in the other five regions did not significantly deviate from the overall frequency across regions. The occurrence of lodging also varied across seasons. Much of the variation in lodging was significantly associated with the SOI over the growing months of the sorghum crops ($R^2 = 29\%$). The SOI was related to lodging possibly through the seasonal effect on in-crop rainfall. Beside the SOI, other factors such as on-farm management strategies can also affect water availability and its spatial and temporal patterns, and likely lodging as well. Over the period of the 14 seasons investigated in the study, the levels of resistance to lodging of commercial hybrids did not improve. It is likely that this occurred because sorghum breeders maintained resistance to lodging at a level that farmers could accept and used any improvements in underlying lodging resistance to increase yield potential.

Author contributions

XW and DJ conceived the project. XW conducted the analysis and wrote the manuscript. All other authors read, revised and approved the manuscript.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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