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Understanding the genetic control of lodging-associated plant characters in winter wheat (*Triticum aestivum* L.)

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Abstract A genetic analysis of plant characters associated with lodging resistance, yield and other agronomic traits was made on two doubled haploid winter wheat populations grown at two UK locations in the 2004/2005, 2005/2006 and 2006/2007 seasons. Wide genetic variation was found for traits that affect lodging, including plant height, components of stem strength (stem diameter, wall width and material strength), components of anchorage strength (spread and depth of the root plate), ear area and shoot number per plant. Heritabilities were estimated for each of the key lodging traits, with plant height having the highest heritability and anchorage traits the lowest values. Six quantitative trait loci (QTL) controlling plant height had individual height effects (2 × the additive effect) of 3–9 cm and taken together, could potentially increase plant height by up to 34 cm. Three of the height QTL were also associated with greater yield or greater thousand grain weight, and three were associated with components of stem strength or anchorage strength. QTL were also identified for each of the measured lodging traits, which were unrelated to height. Individual QTL with the largest estimated effects on lodging resistance were for height, stem diameter, stem material strength, stem failure moment, root plate spread and root plate depth. Diagnostic genetic markers for the most important QTL regions are now required to enable breeders to efficiently combine multiple traits together in a single variety that will increase lodging resistance and yield simultaneously.

Keywords Height · Lodging · QTL · Straw strength · Yield · Wheat

Introduction

Lodging is the permanent displacement of plant shoots from an upright position. It causes reduction in grain yields of up to 50 % (Stapper and Fischer 1990) and loss of bread making quality (Berry et al. 2004).In the past, plant breeders have reduced lodging risk by introducing the semi-dwarfing genes *Rht-B1b* and *Rht-D1b* into breeding programs (Wilhelm et al. 2013) to produce shorter varieties. Farmers also employ a range of methods to reduce lodging, including the use of plant growth regulators (PGRs) to shorten crops, reduced seed rate, delayed sowing, reduced and delayed nitrogen fertiliser and rolling the soil (Berry et al. 2004). Plant breeders and farmers must keep improving lodging resistance to counter the escalating lodging risk arising from the continued yield

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improvements achieved in the UK (Mackay et al. 2011). However, the tools that have been used most successfully in the past, semi-dwarfing genes and PGRs, may not provide a full solution in the future. Several studies have shown that yield is reduced when plant height is shortened too much with dwarfing genes (Allan 1986; Baylan and Singh 1994; Flintham et al. 1997; Kertesz et al. 1991; Miralles and Slafer 1995; Richards 1992). In these studies the optimum plant height for yield was often found to lie between 0.7 and 1.0 m. The lower end of this height range is already being approached by some modern varieties. Whilst there may be scope for further shortening with PGRs through sequential applications, pressure may be brought to bear to reduce their use because some PGRs leave residues in the grain (Spink et al. 2004). If there is limited scope for reducing crop height, and therefore the 'leverage' that is imposed by the aerial parts of the plant, it follows that the strength of the structures that support the plant must be improved in order to decrease lodging risk. In wheat, lodging can arise from over-turning of the anchorage system (root lodging) or buckling of the stem base (stem lodging). A validated model of lodging risk (Berry et al. 2003a) predicts stem lodging when the leverage of a shoot (calculated from the shoot height at the centre of gravity, natural frequency and ear area) exceeds the failure moment of the stem base (calculated from the stem diameter, wall width and material strength of the stem wall). Root lodging is predicted when the sum of the leverage of each shoot on a plant exceeds the anchorage failure moment (calculated from the spread and depth of the root plate). The failure moment of a structure may be defined as the strength at the point of failure. An investigation of the characteristics that a wheat plant would require to avoid lodging showed that improvements in stem failure moment and anchorage failure moment would be required (Berry et al. (2007). This study showed that, in order to maximise stem strength for the least investment in dry matter, it is necessary to increase the stem diameter and material strength of the stem wall, whilst minimising the stem wall width. Increasing anchorage failure moment requires a wider and deeper root plate. Large variation has been observed for traits that determine stem failure moment and anchorage failure moment within winter wheat varieties currently grown in the UK (Berry et al. 2007). However, plant breeders are unlikely to have intentionally exploited the variation in these traits due to the lack of rapid screening methodologies.

The time-consuming nature of measuring traits associated with stem failure moment and anchorage makes them good candidates for genetic marker assisted selection. However, in general, little is known about the genetic control of anchorage and stem strength traits in wheat and the other *Poaceae* and whether or not they are related to other agronomically important characters. Keller et al. (1999) identified two quantitative trait loci (QTL) for stem diameter within a wheat x spelt cross, and Hai et al. (2005) identified one QTL for each of stem diameter and stem wall width and two QTL for stem pushing resistance. Ma (2009) showed that a gene involved in the biosynthesis of lignin (COMT) was expressed more in a lodging resistant variety than a lodging susceptible variety. In a pot study carried out in a glasshouse (Verma et al. 2005) identified one QTL for each of stem width of the lowest internode and structural rooting depth in winter wheat. In maize Guingo et al. (1998) identified QTL for traits associated with stem and anchorage strength (stem diameter, root diameter, root number). In rice six QTL were identified for stem diameter and five QTL identified for the pushing resistance of the lower part of the stem (Kashiwagi and Ishimura 2004). A substantial amount of work has been done on the genetic control of root architecture in rice (e.g. Price and Tomos 1997), but none has investigated the genetic control of anchorage traits in wheat under field conditions.

Understanding the genetic control of stem and anchorage strength is poor in wheat for several reasons; these include 1) the correct measure of stem strength, stem failure moment, has not been investigated, 2) the most relevant sub-traits of anchorage strength, spread and depth of the root plate, have not been measured in field-grown crops, and 3) previous investigations have been done on a limited range of germplasm and growing seasons. The aim of this study was to improve understanding of the genetic control of stem strength and anchorage strength, together with their relevant component sub-traits, by investigating two winter wheat mapping populations grown in a range of locations and growing seasons. The relationships between stem and anchorage strength traits with other lodging-related and agronomically important traits were also investigated to understand the extent to which breeders may increase lodging resistance and yield simultaneously.

Materials and methods

Experiments

Two doubled haploid (DH) mapping populations from crosses between elite winter wheat varieties Savannah x Rialto and Solstice x Xi19 were investigated. These DH populations were chosen on the basis of data from Berry et al. (2003b) and an earlier screening experiment which showed that Savannah possessed a greater anchorage strength and weaker stem strength compared with Rialto, and that Solstice had a greater anchorage and stem strength than Xi19. The Rialto × Savannah (RiSa) population comprised 126 DH lines and the Solstice × Xi19 (SoXi) population comprised 120 DH lines, respectively. The treatments were arranged in a resolvable incomplete block design known as an alpha design. Each treatment was replicated twice in main plots measuring 12 × 2 m. Each replicate block contained 13 sub-blocks, each containing 10 treatment plots. A 6 m length of each main plot (referred to as a sub plot) was treated with a plant growth regulator (PGR) program. This included BASF 3C Chlormequat 720 (chlormequat chloride (720 g/l) applied at 2.25 l/ha at GS30/31 followed by Terpal (2-chloroethylphosphonic acid (155 g/l) plus mepiquat chloride (305 g/l)) applied at 0.75 l/ha at GS37/39.

Each mapping population was grown in three seasons at either Boxworth (52·2°N, 0·0°W) or Rosemaund (52·1°N, 2·5°W) as described in Table 1. The seeding rate was either 200 or 250 seeds/m^2. Boxworth has a clay soil type (Hanslope series) and Rosemaund has a silty clay loam (Bromyard series).

Weather

In the 2004/2005 season the weather for both the Boxworth and Rosemaund sites was characterised by warmer than average temperatures throughout the growing season and below average rainfall during winter (December–February) (Table 2). Otherwise, the rainfall and sunshine hours were similar to the long-term mean (LTM). The 2005/2006 season had a warmer than average autumn (September–November) and summer (June–August) periods. The winter period was dryer than average and at Rosemaund the summer period had less than 50 % of average rainfall due to very low rainfall in June and July. Both sites experienced more sunshine hours than average during summer. The 2006/2007 season was warmer than average between September and May at both sites. At Rosemaund only 8 mm of rain fell in April and May compared with a LTM of 93 mm and rainfall in June was above average. At Boxworth only 1 mm of rain fell in April following a dry second half of March. More than twice as much rain then fell in May compared with the LTM. Rosemaund received fewer sunshine hours than average in summer, mainly due to cloudy conditions in June and July.

Measurements

In all experiments grain yield was determined using a small plot combine, specific weight and grain moisture were measured using a Dickey John GAC 2000 grain analysis computer (Church Industries, Minneapolis, USA), and the percentages of stem and root lodging in each plot were recorded. Plant numbers in the variety screening and mapping population experiments were determined between GS11 and GS13 by recording the plant numbers in rows on either side of a 0.5 m length of row at 5 positions within each plot.

The plant characters associated with lodging were measured between GS69 and GS85 in the variety screening and mapping population experiments. Plants were always selected from the non-PGR sub plot of each main plot, except at Boxworth in 2007

Table 1 Location, sowing date and seeding rate for each mapping population experiment

Mapping population	Year	Site	Sowing date	Seeding rate seeds/m^2
RiSa	2004–2005	Boxworth	22/10/04	200
RiSa	2005–2006	Rosemaund	14/10/05	250
RiSa	2006–2007	Boxworth	7/10/06	250
SoXi	2004–2005	Rosemaund	19/10/04	200
SoXi	2005–2006	Boxworth	3/10/05	250
SoXi	2006–2007	Rosemaund	9/10/05	250

Table 2 Weather observations. BX, Boxworth; RM, Rosemaund

	BX 04-05	BX 05-06	BX 06-07	BX LTM[a]	RM 04-05	RM 05-06	RM 06-07	RM LTM[a]
Minimum daily temperature (°C)								
Autumn	8.3	8.3	9.1	6.7	6.5	7.2	8.0	5.8
Winter	2.3	1.2	3.2	0.9	1.9	0.8	3.4	1.2
Spring	6.0	4.6	5.2	3.9	4.6	4.6	5.1	4.0
Summer	12.2	12.4	10.9	10.5	10.6	11.9	10.7	10.1
Maximum daily temperature (°C)								
Autumn	16.2	16.8	17.3	14.2	13.8	15.6	16.5	13.9
Winter	8.6	6.8	9.5	6.7	7.5	6.9	9.6	7.4
Spring	14.8	13.3	16.0	12.7	13.4	12.8	15.1	12.7
Summer	23.9	24.9	20.9	20.9	21.1	23.0	19.9	20.5
Average monthly sunshine hours								
Autumn	143.3	108.6	120.8	107.9	112.5	109.0	110.2	92.7
Winter	64.8	57.1	64.7	58.2	71.6	62.2	66.2	52.3
Spring	145.0	141.8	173.7	150.5	156.0	152.6	170.2	140.7
Summer	184.1	226.9	178.3	194.3	200.4	234.1	119.2	171.9
Average monthly rainfall (mm)								
Autumn	34.7	64.3	55.3	50.3	61.3	71.3	74.2	60.0
Winter	28.0	22.7	66.0	41.7	34.0	33.3	37.5	62.3
Spring	38.0	45.7	50.7	44.0	46.0	54.3	18.4	47.0
Summer	47.0	46.7	58.3	48.7	41.3	22.7	72.4	51.0

[a] *LTM* long term mean (1971–2000)

when severe lodging in the sub plots without PGR meant that the plants had to be taken from the PGR-treated sub plots. Ten plants were selected randomly, avoiding the outer three rows, and excavated with a hand fork to completely recover the structural crown roots to a depth of 100 mm. Soil was washed from the roots and the section of crown roots responsible for anchoring the plant was identified by its inherent rigidity and by the tendency for soil particles to adhere to the dense covering of root hairs, or rhizosheath (see Berry et al. 2000 for more details). The depth of soil to which the rhizosheath extended was measured and this was termed the ‘structural rooting depth’. The horizontal spread of the roots at the structural rooting depth was also measured and termed ‘root plate spread’.

Fertile shoots per plant were counted in the laboratory. The main shoot of each plant was identified according to Kirby and Appleyard (1984) and all subsequent measurements were carried out on this shoot. Natural frequency (Hz) was measured by plant oscillation tests. The main shoot was clamped at its base and was pulled back (at the collar of the ear) 10 cm from the vertical and released. The time for three complete oscillations in the line of displacement was recorded. Natural frequency was calculated as the number of oscillations per second (Hz). The height to the tip of the ear was measured, and height at the centre of gravity (m) was determined by cutting off the roots and balancing the isolated shoot on a ruler (leaves and ear still attached). The distance from the point of balance to the base of the stem was recorded. The length from the ear collar to the tip of the ear was measured (mm). This measurement was used to estimate the area of the ear using a relationship derived from data collected by Berry et al. (2003b) in which ear length and ear area were shown to be linearly related across 15 varieties (ear area (cm^2) = ear length (mm) * 0.20–7.72).

The first internode of more than 10 mm, which originated at, or just below, the surface of the ground was defined as internode 1. Subsequent internodes up the stem were numbered from two, with the uppermost internode referred to as the peduncle. Internodes shorter than 10 mm were occasionally observed, but were too short to enable tensile failure strength to be measured. These ‘basal’ internodes (Kirby and Appleyard 1984) always preceded internode 1 and never exceeded one per stem. Measurements of the stem base were carried out on internodes 1 and 2 of each main shoot. Stem diameter (mm) was measured at the middle of each internode, using digital callipers (Etalon, Switzerland). The lengths of internodes 1 and 2 were measured from the mid-point of their adjacent nodes. The breaking strengths (Newtons) of internodes 1 and 2 were determined using a three-point bending test (Easson et al. 1992; Graham 1983). The nodes adjacent to the internode were supported and an even pulling pressure was applied at its middle using a digital spring balance (Mecmesin Ltd, Horsham, UK) pulled at an even rate. The force recorded at the point when the internode buckled was taken as its breaking strength. Internodes were then cut at their centre points and digital callipers were used to measure the stem wall width (mm). Two measurements of stem wall width were taken on opposite sides of the stem, from which a mean value was calculated.

Calculations

The stem failure moment (B_s) is the force required to buckle a stem measured in Nmm. B_s was calculated from Eq. 1 where F_s is the breaking strength of the internode measured in Newtons and h is the internode length (mm):

$$B_S = \frac{F_S h}{4} \tag{1}$$

The failure yield stress (material strength) of the stem wall (σ) was calculated for internodes 1 and 2 from the breaking strength of the internode (F_s), its length (h), radius (a) and wall width (t):

$$\sigma = \frac{F_S h a}{\pi\left(a^4 - (a-t)^4\right)} \tag{2}$$

Statistical analysis

ANOVA and REML were used within Genstat 8 to estimate the treatment means and calculate the average standard error of difference. Correlation coefficients were calculated using Genstat 8 to assess whether two sets of variables were significantly related.

Heritability

Heritability at the plot level was calculated as:

$$\text{Genetic variance}/\text{Genetic variance} + \text{Residual variance}$$

Heritability at the trial level was calculated according to Hallauer and Miranda (1981) as follows;

$$\text{Genetic variance}/(\text{Genetic variance} + (\text{Residual variance}/\text{No.obs.})).$$

REML was used to calculate the levels of variance using a Linear Mixed Model. Within this model, the Fixed Model was Site/season and the Random model was Variety + Variety.Site/season. In general, the heritability at the trial level is of greatest relevance to plant breeders (Bruno Poupard, Biostatistician, Limagrain, pers comm).

Production of genetic maps

Leaf tissue was sampled from 7-day-old seedlings directly into deep-well microtitre plates, frozen at −80 °C, and then freeze-dried overnight. The tissue was then ground to fine powder in a Qiagen mixer mill following addition of two stainless steel ball-bearings per well. DNA was extracted using a proprietary method.

Microsatellite markers from several different sources were used in the project including; BARC—Song et al. (2005), CFD—Guyomarc’h et al. (2002), CFA—http://wheat.pw.usda.gov/GG2/index.shtml, WMS—Roder et al. (1998) and http://www.traitgenetics.com/en/, PSP—Bryan et al. (1997), STM—Hayden et al. (2004) and WMC—Wheat Microsatellite Consortium. PCR conditions were as recommended by the various authors above, with the forward PCR primer labelled with either an IRD700 or IRD800 infra-red dye. PCR products were denatured in formamide at 95 °C for 5 min and separated on 6 % acrylamide gels containing urea run on a Li-COR 4200 DNA sequencer. The gel images were printed-out, scored and the data entered into an Excel spreadsheet.

Over 500 hundred publicly available microsatellite or simple sequence repeat (SSR) markers were used to screen the four parental lines in order to check for DNA polymorphisms within the two DH populations. For RiSa, mapping was carried out on all 126 DH lines, but for SoXi, a number of lines containing a large number of non-parental alleles were removed, leaving 112 DH lines. In total 219 SSRs were mapped on the entire SoXi DH population and 180 were mapped on the RiSa population. DNA from the first 94 individuals of both populations was also sent to Triticarte (http://www.diversityarrays.com/) to add DArT markers (coded with the prefix wPt; Akbari et al. 2006) to both maps with the aim of improving the genome coverage.

The marker data were entered into MapDisto version 1.7.0 (http://mapdisto.free.fr/MapDisto/index.html; Lorieux 2012) and the expected 1:1 segregation of alleles at each marker locus, in a DH population, was checked using a Chi squared test. Loci with highly distorted segregation ratios were removed from any further analysis. The linkage maps were constructed using a LOD score of 5 and a maximum recombination fraction of 0.35.

QTL analysis

Prior to QTL analysis, a sub-set of evenly-spaced marker loci was selected (~15–20 cM intervals). This provided good map coverage, a minimal amount of missing data, and, where possible, were common between the two populations to facilitate alignment of QTL. The QTL detection framework comprised 161 loci for RiSa and 193 loci for SoXi. Marker data and 3 years of phenotypic data, plus three-year means for all traits were entered into the software package QTL Cartographer Version 2.0 (http://statgen.ncsu.edu/qtlcart/) and MapDisto. MapDisto was used to perform single marker analysis of variance (ANOVA) and QTL Cartographer was used to predict the size and position of each QTL using the composite interval mapping (CIM) procedure with the standard defaults. A QTL was declared if the LOD score was greater than 2.5 according to CIM and if there was a significant difference ($p < 0.05$) between the means of the two allelic classes at the marker loci flanking the QTL.

Results

Measurement precision

Measurement precision can be estimated in terms of the coefficient of variation (cv), calculated as the standard deviation ÷ mean and expressed as a percentage. Grain yield cvs of 4 % were achieved in the DH mapping population experiments across 3 seasons (Table 5). For traits associated with lodging the lowest cvs of 5 % or less were for plant height, height at the centre of gravity, ear area and internode diameter. Moderate cvs of 6 to 9 % were associated with shoot natural frequency, shoot number per plant, root plate spread, root plate depth, internode wall width, and stem failure wind speed. The highest cvs of 10 % or more were associated with calculations of stem failure moment and stem material strength. Only results with statistically significant differences are discussed in the following sections.

Environmental variation

Moderate or large differences were observed for the mean measurements of each DH population between the site seasons (Tables 3 , 4). Site/season differences were statistically significant ($P < 0.05$) for all measurements, apart from the spread of the root plate, natural frequency and grain moisture in SoXi, and for the spread and depth of the root plate in RiSa. No systematic differences due to site/soil type could be detected and it appears that most of the variation between the site/seasons was caused by variation in plant establishment and weather during the growing season.

Plant establishment was generally above 100 plants/m^2, sufficient to achieve a good yield potential (Tables 3, 4). More plants were established at both sites in 2005–2006 than the other seasons due to more favourable soil and weather conditions during drilling and plant emergence. The higher number of plants in 2005–2006 was related to fewer stems per plant, weaker stem strength, a thinner stem wall, thinner stems in SoXi and a lower material strength in RiSa. Grain yields ranged from an average of 7.7 t/ha in 2006–2007 to 10.3 t/ha in 2004–2005 for the RiSa population (Table 3) and from 8.2 t/ha in 2006–2007 to 10.9 t/ha in 2004–2005 for the SoXi DH population (Table 4). Lower yields recorded in 2006–2007 were probably caused by a combination of the dry spring, and cloudy conditions during June and July. Levels of lodging recorded at harvest were low in all experiments apart from the RiSa population at Boxworth in 2006–2007. The plants were shortest in 2004–2005 and tallest in 2006–2007. Average plant height varied by as much as 112 mm between seasons.

Table 3 Summary of measurements on the Rialto × Savannah DH population

	2004–2005			2005–2006		
	Mean	Range	SED	Mean	Range	SED
Grain yield (t/ha)	10.26	8.46 –11.70	0.62***	9.19	7.12–10.83	0.57***
Grain moisture (%)	13.4	12.3–14.4	0.37***	14.8	14.3–15.6	0.26***
Specific weight (kg/hl)	78.9	73.2–82.5	0.87***	76.9	70.5–81.9	1.12***
Thousand grain weight (g)	44.4	35.6–53.6	–	53	44–63	–
Plants/m^2	142	111–210	17.6*	203	146–222	16.0***
Ear emergence (June date)	8	4–12	–	8	4–14	–
Lodging (%)	10	0–95	–	2	0–45	–
Height to ear tip (mm)	863	631–1051	28.7***	912	690–1092	35.9***
Height centre gravity (mm)	445	335–558	16.2***	568	423–669	33.8***
Natural frequency (Hz)	1.18	0.51–1.81	0.116***	0.861	0.57–1.35	0.079***
Ear area (cm^2)	13.3	10.1–17.5	0.82***	15.1	12.2–19.2	0.70***
Shoot number per plant	4.41	3.36–5.76	0.751	3.64	3.03–4.37	0.338***
Root plate spread (mm)	48.5	35.8–63.7	5.69***	40.1	34.1–46.6	3.63*
Root plate depth (mm)	56.1	44.9–71.0	5.69***	44.8	37.8–50.5	3.10***
Int 1 length (mm)	47	35–59	6.8***	87	59–118	5.6***
Int 2 length (mm)	83	56–112	5.5***	115	81–151	7.1***
Int 1 diameter (mm)	4.00	3.49–4.57	0.215***	4.30	3.61–4.75	0.199***
Int 2 diameter (mm)	4.40	3.63–4.98	0.217***	4.60	3.81–5.13	0.247***
Int 1 wall width (mm)	0.83	0.68–1.08	0.076***	0.47	0.34–0.64	0.055***
Int 2 wall width (mm)	0.91	0.71–1.28	0.093***	0.52	0.36–0.62	0.054***
Int 1 material strength (Mpa)	46	32–62	6.2***	30	20–43	4.5***
Int 2 material strength (Mpa)	36	24–67	5.7***	24	16–34	4.0***
Int 1 failure moment (Nmm)	243	164–359	33.0***	148	87–228	30.8***
Int 2 failure moment (Nmm)	252	165–469	38.3***	176	87–237	18.9***

	2006–2007			Mean 2004–2007			
	Mean	Range	SED	Mean	Range	SED	Year × variety
Grain yield (t/ha)	7.66	5.68–9.02	0.567***	7.3	5.2–10.7	0.371***	***
Grain moisture (%)	13.6	12.8–14.7	0.381**	9.04	7.68–10.05	0.20***	**
Specific weight (kg/hl)	77.4	72.8–80.6	1.39***	13.9	13.3–14.5	0.85***	***
Thousand grain weight (g)				77.7	74.3–80.7	–	–
Plants/m^2	162	130–196	16.1*	164	142–196	10.3***	***
Ear emergence (June date)	−6.8	−10 to −5	–	3	−1 to 7	–	–
Lodging (%)	78	0–100	17.0***	22	0–75	–	–
Height to ear tip (mm)	852	667–1035	51.5***	906	695–1080	19.5***	***
Height centre gravity (mm)	501	408–593	32.8***	469	359–571	18.7***	***
Natural frequency (Hz)	1.13	0.75–1.75	0.144***	1.06	0.71–1.50	0.071***	***
Ear area (cm^2)	9.74	6.5–13.1	1.33***	13.5	11.0–16.8	0.69***	***
Shoot number per plant	2.54	2.05–3.14	0.256***	3.51	3.08–3.97	0.269**	***
Root plate spread (mm)	32.6	25.0–41.7	3.40**	40.4	34.6–46.6	3.63***	***
Root plate depth (mm)	50.5	23.0–77.1	10.80***	50.5	39.2–60.8	4.77***	***
Int 1 length (mm)	39.8	28.6–57.2	5.46***	57.9	43.3–72.6	4.52***	***
Int 2 length (mm)	66.0	49.5–89.1	6.23***	87.6	65.7–114.1	4.47***	***

Table 3 continued

	2006–2007			Mean 2004–2007			
	Mean	Range	SED	Mean	Range	SED	Year × variety
Int 1 diameter (mm)	3.62	3.03–4.17	0.253***	3.98	3.50–4.45	0.137***	***
Int 2 diameter (mm)	3.94	3.30–4.55	0.316*	4.30	3.64–4.73	0.157***	**
Int 1 wall width (mm)	0.70	0.48–0.95	0.111	0.67	0.54–0.83	0.0541***	***
Int 2 wall width (mm)	0.72	0.51–1.06	0.122***	0.72	0.58–0.92	0.0671***	***
Int 1 material strength (Mpa)	57	37–100	12.1***	44	32–64	5.58***	***
Int 2 material strength (Mpa)	45	27–88	10.9***	35	24–47	5.57***	***
Int 1 failure moment (Nmm)	223	134–362	41.2***	204	140–259	23.4***	***
Int 2 failure moment (Nmm)	220	146–332	35.4***	204	140–277	25.5***	***

Int 1 internode 1 (bottom internode), *Int 2* internode 2

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Genetic range of traits

The DH lines exhibited transgressive segregation beyond the range of the parental values in both populations. There was also significant variety x experiment effects for each trait. Significant variation was observed for number of plants established even though the same number of seeds was drilled in each plot. The range in plant number between the DH line with fewest plants to the DH line with most plants (across experiments) was 142–196 plants/m^2 for RiSa (Table 3) and 139–192 plants/m^2 for SoXi (Table 4). Across all experiments the range in yields between the lowest and highest yielding DH lines was 5.7 t/ha for RiSa and 1.7 t/ha for SoXi. In both DH populations the date of ear emergence varied by 7–8 days between the slowest and fastest developing DH lines.

The genetic ranges of the key lodging-associated characters are compared with the lodging-proof ideotype targets for a UK environment as calculated by Berry et al. (2007). The ideotype target for crop height was estimated at 0.7 m; taken as the minimum height likely to be compatible with high yield. Across the RiSa experiments the shortest DH line averaged 0.70 m and the tallest line averaged 1.08 m (Table 3). Across the SoXi experiments the shortest DH line averaged 0.82 m and the tallest line averaged 1.06 m (Table 4). Wide genetic variation was also observed for other traits that determine the wind-induced leverage of the shoot, including shoot height at the centre of gravity, natural frequency and ear area (Tables 3, 4). Shoot number per plant varied from approximately 3 to 4 between the least and most profuse tillering DH line in each population.

On average across experiments several DH lines in the RiSa and SoXi populations did achieve the ideotype target for the overall strength for internodes 1 and 2 of 250 and 230 Nmm, respectively (Tables 3, 4). A wide range of overall stem strengths was observed between the DH lines, e.g. the strength of the bottom internode varied from 140 to 259 Nmm over the 3 seasons that RiSa was grown (Table 3). The stem diameter of internode 1 ranged 3.50 to 4.45 mm in RiSa and 3.75 to 4.32 mm for SoXi, compared to the ideotype target of 4.94 mm. The ideotype target of internode 2 is 4.77 mm, which was almost achieved with the RiSa DH line with the thickest stem achieving 4.73 mm and thickest SoXi DH line achieving 4.69 mm across seasons. Increasing wall width results in a relatively modest increase in stem strength, but greatly increases the amount of biomass that must be invested in the stem. Therefore a maximum wall width of 0.65 mm was chosen for the bottom two internodes. Wall widths as low as 0.54 mm for internode 1 were observed in both populations, and as low as 0.47 and 0.58 mm for internode 2. Stem wall material strengths ranged from 32.0 to 63.6 MPa for RiSa and 34.1 to 54.4 MPa for SoXi against an ideotype target of 30 MPa.

The ideotype targets for the spread and depth of the root plate were 57 and 150 mm, however, these targets were not achieved in either DH population. Across experiments there was a range in root plate spread of 34.6 to 46.6 mm for RiSa and 37.7 to 49.5 mm for

Table 4 Summary of measurements on the Solstice × Xi19 DH population

	2004–2005			2005–2006		
	Mean	Range	SED	Mean	Range	SED
Grain yield (t/ha)	8.85	7.16–10.79	0.62***	10.93	9.91–11.92	0.49***
Grain moisture (%)	15.7	14.7–18.7	0.44***	15.0	14.6–15.8	0.35*
Specific weight (kg/hl)	78.2	69.0–82.4	1.77***	77.3	73.9–80.1	0.795***
Thousand grain weight (g)	46.8	38.9–56.2	–	47.1	39.8–56.7	–
Plants/m^2	135	82–196	20.0***	197	140–241	10.7***
Ear emergence (June date)	12	8–16	–	5	2–8	–
Lodging (%)	7	0–93	–	0	0–0	–
Height to ear tip (mm)	881	726–1037	34.1***	946	786–1105	24.4***
Height centre gravity (mm)	492	387–571	23.6***	511	413–651	32.4***
Natural frequency (Hz)	1.06	0.75–1.40	0.099***	0.90	0.62–1.16	0.058***
Ear area (cm^2)	13.7	10.3–19.9	0.68***	11.3	9.2–15.3	0.70***
Shoot number per plant	4.45	3.25–5.89	0.489***	2.82	2.12–3.74	0.346***
Root plate spread (mm)	42.9	32.0–57.9	4.26***	41.0	32.3–49.4	3.67***
Root plate depth (mm)	25.2	36.9–19.9	5.01 (ns)	26.6	23.3–31.3	1.88***
Int 1 length (mm)	70	48–95	4.8***	43	34–58	5.3***
Int 2 length (mm)	101	71–149	6.8***	85	69–104	4.2***
Int 1 diameter (mm)	4.41	3.97–5.00	0.191***	3.60	3.17–3.99	0.132***
Int 2 diameter (mm)	4.69	4.07–5.33	0.190***	3.90	3.46–4.29	0.164***
Int 1 wall width (mm)	0.62	0.46–0.76	0.058***	0.52	0.35–0.71	0.068***
Int 2 wall width (mm)	0.63	0.46–0.83	0.065***	0.44	0.25–0.59	0.056***
Int 1 material strength (Mpa)	37	27–51	5.3***	51	34–93	8.3***
Int 2 material strength (Mpa)	26	19–39	4.1***	36	21–59	6.2***
Int 1 failure moment (Nmm)	222	152–336	27.7***	167	94–250	24.1***
Int 2 failure moment (Nmm)	181	110–286	26.4***	128	63–186	20.8***

	2006–2007			Mean 2004–2007			
	Mean	Range	SED	Mean	Range	SED	Year × cv
Grain yield (t/ha)	8.22	5.24–9.21	0.398***	9.35	8.57–10.22	0.352***	***
Grain moisture (%)	14.9	14.1–15.4	0.17**	15.2	14.7–16.1	0.23***	**
Specific weight (kg/hl)	75.3	62.6–80.7	3.91***	77.0	73.1–79.8	1.67***	***
Thousand grain weight (g)				47.0	41.4–52.1	–	–
Plants/m^2	160	128–197	10.9***	164	139–192	12***	***
Ear emergence (June date)	−7	−10 to −4		4	0 to 7	–	–
Lodging (%)	11	0–88	8.9***	9	0–78	–	–
Height to ear tip (mm)	996	857–1,111	38.1***	939	817–1,062	27.5***	***
Height centre gravity (mm)	590	516–680	41.9***	521	451–602	21.4***	***
Natural frequency (Hz)	1.34	0.75–1.90	0.221***	1.10	0.84–1.48	0.091***	***
Ear area (cm^2)	14.6	11.8–18.0	1.22***	14.0	11.7–17.7	0.72***	***
Shoot number per plant	3.46	2.75–4.26	0.408**	3.57	3.06–4.18	0.270***	***
Root plate spread (mm)	42.9	36.5–50.7	3.32*	42.2	37.7–49.5	2.45***	***
Root plate depth (mm)	100.1	87.1–119.8	5.90***	50.6	45.5–57.3	2.86***	***
Int 1 length (mm)	73	56.9–87.8	5.59***	62	51.8–73.4	3.73***	***
Int 2 length (mm)	94	76.6–109.9	7.65***	93	78.1–108.4	4.56***	***

Table 4 continued

	2006–2007			Mean 2004–2007			
	Mean	Range	SED	Mean	Range	SED	Year × cv
Int 1 diameter (mm)	4.13	3.70–4.58	0.20**	4.04	3.75–4.32	0.113***	***
Int 2 diameter (mm)	4.32	3.91–4.74	0.20***	4.29	3.95–4.69	0.124***	**
Int 1 wall width (mm)	0.73	0.59–1.02	0.075***	0.62	0.53–0.79	0.0469***	***
Int 2 wall width (mm)	0.62	0.49–0.77	0.063***	0.57	0.47–0.67	0.0420***	***
Int 1 material strength (Mpa)	38	28.3–49.0	4.81	42	34.1–54.4	4.26***	***
Int 2 material strength (Mpa)	33	24.0–41.7	4.62*	32	24.7–48.9	3.59***	***
Int 1 failure moment (Nmm)	211	147–296	29.2***	200	154–258	21.2***	***
Int 2 failure moment (Nmm)	190	133–275	28.5***	166	110–209	18.2***	***

Int 1 internode 1 (bottom internode), *Int 2* internode 2

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

SoXi. The depth of the root plate ranged from 39.2 to 60.8 mm for RiSa and 45.5 to 57.3 mm for SoXi.

Heritability

Significant GxE interactions observed for all of the lodging-associated traits measured in the DH populations (Table 5) reduced the heritabilities, which were generally greater in RiSa than in SoXi. Traits associated with height to the ear tip (natural frequency, height at centre of gravity, internode length) had the highest heritability. Shoot number per plant and the depth of the root plate had the lowest heritabilities. Of the traits associated with stem strength or anchorage strength, stem diameter had the highest heritability of 0.37 to 0.56, slightly higher than the heritability of grain yield (0.34 to 0.49). Other traits associated with strength (wall width, material strength, failure moment and the spread of the root plate) generally had heritabilities of between 0.3 and 0.4.

Genetic correlations

Correlations with height

Height to the ear tip was noticeably correlated with several traits. Height was very closely correlated with the height to the shoot centre of gravity ($r = 0.9$) in both the RiSa population and the SoXi population (Table 6). Height was also strongly and negatively correlated with shoot natural frequency ($r = -0.53$ in the variety screen and -0.81 to -0.90 within the DH populations). These relationships confirm that height is of overriding importance in determining the shoot height at the centre of gravity and natural frequency. Height was positively correlated with ear area in both RiSa and SoXi ($r = 0.35$ and 0.31. respectively). Height was also strongly correlated with the length of the bottom two internodes. Correlation coefficients of 0.68 to 0.86 were observed within the DH populations. The correlation between height and internode length was not perfect which indicates that height genes may have different sized effects on different internodes.

In the seasons with significant lodging there was a strong positive relationship between height and the percentage of plot lodged. RiSa showed moderate lodging in 2004-5 ($r = 0.61$) and severe lodging in 2006–2007 ($r = 0.75$). SoXi exhibited moderate lodging in 2004–2005 and 2006–2007 when the r values were 0.61 and 0.45, respectively (data not presented). Across all experiments the relationship between height and lodging had a correlation coefficient of 0.78 for RiSa and 0.55 for SoXi (Table 6).

Height and yield were positively correlated in RiSa with r values of 0.51 in 2004–2005, 0.44 in 2005–2006, 0.13 in 2006–2007, and 0.42 across all experiments. The severe lodging in 2006–2007 may have weakened the positive relationship between yield and lodging in that year. In SoXi, there was an inconsistent relationship between height and yield, with r values of 0.24 in 2004–2005, −0.30 in 2005–2006, −0.39 in 2006–2007 and −0.15 across all experiments. Differences in the relationship were not related to the amount of lodging, since even in 2005–2006 when no lodging occurred there was a negative relationship.

Table 5 Coefficients of variation and broad sense heritabilities

	Coefficient of variation[a]		Heritability	
	RiSa	SoXi	RiSa	SoXi
Plants/m^2	6	7	0.151	0.122
Height to ear tip (mm)	2	3	0.950	0.846
Height at centre of gravity (mm)	4	4	0.826	0.683
Natural frequency (Hz)	7	8	0.828	0.531
Ear area (cm^2)	5	5	0.803	0.630
Shoot number per plant	8	8	0.060	0.286
Root plate spread (mm)	9	6	0.344	0.310
Root plate depth (mm)	9	6	0.233	0.172
Internode 1 length (mm)	8	6	0.678	0.602
Internode 2 length (mm)	5	5	0.869	0.694
Internode 1 diameter (mm)	3	3	0.555	0.370
Internode 2 diameter (mm)	4	3	0.532	0.443
Internode 1 wall width (mm)	8	8	0.336	0.297
Internode 2 wall width (mm)	9	7	0.314	0.421
Internode 1 material strength (Mpa)	13	10	0.393	0.208
Internode 2 material strength (Mpa)	16	11	0.321	0.270
Internode 1 failure moment (Nmm)	11	11	0.354	0.384
Internode 2 failure moment (Nmm)	13	11	0.360	0.352
Grain yield (t/ha)	4	4	0.491	0.342
Grain moisture (%)	1	2	0.449	0.256
Specific weight (kg/hl)	1	2	0.761	0.139
Lodging (% area lodged)	–	–	0.622	0.581

[a] Average across experiments

Height was positively related to the material strength of the bottom two internodes. On average, r = 0.31 in the variety screen and r = 0.31 in the DH populations. Height was negatively correlated with wall width, −0.29 in the DH populations. Height was correlated less strongly with stem diameter, with an average correlation coefficient of −0.31 in RiSa, and −0.18 in SoXi. In general height did not correlate with overall stem strength (stem failure moment), although there were weak positive relationships with the strength of internode 1 in RiSa (r = 0.17).

Stem strength traits

The diameter, wall width, material strength and overall strength (stem failure moment) of internode 1 were all strongly correlated with the corresponding measurements made on internode 2 (average r value of 0.78). Mean r values for the bottom two internodes are therefore described in this section. In general, stem diameter, wall width and the overall stem strength (stem failure moment) were weakly and negatively correlated with plants/m^2 and shoots/plant in both DH populations. Previous studies showed that increasing seed rate reduced stem strength, stem diameter and wall width (Berry et al. 2000). It seems likely that the negative relationships with plants/m^2 and shoots/plant were caused by increased competition between shoots for resources.

There was a positive relationship between stem diameter and stem wall width and a negative relationship between stem diameter and material strength in both DH populations. The diameter and wall width of the bottom two internodes were positively related in RiSa and SoXi (average r values = 0.43 and 0.42, respectively). The negative correlations between material strength and diameter were −0.56 in RiSa and −0.48 in SoXi. There was also a negative correlation between material strength and wall width in RiSa (−0.50). The diameter, wall width and material strength were positively correlated with overall stem strength (stem failure moment) in the DH populations. Across all sets of germplasm and each of the bottom 2 internodes the correlation coefficients between stem

Table 6 Mean correlation coefficients for the Rialto × Savannah and Solstice × Xi19 populations across 2004–2007 (bold text denotes significant correlations (P < 0.05)

		1	2	3	4	5	6	7	8	9	10	11
2. Ear emergence date	RiSa	−0.05										
	SoXi	−0.09										
3. Crop height	RiSa	−0.02	−0.35									
	SoXi	0.00	−0.08									
4. Height centre of gravity	RiSa	0.02	−**0.40**	**0.95**								
	SoXi	0.04	−0.16	**0.92**								
5. natural frequency	RiSa	0.01	0.29	−**0.90**	−**0.90**							
	SoXi	0.01	0.09	−**0.81**	−**0.75**							
6. ear area	RiSa	0.11	0.08	0.35	0.36	−0.35						
	SoXi	−**0.42**	0.06	0.31	0.32	−0.29						
7. Shoot number	RiSa	0.09	0.03	−0.01	0.04	−0.04	0.12					
	SoXi	−.006	0.09	0.01	−0.04	0.00	−0.10					
8. Root plate spread	RiSa	−0.20	0.13	−0.11	−0.12	0.13	−0.07	0.08				
	SoXi	−0.05	0.09	−0.09	−0.08	0.00	−0.03	0.02				
9. Root plate depth	RiSa	−0.16	0.23	−0.13	−0.19	0.18	−0.12	−0.05	**0.45**			
	SoXi	0.09	−0.02	0.12	0.12	−0.07	−0.02	−0.15	0.28			
10. Int 1 length	RiSa	0.07	−0.36	**0.84**	**0.87**	−**0.77**	0.19	0.02	−0.08	−0.10		
	SoXi	0.04	−0.17	**0.69**	**0.68**	**0.58**	0.18	0.05	0.11	0.15		
11. Int 2 length	RiSa	0.01	−0.35	**0.86**	**0.86**	−**0.77**	0.14	−0.03	−0.07	−0.05	**0.95**	
	SoXi	−0.01	−0.10	**0.68**	**0.65**	−**0.55**	0.18	0.06	0.13	0.25	**0.92**	
I2. Int 1 diameter	RiSa	−0.00	0.20	−0.33	−0.33	**0.46**	0.00	−0.23	0.07	0.16	−0.25	−0.26
	SoXi	−0.23	0.12	−0.18	−0.17	0.22	**0.39**	−0.28	0.05	0.12	−0.20	−0.10
13. Int 2 diameter	RiSa	−0.09	0.15	−0.28	−0.28	**0.41**	0.02	−0.32	0.05	0.11	−0.22	−0.20
	SoXi	−0.27	0.17	−0.17	−0.17	0.23	**0.40**	−0.32	0.05	0.05	−0.17	−0.09
14. Int 1 wall width	RiSa	−0.17	0.14	−0.23	−0.24	0.23	−0.18	−0.11	0.13	0.18	−0.24	−0.18
	SoXi	−0.15	0.11	−0.28	−0.34	0.25	0.15	−0.20	0.11	−0.03	−0.33	−0.27
15. Int 2 wall width	RiSa	−0.22	0.15	−0.32	−0.33	0.31	−0.11	−0.05	0.20	0.24	−0.35	−0.30
	SoXi	−0.18	0.13	−0.32	−**0.38**	0.29	0.18	−0.23	0.09	−0.05	−**0.37**	−0.33
16. Int 1 material strength	RiSa	0.03	−0.26	**0.50**	**0.50**	−**0.41**	0.06	0.07	0.02	0.05	**0.45**	**0.47**
	SoXi	0.09	0.01	0.27	0.24	−0.18	0.00	0.03	−0.08	−0.11	0.18	0.13
17. Int 2 material strength	RiSa	0.15	−0.16	0.29	0.30	−0.23	−0.07	0.06	−0.10	−0.01	0.27	0.25
	SoXi	0.05	−0.04	0.19	0.17	−0.10	−0.04	0.16	−0.10	−0.06	0.05	0.09
18. Int 1 failure moment	RiSa	0.01	−0.09	0.17	0.17	0.04	−0.04	−0.21	0.15	0.25	0.22	0.24
	SoXi	-0.18	0.07	0.05	0.04	0.06	0.37	−0.28	0.03	−0.02	−0.06	−0.04
19. Int 2 failure moment	RiSa	0.02	−0.04	0.09	0.12	0.07	−0.03	−0.26	0.12	0.26	0.14	0.16
	SoXi	0.19	0.03	−0.02	−0.04	0.09	0.34	−0.27	0.04	0.00	−0.18	−0.14
20. Grain yield	RiSa	0.13	−0.28	**0.42**	**0.48**	−**0.43**	0.10	0.15	−0.29	−**0.45**	0.38	0.34
	SoXi	**0.40**	−0.15	−0.15	−0.11	0.00	−0.18	−0.06	0.17	0.06	0.01	−0.08
21. Moisture	RiSa	−0.07	−0.02	**0.45**	**0.40**	−**0.47**	0.13	0.01	0.03	−0.04	0.35	0.37
	SoXi	−0.25	0.15	0.12	0.01	−0.14	0.26	0.17	0.13	−0.17	0.10	0.12
22. Specific wt	RiSa	0.02	−0.28	**0.54**	**0.46**	−**0.48**	−0.15	−0.04	−0.07	−0.03	**0.43**	0.47
	SoXi	0.10	−0.17	0.04	−0.03	−0.03	−0.04	−0.17	−0.06	0.04	−0.02	−0.01
23. TGW	RiSa	0.10	−**0.41**	0.32	0.34	−0.23	−0.24	−0.16	−0.05	−0.08	0.30	0.31
	SoXi	0.03	−0.22	0.12	0.13	−0.24	−0.02	−0.20	0.02	−0.08	0.20	0.15
24. Natural lodging	RiSa	−0.01	−**0.40**	**0.78**	**0.78**	−**0.76**	0.22	0.13	−0.10	−0.13	**0.75**	**0.76**
	SoXi	−0.14	0.01	**0.52**	**0.45**	−**0.46**	0.10	0.17	−0.25	−0.05	**0.46**	**0.39**

Table 6 continued

		12	13	14	15	16	17	18	19	20	21	22	23
13. Int 2 diameter	RiSa	**0.92**											
	SoXi	**0.89**											
14. Int 1 wall width	RiSa	**0.43**	**0.44**										
	SoXi	**0.39**	**0.40**										
15. Int 2 wall width	RiSa	**0.43**	**0.43**	**0.88**									
	SoXi	**0.41**	**0.44**	**0.84**									
16. Int 1 material strength	RiSa	**-0.58**	**-0.54**	**-0.43**	**-0.49**								
	SoXi	−**0.45**	−**0.37**	−0.06	−0.08								
17. Int 2 material strength	RiSa	−**0.43**	−**0.54**	−**0.47**	−**0.57**	**0.70**							
	SoXi	−**0.42**	−**0.50**	−0.07	−0.11	**0.69**							
18. Int 1 failure moment	RiSa	**0.43**	**0.43**	0.27	0.15	0.34	0.19						
	SoXi	**0.43**	**0.44**	**0.47**	**0.48**	**0.48**	0.24						
19. Int 2 failure moment	RiSa	**0.42**	**0.41**	0.10	0.01	0.23	0.35	**0.80**					
	SoXi	**0.40**	**0.41**	**0.54**	**0.57**	0.35	0.35	**0.85**					
20. Grain yield	RiSa	−0.15	−0.16	−0.18	−0.23	0.18	0.20	0.04	0.00				
	SoXi	−0.22	−0.26	0.03	−0.04	0.11	0.05	−0.07	−0.10				
21. Moisture	RiSa	−**0.40**	−0.35	−0.11	−0.16	0.36	0.19	0.01	0.00	0.20			
	SoXi	−0.09	−0.05	0.18	0.18	0.02	0.04	0.00	0.06	0.02			
22. Specific wt	RiSa	−**0.41**	−0.37	0.03	−0.07	**0.43**0	0.27.	0.13-	0.00	0.33	**0.46**.		
	SoXi	−0.03	0.02	0.11	0.05	0.03	0.01	−0.01	0.03	0.27	0.09		
23. TGW	RiSa	0.09	0.07	−0.09	−0.21	0.24	0.24	0.31	0.28	**0.40**	0.10	0.36	
	SoXi	−0.20	−0.08	0.00	0.06	0.17	0.08	0.05	0.06	0.05	0.06	−0.01	
24. Natural lodging	RiSa	−**0.45**	−**0.42**	−0.27	−0.37	**0.47**	0.33	0.00	−0.02	0.33	0.35	0.33	0.23
	SoXi	−0.20	−0.16	−0.28	−0.25	0.08	−0.06	−0.15	−0.25	−0.27	0.15	−0.19	0.10

strength and its component traits were 0.46 for stem diameter, 0.39 for wall width and 0.40 for material strength.

Stem diameter, wall width and overall stem strength were positively related with ear area in SoXi (mean r value 0.31). For RiSa, a weak relationship was observed in 2006–2007, but not in the other two seasons. Apart from a weak positive relationship between the width of internode 2 with the spread and depth of the root plate in RiSa, neither stem strength, nor its components were related to the spread or depth of the root plate.

Neither grain yield, grain moisture content nor specific weight was related to overall stem strength. Thousand grain weight was positively related to overall stem strength in RiSa, but not in SoXi. There was a weak negative relationship between diameter and yield in SoXi (r = −0.24), but no significant relationship in RiSa. In RiSa, there was a negative relationship between stem diameter and grain moisture and specific weight (r = −0.35 to −0.41).

Anchorage strength traits

The spread and depth of the root plate were positively correlated in RiSa (r = 0.45) and SoXi (r = 0.28). In RiSa grain yield was negatively correlated with the depth of the root plate (r = −0.45) and the spread of the root plate (r = −0.29). No relationship with yield was observed in SoXi. There tended to be weak negative relationships between plants/m^2 and spread and depth of the root plate in RiSa. This was in agreement with seed rate experiments carried out by Berry et al. (2000). No relationship was observed with shoots per plant.

Natural lodging

It must be recognised that the mean scores for natural lodging tended to be a mixture of stem and root lodging. As described above, natural lodging was correlated most closely with height to the ear tip and its closely related characters (height at centre of gravity, natural frequency and internode length). Stem diameter (r = −0.44 and −0.18) and wall width (−0.32 and −0.27) were negatively related with natural lodging in RiSa and SoXi, respectively. Material strength was negatively related with natural lodging in RiSa (r = −0.40), but not in SoXi. The width of the root plate was negatively related to lodging in SoXi (r = −0.25), but no relationship was observed in RiSa.

Grain yield

The traits correlated most closely with grain yield depended strongly on the germplasm. Natural lodging was negatively related with yield in SoXi (r = −0.27). However, it was positively related with lodging in RiSa (r = 0.33). This difference arose because there was a strong positive relationship between yield and height in RiSa, which more than compensated for the positive relationship between height and lodging and the resulting effect on yield. In SoXi there was either no relationship between height and yield or it was too weak to be detected in the presence of the lodging observed in these experiments.

In RiSa it is clear that the relationship between height, yield and lodging was of great importance in understanding how traits affect yield. Understanding whether height also affects the other traits (wall width and root plate spread/depth) will be important for understanding why these traits were negatively correlated with yield.

In SoXi, yield was positively correlated with plants/m^2, indicating that there were insufficient plants to achieve yield potential. This trend was strongest in the first season when the trial was sown late and the fewest plants established. Higher plant populations are known to reduce stem diameter (Berry et al. 2000), possibly explaining why stem diameter was negatively correlated with yield. In 2005–2006, when most plants were established and there was no lodging, yield was negatively correlated with height (r = −0.30), positively correlated with grain moisture (r = 0.21) and positively correlated with stem wall width (r = 0.19).

Genetic maps

The SoXI map comprised 499 loci, arranged in 43 linkage groups and covering 2,059 cM. In comparison the RiSa map comprised 377 loci in 29 linkage groups and covering 2,162 cM. The addition of DArT marker loci extended the SSR maps by 304 and 444 cM for the RiSa and SoXi, respectively. In both cases there were small numbers of unlinked loci, a common occurrence when constructing linkage maps of wheat due to the large genome size. The ordering of the microsatellite loci was consistent with the Komugi (http://www.shigen.nig.ac.jp/wheat/komugi/top/top.jsp) composite genetic map (data not shown). Several "gaps" of greater than 35 cM occurred on both maps, but these corresponded to known regions (Xue et al. 2008) that are presumably areas of high recombination within the wheat genome. Although more markers were mapped in the SoXi population, the genetic map was very fragmented (43 linkage groups as opposed to 29 in RiSa). Solstice and Xi19 share Rialto as a common parent in their pedigrees and this explains why some chromosomal regions were not polymorphic due to identity by descent.

QTL analysis

All QTL described in Table 7 have LOD scores of at least 2.5 (unless otherwise stated) and were detected using mean data across all three years of field trials. The stem trait effects are also averages of internodes 1 and 2. The size of the mean QTL effect described in Table 7 is twice the additive effect, which is defined as the difference between the trait values with and without the QTL. The directions of the trait effects are given in terms of the effect of the Savannah allele or the Xi19 allele. All height QTL coincided with QTL for height at the centre of gravity and natural frequency. A total of 21 QTL in the RiSa population and 12 in SoXi were associated with yield and traits related to lodging (Table 7). Many of the trait QTL were clustered within specific chromosomal regions, e.g. in RiSa a region of the 3A chromosome contained QTL for yield, height, observed natural lodging, stem wall width, stem material strength, flowering date, thousand grain weight and specific weight. This could be indicative of either a large pleiotropic effect or a series of tightly linked genes individually controlling each trait.

The QTL regions that affected the highest number of lodging-associated traits tended to include the large height effects. Notable examples of this are the QTL on chromosomes 3A and 7D of RiSa that were consistent across years. For RiSa, the QTL for increased height coincided with QTL for higher yield

Table 7 Summary of QTL with LOD scores >2.5 using mean data over 3 years

Chromosome (position cM)	DH population	Closest marker to the QTL peak	R^2 variation accounted for	Mean effect	Experiments with LOD >2.5	Other QTL at this location
Yield						
3A (82)	RiSa	*Xcfa2193*	9.95	−0.29 t/ha	2006	−HT, −TGW, −SPWT, −LDG, +FD, −SD, +SWW, −SMS
3B (72)	RiSa	*Xpsp3144*	10.43	−0.30 t/ha	2007†	−SPWT
6A (42)	SoXi	*Xwmc32*	13.9	−0.22 t/ha	2006	+HT, −SWW, −SFM
7A (23)	RiSa	*wPt-5153*	8.14	−0.26 t/ha	2005	+RPD
7D (4)	RiSa	*Xbarc184*	21.50	+0.43 t/ha	2005, 06, 07	+HT, −SWW, −RPS, −RPD, +EA, −FD
Height						
1D (119)	RiSa	*Xgwm642*	7.97	−45 mm	2005, 06†, 07†	−LDG
2A (16)	RiSa	*Xgdm93*	6.67	+42 mm	2005, 06†, 07	
3A (53)	SoXi	*Xbarc45*	32.10	+63 mm	2005, 06	+LDG, −SWW
3A (63)	RiSa	*Xbarc45*	34.10	−94 mm	2005, 06, 07	−YLD, −TGW, −SPWT, −LDG, +FD, −SD, +SWW, −SMS
4A (16)	SoXi	*Xwmc313*	11.01	−36 mm	2005, 06	
6A (25)	SoXi	*Xgwm570*	6.44	+28 mm	2005, 06	−YLD, −SWW, −SFM
6A (55)	RiSa	*wPt-9690*	20.49	+72 mm	2005, 06, 07	+TGW, +SFM
7D (27)	RiSa	*Xbarc184*	10.56	+53 mm	2005, 06, 07	+YLD, −SWW, −RPS, −RPD, +EA, −FD
Ear area						
2D (10)	RiSa	*Xbarc124*	13.06	−0.99 cm^2	2005, 06, 07	−HT
7A (135)	RiSa	*Xgwm332*	14.12	−1.20 cm^2	2005, 06	+RPD
7D (25)	RiSa	*Xbarc184*	14.16	+1.03 cm^2	2005, 06, 07†	+YLD, −SWW, −RPS, −RPD, +HT, −FD
Stem diameter						
3A (68)	RiSa	*Xwmc264*	9.04	−0.11 mm	2007	−HT, −YLD, −TGW, −SPWT, −LDG, +FD, +SWW, −SMS
4D (26)	RiSa	*wPt−0472*	15.21	−0.14 mm	2006	+GM, +FD
4D (5)	SoXi	*Xwmc48*	8.90	−0.07	2006	
Stem wall width						
3A (65)	SoXi	*Xbarc45*	8.44	−0.021 mm	2005, 06†	+HT, +LDG
3A (68)	RiSa	*Xwmc264*	13.90	+0.042 mm	2005	−HT,−YLD, −TGW, −SPWT, −LDG, +FD, −SD, −SMS
6A (12)	SoXi	*Xgwm1005*	9.45	−0.023 mm	2007	−YLD, +HT
6B (73)	SoXi	*Xwmc398*	16.93	+0.030 mm	2006, 07	
7D (23)	RiSa	*Xgwm1007*	7.38	−0.031 mm	2005	+YLD, +HT, −RPS, −RPD, +EA, −FD
Stem material strength						
3A (12)	SoXi	*Xgwm369*	9.51	+1.98 MPa	2005†, 06	+HT, +LDG, −SFM
3A (59)	RiSa	*Xbarc45*	15.12	−3.73 MPa	2005, 07	−HT, −YLD, −TGW, −SPWT, −LDG, +FD, −SD, +SWW
Stem failure moment						
1A (22)	SoXi	*Xcfa2153*	9.30	−11.1 Nmm	2005	+FD
6A (44)	SoXi	*Xwmc32*	8.96	−11.2 Nmm	2005†, 07	−YLD, +HT, −SWW
6A (58)	RiSa	*Xbarc146*	9.35	+13.0 Nmm	2006	+TGW, +HT
Root plate spread						
5B (10)	SoXi	*wPt-1589*	12.29	+1.44 mm	2005	
7D (27)	RiSa	*Xbarc184*	14.6	−1.99 mm	2005, 06, 07	+YLD, +HT, −SWW, −RPD, +EA, −FD
Root plate depth						
7A (21)	RiSa	*Xgwm681*	11.1	+2.71 mm	2005, 07	−YLD

Table 7 continued

Chromosome (position cM)	DH population	Closest marker to the QTL peak	R^2 variation accounted for	Mean effect	Experiments with LOD >2.5	Other QTL at this location
7D (18)	RiSa	*wPt-6263*	16.5	−3.39 mm	2005, 06	+YLD, +HT, −SWW, −RPS, +EA, −FD

Directions of trait effects are in terms of the effect of the Savannah allele or the Xi19 allele

EA ear area, *HT* height, *FD* flowering date, *GM* grain moisture content, *LDG %* area lodged, *PE* plant establishment, *RPD* root plate spread, *RPS* root plate spread, *SD* stem diameter, *SWW* stem wall width, *SMS* stem material strength, *SFM* stem failure moment, *SNO* shoot number per plant, *YLD* yield

† LOD between 2.0 and 2.5

(3A, 7D), higher thousand grain weight (3A, 6A), greater ear area (2D, 7D), smaller and shallower root plates (7D), with thinner stem walls (3A, 7D), wider stem diameters (3A), greater stem material strength (3A), greater failure moment (6A), and earlier flowering (3A, 7D). Consistent effects on 3A and 6A were also found in SoXi, where increased height also resulted in thinner stem walls, but in this population, this region was not associated with higher yield.

There were a small number of QTL for lodging traits unrelated to height. These included a QTL for overall stem failure moment on 1A in SoXi, a QTL for stem diameter on 4D in both RiSa and SoXi, a QTL for stem wall width on 6B, and a QTL for the width of the root plate on 5B. A QTL for a deeper root plate on 7A in RiSa was associated with decreased yield.

Discussion

Over the three site x seasons the DH lines showed a very wide range of average values for the traits associated with lodging and other agronomic traits (Tables 2, 3). These differences were highly significant. There was often a change in ranking between the DH lines for the traits between experiments, but this variation was usually small compared with the genetic differences across seasons. A model of lodging (Berry et al. 2003b) was used to estimate the effect on lodging risk of altering each trait by the range observed between DH lines. Lodging risk was estimated in terms of the wind speed required to cause either stem or root lodging which was termed either the stem or root failure wind speed. This showed that improving a trait by the range observed between breeding lines could increase the failure wind speeds by 4–6 m/s for changes to height, stem diameter, stem material strength, stem failure moment, root plate spread and root plate depth. Smaller changes in stem failure wind speed of 1 to 3 m/s were estimated for changes to stem wall width, ear area and shoot number per plant. Increasing the failure wind speed from 6 m/s to 10 m/s was estimated by Berry et al. (2003a) to reduce the probability of lodging from 0.9 to 0.2. It is clear that the genetic ranges for several of the lodging traits are sufficient to effect significant changes in lodging risk.

This study indicates that extremely large improvements in lodging resistance could be made if the most lodging resistant traits were combined together in a single variety. An investigation into the correlations between traits indicated that this should be possible because relatively few were strongly correlated with each other. Shorter DH lines tended to be lower yielding, which could act as a constraint for improving lodging resistance by further reduction in height. Shorter DH lines also tended to have a weaker material strength and a thicker stem wall width. However, in general, there was no correlation between height and stem failure moment. The material strength of the stem wall was negatively correlated with the diameter and wall width of the stem, which could constrain the ability of breeders to improve stem failure moment. Despite this correlation, the diameter of the stem was positively correlated with stem failure moment indicating that this trait will be a useful selection criterion for stem failure moment. Positive correlations between the diameter and wall width of the stem and between the spread and depth of the root plate will help breeders select for greater stem strength and anchorage strength.

Calculations of failure wind speed from measurements of lodging-associated traits for the DH lines showed that a significant number had stem and root lodging resistance scores that were 3 m/s greater than cv Solstice, which is one of the most lodging resistant varieties grown in the UK. These transgressive segregants usually had strong stem bases and strong anchorage systems, with heights ranging from 70 cm (short) to 80–90 cm (the height of typical varieties). Yields were either similar to Solstice or up to 0.8 t/ha less. These DH lines could be used as parents for crosses to produce new varieties with high lodging resistance. It therefore seems plausible that significant improvements can be made to lodging resistance without losing yield potential or having to select very short varieties. Increasing yield and lodging resistance together may pose a greater challenge.

The project identified QTL associated with height, stem failure moment, thickness and wall width of the stem, spread and depth of the root plate, grain yield, specific weight, thousand grain weight, flowering date and grain moisture content. The QTL for stem thickness, stem wall width and structural rooting depth were on different chromosomes to those identified in previous studies (Keller et al. 1999; Hai et al. 2005; Verma et al. 2005). In the RiSa DH population, three QTL for increased yield or higher thousand grain weight on chromosomes 3A, 6A and 7D were often associated with traits that increased lodging risk, i.e. greater height and a smaller root plate. These genetic associations are likely to make increasing yield and lodging together more difficult. The project also identified several QTL for each of the lodging subtraits that were not related to yield (i.e. independent QTL for height, stem strength traits and anchorage strength traits were identified). Individual QTL for height, stem diameter, stem material strength, stem failure moment, root plate spread and root plate depth were estimated by the model of lodging (Berry et al. 2003a) to generally affect the failure wind speed by between 0.5 and 1.3 m/s. These effects would be sufficient to have a meaningful effect on lodging risk; whereas QTL for stem wall width and ear area would not.

The QTL identified in this study offer the possibility of using genetic markers to select for increased yield, whilst maintaining or increasing lodging resistance. For example, for the RiSa DH population, combining the increased yield and height QTL on chromosomes 3A and 7D is estimated to increase yield by 0.7 t/ha, but would reduce root and stem lodging failure wind speed by 2–4 m/s mainly due to a height increase of 100 mm. Combining the QTL for increased lodging resistance on 1D and 2A (reduced height) with 4D (thicker stems), that do not affect yield directly, is estimated to counteract the increase in lodging risk. The stem and root failure wind speed may be increased by up to 3 m/s without reducing yield by combining a different set of QTL. In the SoXi DH population, specific combinations of QTL can also be made to either increase failure wind speed by up to 3 m/s without increasing yield, or to increase yield by up to 1 t/ha and make a more modest increase in failure wind speed of 1 to 2 m/s.

This study identified six height QTL that are polymorphic within elite UK wheat varieties and are in addition to the ‘standard’ semi-dwarf genes (*Rht-B1b* and *Rht-D1b*) used by the breeders. The QTL on chromosomes 1D, 2A, 3A and 6A mapped to the same regions as those described by Griffiths et al. (2010). The major height QTL found in the present study can increase plant height by 3–9 cm and taken together all the major QTL would result in a height increase of 34 cm. This discovery may help to explain why UK breeders select for tall plants within semi-dwarf backgrounds (Law et al. 1978). However height QTL having no effect on yield could be used to balance those bringing yield and height increases. It will be important for further work to ascertain whether the associated effects of yield and height are caused by linkage or pleiotropy so that breeders know whether these effects can be separated through recombination.

The genetic markers that were identified as linked to QTL for yield and lodging-related traits are not sufficiently close to the gene(s) underlying the QTL to be predictive of their presence in other breeding populations. Further work is necessary to develop robust, diagnostic genetic markers (i.e. the marker and QTL alleles are in linkage disequilibrium) that can then be used by plant breeders to choose the most appropriate parents for crossing, and enable efficient selection of breeding lines with the most desirable combinations of traits. The development of more diagnostic markers will involve analysis of a greater number of mapping populations and fine mapping. This study showed that some individual QTL increased failure wind speed by 0.5–1.3 m/s; therefore, incorporation of 2 or 3 QTL would be sufficient to achieve a substantial improvement in lodging resistance. If the genetic markers are diagnostic then it would be feasible to incorporate 2 or 3 lodging QTL along with breeding for other traits, such as high yield and disease resistance. However, it would be necessary to understand any linkages between lodging QTL and QTL for other agronomic traits; for example, shorter crops may be more susceptible to splash-borne diseases due to closer proximity of leaves to each other. To improve lodging resistance, emphasis should be placed on developing reliable markers for plant height, spread of the root plate, stem diameter, material strength of the stem wall, and stem failure moment.

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