Ideotype for lodging resistant wheat

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Ideotype design for lodging-resistant wheat

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Abstract The plant characteristics required to make wheat lodging-proof for the least investment of biomass are calculated using a validated model of the lodging process and information about the dry matter costs of altering lodging-associated characters. The plant characteristics required to give a crop yielding 8 t ha^{-1} with 500 shoots m^{-2} and 200 plants m^{-2}, a lodging return period of 25 years include a height of 0.7 m, a root plate spread of 57 mm, and for the bottom internode a wall width of 0.65 mm with a diameter/material strength combination ranging from a diameter of 5.86 mm with a material strength of 20 MPa to a diameter of 4.00 mm with a material strength of 50 MPa. It is estimated that this ideotype would require 7.9 t ha^{-1} of stem biomass and would have a harvest index of 0.42. Observations of a wide range of varieties grown using crop management to maximise lodging resistance without reducing yield potential showed that the root plate of the best variety was 7 mm less than the ideotype target, the stem character targets were achieved but not all in one variety, and the height target was achievable with the use of plant growth regulators. Plant breeders must therefore focus on selecting for a wider root plate and combining the appropriate stem strength characteristics.

Keywords Anchorage · Height · Ideotype · Lodging · Stem strength · Wheat

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Introduction

Lodging is defined as the permanent displacement of plant shoots from an upright position. Severe lodging occurs in UK cereal crops, on average, every 3 or 4 years when 15–20% of the wheat (*Triticum aestivum* L.) area lodges (Berry et al. 2004). Lodging can reduce grain yield by up to 50% (Stapper and Fischer 1990) and cause large reductions in bread-making quality. Plant breeders have reduced lodging risk by introducing dwarfing genes to produce shorter varieties. Farmers employ a range of methods to reduce lodging. The most common is the use of plant growth regulators (PGRs) to shorten crops. In the UK, PGRs were applied to 88% of the winter wheat area in 2004 (Garthwaite et al. 2005). Other lodging-avoidance methods that are less

commonly used include reducing seed rate, delaying sowing, reducing and delaying nitrogen, and rolling the soil. Plant breeders and farmers must keep improving lodging resistance to counter the escalating lodging risk arising from continued yield increases. However, the tools that have been successfully used in the past, dwarfing genes and PGRs, may not provide the full solution in the future. Several studies have shown that yield is reduced when plants are shortened too much with dwarfing genes (Flintham et al. 1997; Kertesz et al. 1991; Miralles and Slafer 1995; Allan 1986; Baylan and Singh 1994; Richards 1992a). The reduction in yield appears to be exacerbated by high temperatures or drought stress (Richards 1992b). In these studies, the optimum plant height for yield is 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. Although 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 the crop's height and therefore the ''leverage'' that is imposed by the aerial parts of the plant, then it follows that the strength of the structures that support the plant must be improved to reduce lodging risk. In wheat, lodging can arise from over-turning of the anchorage system (root lodging) or buckling of the stem base (stem lodging). Recent work has shown that strengthening the stem base and anchorage system by relatively small amounts would cause large reductions in the risk of both types of lodging (Berry et al. 2003a). Furthermore, large variation has been observed for anchorage strength and stem strength within winter wheat varieties currently grown in the UK (Berry et al. 2003b). Plant breeders are unlikely to have exploited this variation yet because the high importance of these traits has only recently been identified and due to the difficulty of rapidly assessing them.

The development of a validated model of wheat lodging (Baker et al. 1998; Berry et al. 2003a) has provided the opportunity to quantify the plant structures that would be required for a wheat plant to avoid lodging in all but the most severe weather conditions. This model was developed with winter wheat but should also be applicable for spring wheat. This process has been initiated by Berry et al. (2004) who quantified the wind-induced leverage imposed at the base of the plant by the shortest wheat plant compatible with high yields when subjected to the maximum wind speed likely in arable areas of the UK. The strength of the anchorage system and stem base required to support this maximum leverage was then calculated.

The development of the root and stem characters associated with lodging continues until anthesis (Crook et al. 1994). Lodging characters therefore compete for resources with the development of grains per m^2, for which the critical period of determination is the 30-day period before anthesis (Fischer 1985), and the production of soluble stem reserves that are later relocated to the grain. Therefore, the ideal combination of lodging-associated characters will require the least investment in biomass in order to minimise any conflict with yield potential. A preliminary investigation of the dry matter costs associated with altering various characteristics has been carried out (Berry 2004).

Thus, it is clear that most of the understanding that is required for designing lodging-proof wheat exists, but it has not yet been brought together. This paper quantifies the dimensions of a lodging-proof wheat plant that requires the least investment in biomass. The aim is to set breeding targets after taking into account feasible improvements that can be made through crop management. The implications of breeding for a lodging-proof plant are discussed. The paper is primarily a review of current understanding. The experiments to quantify the biomass costs of altering lodging characters are unpublished and are therefore described in Materials and methods.

Materials and methods

Experiments

The primary field experiment was done in 2003–2004 at ADAS Rosemaund (52.1°N, 2.5°W) on a silt clay loam (Bromyard series). Twenty-eight

winter wheat varieties were grown in a randomised block design with two replicates (Table 1). Twenty one of the varieties are currently, or have recently been, part of the UK Recommended List or National List trials, three were new breeding lines from Advanta Seeds Ltd., and the remainder were bred in other European countries (Table 1). In 2003–2004, at ADAS High Mowthorpe (54.1°N, 0.5°W), cv. Xi19 was grown in a randomised block design replicated three times on a silty loam over chalk (Wold series). Both experiments were on soil types that are typical of wheat growing areas in the UK. The two field experiments are referred to as the ''Rosemaund experiment'' and the ''High Mowthorpe experiment'' throughout. The experiments were sown in October at 200 and 275 seeds m^{-2} at ADAS Rosemaund and High Mowthorpe, respectively. The amounts and timings of nitrogen fertiliser, applied as granules of ammonium nitrate, were calculated using measurements of soil mineral nitrogen in February and recommendations described in Anon (2000). A prophylactic programme of disease, weed, and pest control was used for both experiments.

Measurements

Measurements of the plant characters associated with lodging were made during the first part of grain filling (GS71–GS79) at ADAS Rosemaund and at GS83 at ADAS High Mowthorpe. Ten plants were selected randomly, avoiding the outer three rows of the plot, and excavated with a hand fork to recover roots to a depth of 100 mm. Soil was washed from the roots and the section of the crown roots that was responsible for anchoring the plant was identified by its inherent rigidity and by the tendency for soil particles to adhere to its dense covering of root hairs, or rhizosheath. 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 the ''root plate spread.'' Measurements also included the number of shoots per plant, and the length, diameter, wall width, and breaking strength of the bottom two internodes (internodes 1 and 2) of the main shoot. The methods for these measurements are described by Berry et al. (2000).

The root biomass was determined for a subset of 13 varieties chosen to represent the greatest range of root plate spread and structural rooting depth. All roots were trimmed from the plant at the point where they joined the stem base, rewashed to remove any soil adhering to the rhizosheath, dried until no further weight loss occurred, and their weight expressed as 100% dry matter. The total length and diameter of the roots were then measured using a winRHIZO scanner (Regent Instruments, Inc., Sainte-Foy, Quebec, Canada). The biomass of the bottom internode (internode 1) of the main stem was determined for a second subset of six varieties chosen to represent a wide range of each of the characters associated with stem strength. At ADAS High Mowthorpe, the length, diameter, wall width, breaking strength, and dry weight were measured on all internodes of the main stems.

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

$$\sigma = \frac{F_S h a}{\pi\left(a^4 - (a-t)^4\right)} \quad (1)$$

PCR analyses for the alleles at the *Rht* genes on chromosomes 4B and 4D were carried out according to Ellis et al. (2002) with minor modifications (Table 1).

Statistical analysis

Analysis-of-variance procedures within Genstat 6 (Lane and Payne 1996) for fully randomised block designs were used to test for differences between treatments and calculate their standard errors of differences. Simple linear regression analysis in Genstat 6 was used to assess whether two sets of variables were significantly related.

Designing a lodging-proof ideotype

A validated model of lodging has identified the characters that determine stem and root lodging

Table 1 Variety characteristics

Cultivar	Origin and breeder	Season of introduction into NL[a]	*Rht* alleles determined by PCR[b]	Standing power[c]
Rosemaund study in 2003–2004				
A31–00	UK, Advanta	2000–2001	*Rht-B1a/Rht-D1b*	–
A32–00	UK, Advanta	2000–2001	*Rht-B1a/Rht-D1b*	–
A33–00	UK, Advanta	2000–2001	*Rht-B1a/Rht-D1b*	–
Access	UK, CPBT	1998–1999	*Rht-B1a/Rht-D1b*	8
R1	Germany	–	*Rht-B1a/Rht-D1a*	–
Badger	UK, Advanta	1997–1998	*Rht-B1a/Rht-D1b*	–
Charger	UK, PBI	1992–1993	*Rht-B1a/Rht-D1b*	5
Chatsworth	UK, Cebeco	1998–1999	*Rht-B1a/Rht-D1b*	–
Claire	UK, Nickerson	1995–1996	*Rht-B1a/Rht-D1b*	7
Goodwill	UK, Cebeco	1999–2000	*Rht-B1a/Rht-D1b*	–
Macro	UK, CPBT	1998–1999	*Rht-B1a/Rht-D1b*	–
Malacca	UK, CPBT	1993–1994	*Rht-B1a/Rht-D1b*	7
Napier	UK, PBI	1996–1997	*Rht-B1a/Rht-D1b*	7
Option	UK, PBI	1997–1998	*Rht-B1a/Rht-D1b*	6
Phelbas	UK, CPBT	1998–1999	*Rht-B1a/Rht-D1b*	–
Piko	Secobra	–	*Rht-B1a/Rht-D1a*	–
R2	Czech Republic, Novi Sad	–	*Rht-B1a/Rht-D1a*	–
Rialto	UK, PBI	1990–1991	*Rht-B1a/Rht-D1b*	7
Robigus	UK, CPBT	1999–2000	Rht-B1b/Rht-D1a	7
Savannah	UK, Advanta	1994–1995	*Rht-B1a/Rht-D1b*	7
Scorpion-25	UK, Advanta	1999–2000	*Rht-B1a/Rht-D1b*	–
Solstice	UK, Advanta	1998–1999	*Rht-B1a/Rht-D1b*	8
Spark	UK, Nickerson	1989–1990	*Rht-B1a/Rht-D1a*	7
Trintella	Holland, VDH	–	*Rht-B1a/Rht-D1b*	–
Vector	UK, Advanta	2000–2001	*Rht-B1a/Rht-D1b*	–
Warlock	UK, Advanta	1999–2000	*Rht-B1a/Rht-D1b*	–
Wizard	UK, CPBT	1999–2000	*Rht-B1a/Rht-D1b*	–
Xi19	UK, Advanta	1998–1999	*Rht-B1a/Rht-D1b*	5
Berry et al. (2003a,b)				
Buster	UK, Nickerson	1990–1991	*Rht-B1a/Rht-D1b*	9
Cadenza	UK, CPBT	1989–1990	*Rht-B1a/Rht-D1a*	6
Charger	UK, PBI	1992–1993	*Rht-B1a/Rht-D1b*	5
Consort	UK, PBI	1991–1992	*Rht-B1a/Rht-D1b*	8
Equinox	UK, CPBT	1993–1994	*Rht-B1a/Rht-D1b*	9
Harrier	UK, Advanta	1993–1994	*Rht-B1a/Rht-D1b*	6
Hereward	UK, PBI	1987–1988	*Rht-B1a/Rht-D1b*	8
Hussar	UK, Advanta	1988–1989	*Rht-B1a/Rht-D1b*	6
Madrigal	UK, PBI	1993–1994	*Rht-B1a/Rht-D1b*	8
Mercia	UK, PBI	1982–1983	*Rht-B1a/Rht-D1a*	6
Reaper	UK, Syngenta	1993–1994	*Rht-B1a/Rht-D1b*	6
Rialto	UK, PBI	1990–1991	*Rht-B1a/Rht-D1b*	7
Savannah	UK, Advanta	1994–1995	*Rht-B1a/Rht-D1b*	7
Shamrock	UK, Advanta	1995–1996	*Rht-B1a/Rht-D1b*	8
Spark	UK, Nickerson	1989–1990	*Rht-B1a/Rht-D1a*	7

[a] NL is the UK National List testing system

[b] Semidwarf alleles include *Rht-B1b* (formerly termed *Rht*1), *Rht-D1b* (*Rht*2), wild-type alleles include *Rht-B1a* (*rht*1) and *Rht-D1a* (*rh*t2)

[c] Standing power scores are assigned to UK varieties after several years in the National and Recommended List testing system. Scores are out of 9, with high scores representing high lodging resistance

risk (Baker et al. 1998; Berry et al. 2003a). The steps involved in calculating lodging risk are described in Fig. 1 and the equations used to link the characters are described in Berry et al. (2003a). The risk of stem and root lodging is calculated in terms of the wind speeds required to cause failure of the stem base and the anchorage system. Stem lodging is predicted when the wind-induced leverage of a single shoot exceeds the strength of the stem base. Root lodging is predicted when the wind-induced leverage of all shoots belonging to a single plant exceeds the anchorage strength. The wind-induced leverage of a shoot is calculated from its height at centre of gravity, the rate at which the shoot sways (natural frequency), and the projected area of the ear. In turn, these characters can be calculated from the height to the ear tip, grain yield per unit area, and shoot number per unit area (Berry et al. 2004). The strength of the stem is calculated from the diameter, wall width, and material strength of the stem wall. Root anchorage strength is calculated from the spread and depth of the root plate and the shear strength of the surrounding soil.

The model described above is used as the basis for calculating the dimensions of a lodging-proof wheat crop. The following sections first quantify the characteristics of the shoot required to minimise the wind-induced leverage. The characteristics of the stem and anchorage system required to support this leverage are then calculated. Wherever possible, the combination of characters that require the least biomass is chosen.

Wind-induced leverage

The strength of the stem and anchorage system that are required to support wheat is determined by the maximum wind-induced leverage that is likely to be imposed by the shoot. The wind-induced leverage exerted on the stem base can be calculated from the maximum wind speed, crop height, grain yield per unit area, and shoot number per unit area using methods described by Berry et al. (2004). If we take a lodging return period of 25 years as our target for a lodging-proof state, then the maximum wind speed that must be withstood in cereal growing areas of the UK between mid-June and mid-August (taken as the main period of lodging risk) is 18 m s^{-1} (Berry et al. 2003a). In the first instance, this is calculated for a crop yielding 8 t ha^{-1} as this is the average winter wheat yield achieved on UK farms.

Shoot leverage is minimised by choosing a short crop. Flintham et al. (1997) estimated that UK plant breeders may have difficulty shortening

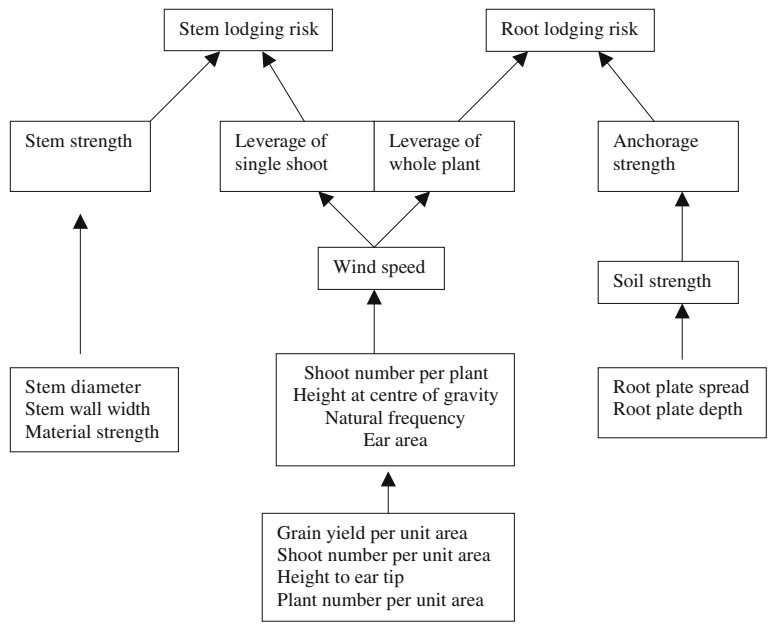

Fig. 1 Plant characters associated with stem and root lodging risk

crops below 0.7 m without reducing yield potential. It is not known whether PGRs could be used to shorten height below 0.7 m without reducing yield. It should also be noted that growth regulator chemicals are not acceptable in organic farming systems and the presence of residues from some growth regulators means they are not suitable for all grain markets. Even if crops can be shortened below 0.7 m without reducing yield through breeding or the use of growth regulators, the impaired ability of short crops to escape foliar disease (Parker et al. 2002) or tolerate weeds (Cosser et al. 1997) is likely to reduce the productivity of a very short ideotype. On balance, it seems sensible to take 0.7 m has the minimum crop height that is compatible with high yields.

Shoot leverage is reduced by increasing the number of shoots m^{-2}, but this also increases the leverage that all the shoots belonging to one plant exert on the anchorage system. The negative effect of increasing shoots m^{-2} could be minimised by establishing more plants, but this would exacerbate the problem by reducing the strength of the anchorage system more than the leverage exerted upon it (Berry et al. 2002). If the minimum plant population at which potential yield can be realised for sowing dates up to mid-October is assumed to be 200 plants m^{-2} (Spink et al. 2005), then the shoot number m^{-2} at which the combined shoot and plant leverage is minimised lies anywhere between 400 and 600 shoots m^{-2}. The maximum wind-induced leverage that would be exerted at the base of the bottom internode (internode 1) by a single shoot of a 0.7 m tall crop with 500 shoots m^{-2} and yielding 8 t ha^{-1} has been estimated at 250 N mm (Berry et al. 2004). If it is assumed that the lodging-proof crop establishes 200 plants m^{-2} then each plant will possess two or three shoots (2.5 shoots on average) and the leverage exerted on the root anchorage system of an individual plant will vary between 500 and 750 N mm (625 N mm on average).

Leverage decreases linearly with height up the stem for relatively rigid cereal stems such as wheat (Berry et al. 2006). The ratio of internode length to the height at the midpoint of the ear for a typical wheat shoot has been measured in the High Mowthorpe experiment at 0.08 for the bottom internode, 0.12 (internode 2), 0.17 (internode 3), 0.24 (internode 4), and 0.39 for the peduncle (Berry 2004). This means that the leverage exerted at the base of internodes 2, 3, 4, and 5 must be 92, 80, 63, and 39%, respectively, of the leverage exerted at the base of internode 1.

If it is assumed that all internodes, apart from the peduncle, have uniform geometric and material properties along their length, then the minimum strength of a particular internode must equate to the leverage exerted at its base. If the properties of the peduncle are assumed to taper in a similar way to its diameter, then its strength requirements can be allowed to decrease in proportion with the reduction in leverage it must support. We will quantify the leverage exerted at the midpoint of the peduncle, which based on typical internode length ratios (Berry 2004) is 20% of the leverage exerted on internode 1.

Stem characteristics

The optimum stem structure must not only provide sufficient strength, but must achieve this for the minimum investment in biomass. Stem strength (B_s) is determined by the radius (a), wall width (t), and the material strength of the stem wall (σ) as described by Eq. (2). Weight (mg) per mm of stem (W) is given by Eq. (3) where α is the density of the stem wall material. Stem weight per N mm of strength (Eq. (3) divided by Eq. (2)) can be used to predict the combination of stem characters that gives the greatest strength with the least stem biomass.

$$B_s = \frac{\sigma \pi a^3}{4}\left(1 - \left(\frac{a-t}{a}\right)^4\right) \quad (2)$$

$$W = \alpha\left[\pi a^2 - \pi(a-t)^2\right] \quad (3)$$

The Rosemaund experiment showed the stem wall density of internode 1 to vary from 0.46–0.60 mg mm^{-3} for different varieties. The High Mowthorpe experiment measured stem wall density at 0.50 mg mm^{-3} for internode 1 and 0.38 mg mm^{-3} for internode 2. These results are similar to previous measurements by Mulder (1954) who showed that the density of the stem walls of the 2nd lowest internode varied from

0.27–0.38 mg mm^{-3} within wheat crops grown with different amounts of nitrogen fertiliser. Results from the Rosemaund experiment showed that the material strength of the stem wall was positively related to the density of the stem wall across six varieties ($P < 0.01$) (Fig. 2). A positive relationship was also observed for variation in these characters across all five internodes of a single variety ($P < 0.001$) (Fig. 2). In this analysis, the bottom internode (internode 1) had the greatest values for material strength and density, which were 67 and 39%, respectively, greater than the corresponding characters of internode 2. These characters became successively smaller for internodes 3 and 4, then rose significantly for internode 5 (the peduncle) ($P < 0.001$; Fig. 2). The similarly uneven pattern of changes along the height of the stem for both material strength and density, together with data from the Rosemaund experiment, provide good evidence that these two characters are positively related. At this stage, there is insufficient data to justify investigating whether the slopes of the two data sets differ. More testing is required to confirm and quantify the relationship. In order to provide an initial estimate for the slope, which will then be used to estimate the effect of increasing material strength on the dry weight of internodes 1–5, it seems sensible to combine the two data sets. This gives a linear regression with a slope of 0.0069 ($P < 0.001$) and an R^2 value of 0.86. Neither stem diameter nor wall width was related to stem wall density across varieties. Across internodes, stem diameter showed a weak negative regression with the density of the stem wall ($P < 0.05$; $R^2 = 0.28$) and wall width was not related to density.

Equations (2) and (3) can be used to show that, after accounting for the positive relationship between material strength and the density of the stem wall, both increasing radius and material strength reduce the stem biomass per unit of strength. In contrast, increasing wall width for any value of radius or material strength increases the biomass per unit of strength. So it is immediately clear that wall width should be minimised. The smallest wall width that has been measured for a single variety over a number of seasons is 0.65 mm (Berry et al. 2003b). Wall width has been shown to be uniform for the first four internodes and to be 0.1 mm thinner for the peduncle (Berry 2004). With these wall widths, the combinations of stem diameter and material strength required to support the leverage exerted upon each internode by a 0.7-m high crop yielding 8 t ha^{-1} can be calculated using Eq. (2) (Fig. 3).

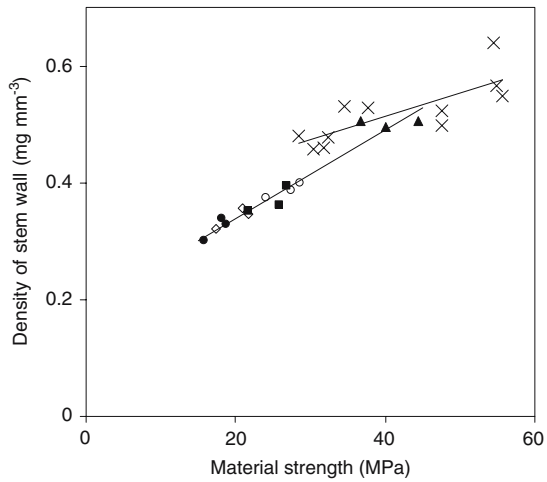

Fig. 2 Material strength of the stem wall plotted against stem wall density for (×) internode 1 of six varieties ($y = 0.0039x + 0.357$; $R^2 = 0.62$; $P < 0.01$); and for internode 1 (▲), internode 2 (■), internode 3 (◇), internode 4 (●), and internode 5 (○) of a single variety cv. Xi19 ($y = 0.0076x + 0.187$; $R^2 = 0.95$; $P < 0.001$)

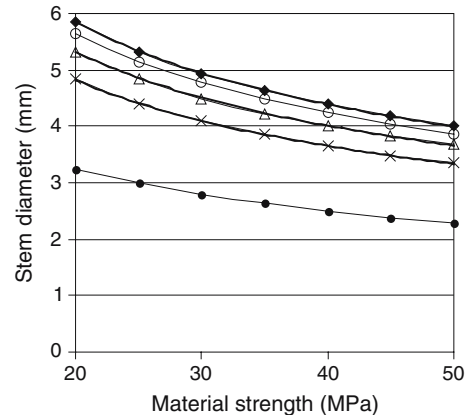

Fig. 3 Combinations of diameter and material strength required for internode 1 (♦), internode 2 (○), internode 3 (△), internode 4 (×), and internode 5 (●) to enable a 0.7-m crop yielding 8 t ha^{-1} to have an average stem lodging frequency of once every 25 years. Internodes 1–4 have a wall width of 0.65 mm and internode 5 has a wall width of 0.55 mm

Equation (3) can then be used to show that for each internode the minimum stem weight per N mm of strength occurs when the material strength is 30 MPa. Using material strength values of 50 or 20 MPa increases the stem weight per N mm by only 3%. It therefore appears that the optimum stem biomass for strength for a thin-walled stem can be achieved for a wide range of stem diameter (D) and material strength (σ) combinations, such that for internode 1, $D = 20.3\sigma^{-0.415}$. This means that the optimum dimensions for internode 1 could range from a diameter of 5.86 mm with a material strength of 20 MPa to a diameter of 4.00 mm with a material strength of 50 MPa.

Anchorage characteristics

The anchorage failure moment (anchorage strength) (B_R) can be calculated from

$$B_R = k_3 s d^3 \quad (4)$$

where k_3 is taken as 0.43 (Baker et al. 1998), s is the soil shear strength, and d the root plate spread. Soil shear strength can be calculated using Eq. (5), in which i is the daily rainfall, l the structural rooting depth, f the soil moisture content at field capacity, w the soil moisture content at permanent wilting point, ρ_s the density of soil, and ρ_w the density of water. Typical values for a silt clay loam include: f at 0.27 g g^{-1}, w at 0.15 g g^{-1}, ρ_s at 1.4 g cm^{-3}, S_D at 51 kPa, and at S_W 6 kPa (Baker et al. 1998):

$$s = s_D - \frac{i}{\frac{\rho_s}{\rho_w}(f - w)l}(s_D - s_w) \quad (5)$$

Anchorage strength increases to the third power in response to increasing the spread of the root plate (Eq. (4)). The model predicts that the structural rooting depth interacts with the daily rainfall to affect soil strength and anchorage strength (Eq. (5)). This is because soil strength is strongly affected by its moisture content, and the moisture content of the soil surrounding the structural roots is calculated from the depth of the structural roots and the daily rainfall. The maximum daily rainfall expected during the lodging risk period once every 25 years is estimated at greater than 25 mm (Baker et al. 1998). A lodging-proof plant must be designed to withstand this and the maximum gust speed of 18 m s^{-1} occurring together. Under this level of rainfall, the depth of the structural roots must be greater than 150 mm to alter anchorage strength. Varietal differences in rooting depth ranged from 32–47 mm (Table 2), so it appears that varying the depth of the root plate is not helpful for avoiding lodging in heavy rainfall.

The target anchorage strength required to give a 0.7-m tall crop yielding 8 t ha^{-1} a lodging return period of 25 years has been estimated at 625 N mm. If the soil is at field capacity and has a strength of 6 kPa, then a root plate spread of 61.5 mm is required to produce an anchorage strength of 625 N mm. Rolling the soil after sowing, but before stem extension, reduces root lodging risk by strengthening the soil surface by approximately 30% (Berry et al. 2002). If rolling can be used to strengthen the soil surface by 30%, then the required root plate spread is reduced to 56.5 mm.

Achieving the lodging-proof ideotype

The plant dimensions required to give a crop yielding 8 t ha^{-1} with 500 shoots m^{-2} and 200 plants m^{-2} a lodging return period of 25 years, for

Table 2 A summary of the ideotype targets and progress towards them

Character	Minimum ideotype target	Best observed value
Root plate spread (mm)	56.5	49.7 (cv. Savannah)
Internode 1 diameter (mm)	4.00–5.86	4.12 (cv. Phelbas)
Internode 1 material strength (MPa)	20–50	54.6 (cv. Alcedo)
Internode 1 wall width (mm)	0.65 (maximum)	0.65 (cv. Charger)
Internode 1 strength (N mm)	250	230 (cv. Wizard)
Height (m)	0.70	0.74 (cv. Access)

the minimum investment in biomass, include a height of 0.7 m, root plate spread of 56.5 mm (assuming the soil is rolled), a stem wall width of 0.65 mm for the bottom four internodes, and 0.55 mm for the midpoint of the top internode, a material strength of 30 kPa for all internodes and a stem diameter of 4.94 mm for internode 1, 4.77 mm for internode 2, 4.50 mm for internode 3, 4.09 mm for internode 4, and 2.79 mm for the midpoint of internode 5 (Table 2). Progress towards the ideotype described in this paper can be made using careful selection of existing germplasm and crop management. Any gap between the best achievable structures and the ideotype must then be closed by further breeding efforts.

Germplasm selection and crop management

Large and statistically significant varietal differences have been observed for all of the lodging-associated characters (Table 3). The ranges described for 15 varieties in Berry et al. (2003b) are a mean of six experiments across three seasons. Larger ranges were observed for the 28 varieties investigated in the Rosemaund experiment, albeit in a single season. Four varieties were common between the two experiments and these showed consistent rankings for the lodging-associated characters in each experiment. The results illustrate the large amount of genetic variation for the lodging-associated characters within elite wheat germplasm. The heritability values estimated from Berry et al. (2003b) range from 0.73–0.98 for the lodging traits which illustrates that selecting varieties based on these traits should result in improved lodging resistance across a range of environments. The variety ranges observed for the spread and depth of the root plate, ear area, and stem diameter are calculated to have the greatest effect on lodging risk.

After choosing the best germplasm, lodging resistance can be increased further by delaying sowing, reducing seed rate, smaller levels of residual nitrogen in the soil, delaying and reducing nitrogen fertiliser, and using PGRs (Easson et al. 1993; Crook and Ennos 1995; Berry et al. 2000). These crop management practices alter lodging risk through the control of several lodging-associated characters (Table 4). The extent to which crop management affects these plant characters is described more fully in Berry et al. (2000). Rolling the soil after sowing reduces root lodging risk by strengthening the soil surface (Berry et al. 2002). However, use of this management practice may not always be practical on certain soil types in wet conditions.

The extent to which crop management can be altered to increase lodging resistance is

Table 3 Genetic range of lodging-related traits

Parameter	Berry et al. (2003a,b)		Rosemaund (2004)	
	Range	SED (152df)	Range	SED (28 df)
Anchorage characters				
Root plate spread (mm)	44.3–49.7	1.67	25.5–42.2	2.86
Root plate depth (mm)	41.4–46.9	1.54	31.7–42.7	2.45
Root length per plant (cm)[a]	NA	NA	55.5–124.9	31.5 (9 df)
Average root thickness (μm)[a]	NA	NA	41.3–80.2	10.29 (9 df)
Stem strength characters				
Diameter (mm)	3.63–3.94	0.056	3.24–4.12	0.144
Wall width (mm)	0.732–0.807	0.0755	0.76–1.11	0.089
Material strength (Mpa)	36.3–42.5	1.61	29.0–54.6	4.62
Stem wall density (mg mm^{-3})[b]	NA	NA	0.459–0.602	0.0242 (4 df)
Leverage characters				
Height at centre of gravity (mm)	473–625	5.1	471–668	11.5
Natural frequency (Hz)	0.77–0.96	0.19	0.66–1.02	0.17
Ear area (cm^2)	10.53–12.53	0.279	9.00–14.20	0.70
Shoot number per plant	2.94–3.46	0.172	2.40–5.50	0.40

[a] Thirteen varieties

[b] Six varieties

Table 4 Summary of the effects of crop management on plant characters associated with lodging (arrow marks in parentheses denote an increase in lodging risk), adapted from Berry et al. (2000)

	Crop parameter	Low soil N	Late sowing	Low seed rate	Low spring N	With PGR
Shoot	Centre of gravity (m)	–	↓	–	↓[a]	↓
Leverage	Natural frequency (Hz)	–	↑	–	–	↑
	Ear area (cm^2)	–	–	–	↓[c]	–
Plant leverage	Shoot number per plant	–	–	(↑)	↓	–
Stem strength	Stem diameter (mm)	↑[a]	↑[b]	↑	↑[b]	–
	Stem wall width (mm)	↑	↑	–	↑[b]	–
	Material strength (MPa)	↑[a]	↑[b]	(↓)	–	–
Anchorage	Root plate spread (mm)	–	↑	↑	–	–
Strength	Structural root depth (mm)	–	–	↑	–	–

[a] Early sown treatments only

[b] High levels of residual N only

[c] Normal levels of residual N only

constrained by the requirement for high yield potential. For example, sowing cannot be delayed much later than mid-October in the UK before yield potential decreases. Reducing plant population probably offers the greatest scope for improving lodging resistance because growers often establish more than the economically optimum number of plants, which often lies between 100 and 200 plants m^{-2} (Spink et al. 2005). Lowering plant population from 400 plants m^{-2} to 200 plants m^{-2} increased stem diameter by 0.4 mm, root plate spread by 7 mm, root plate depth by 4 mm and shoot number by 1.4 shoots per plant, and reduced material strength by 5 MPa (Berry et al. 2000). The negative effects of reducing material strength and increasing shoot number on lodging resistance were significantly outweighed by the positive effects of increasing root plate spread and depth and the stem diameter. However, uncertainty about establishment often means that more seeds must be sown to avoid falling below the optimum plant number. This will restrict the potential for improving lodging resistance by reducing seed rate. Other crop management methods include avoiding early sowing on soils with a high level of residual N, and delaying and reducing fertiliser N where soil N levels allow. The shortest UK varieties are about 0.8 m, so PGRs will play an important role in reducing height towards the 0.7-m target, until shorter varieties that are compatible with high yield are bred.

The variety trials described by Berry et al. (2003b) and in this paper were sown in October, established close to 200 plants m^{-2} and used economically optimum amounts of fertiliser N. The lodging-associated characters measured in these trials therefore represent the best that could be achieved using current varieties without using growth regulators or reducing yield potential. The difference between the most lodging-resistant characters that have been observed in these trials and the ideotype target (Table 2) therefore represents the gap that must be closed by breeding.

Breeding

The ability of breeders to achieve the lodging-proof ideotype could be constrained by genetic linkage between the lodging-associated traits. Many pairs of lodging traits were found to be genetically correlated ($P < 0{\cdot}05$) by Berry et al. (2003b). However, only two correlations were detrimental; a negative correlation between stem diameter and the material strength of the stem wall, and a positive correlation between stem diameter and stem wall width, which accounted for 33 and 20% of the genetic variation, respectively. No correlations were found between the traits for stem strength and anchorage strength. Correlation coefficients from the Rosemaund experiment were also consistent with those found by Berry et al. (2003a,b). It therefore appears that genetic linkages between lodging traits are unlikely to be significant barriers for breeders to achieve a lodging-proof ideotype.

The height target of 0.7 m has almost been achieved by cv. Access (Table 2) and is unlikely

to present any difficulty to breeders. Root plate spread must be increased by a further 7 mm. Significant genetic variation has been observed for the spread of the root plate (Table 3) and it seems feasible that the target root plate spread could be discovered if more diverse germplasm is screened. No genetic linkage was observed between root plate spread and shoot number per plant either by Berry et al. (2003b) or in the Rosemaund experiment that may reduce the effectiveness of wider root plates for reducing lodging risk. In fact, the weak positive correlation with the depth of the root plate will help to further increase lodging resistance.

The target diameter for the bottom internode of 4.00 mm was achieved in one variety in the Rosemaund experiment (Table 2). The challenge now is to combine this with a material strength of approximately 50 MPa. This seems possible given that a variety with a material strength of greater than 50 MPa has been observed (Table 2) and the negative relationship between stem diameter and material strength observed by Berry et al. (2003b) was weak. The weak positive correlation between stem diameter and wall width will also increase the difficulty of combining a wide stem diameter with a thin wall but this should be easily surmountable. Achieving a thin wall will be important for minimising the dry matter costs of strengthening the stem. The very strong positive correlations between corresponding characteristics on internodes 1 and 2 (Berry et al. 2003b) indicate that selecting for traits on the bottom internode will result in similar improvements for the upper internodes, however this must be tested.

The production of a lodging-proof wheat plant appears to be feasible with further breeding efforts. However, many of the lodging-associated traits are very time-consuming to measure and rapid screening methods such as genetic markers must be developed to enable the large genetic variation for the traits to be exploited. Clearly plant breeders cannot improve all of the lodging traits simultaneously. The spread of the root plate and stem diameter have been shown to have the greatest effect on lodging risk, so focussing on these traits first is likely to pay the greatest dividends.

Implications of breeding for lodging resistance

One possible detrimental effect of breeding for lodging resistance is that extra dry matter will be required for the stems and roots. The stem biomass (t ha^{-1}) required by a crop of plants with lodging-proof dimensions can be estimated using the relationship for stem wall density and material strength given in Fig. 3, Eq. (3), the lengths of each internode and assuming 500 shoots m^{-2}. This gives a total stem biomass of 7.93 t ha^{-1} for a 0.7-m tall yielding 8 t ha^{-1}. At harvest, UK wheat crops have been recorded to contain 16.5 t ha^{-1}, of which 7.8 t ha^{-1} was grain, 1.7 t ha^{-1} was chaff, and the remaining 7.1 t ha^{-1} was predominantly straw (Sylvester-Bradley et al. 1998). It therefore seems likely that additional stem biomass will be required.

Results from the Rosemaund experiment show that the significant varietal differences between the spread of the root plate were linearly related to the root biomass per plant to a depth of 10 cm (Fig. 4; $P < 0.001$). After accounting for the plant population density, which ranged between 135 and 225 plants m^{-2}, it can be shown that root biomass in the top 10 cm of soil varied from 0.2–0.6 t ha^{-1}. The root biomass in the top 10 cm of soil has been estimated to make up 20–40% of the total root biomass (Barraclough and Leigh 1984). Therefore observations of 1.01–1.72 t ha^{-1}

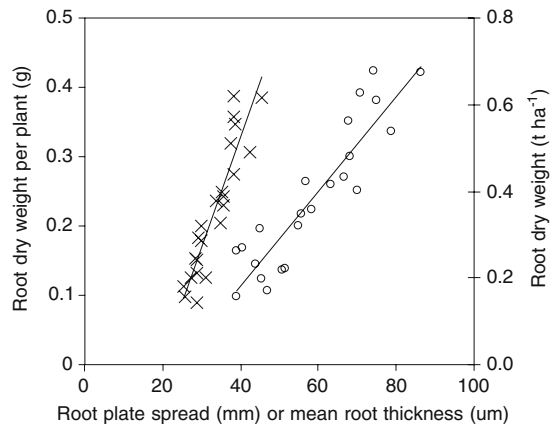

Fig. 4 Root plate spread plotted against root biomass per plant in the top 100 mm of soil (×) 1st *y*-axis: $y = 0.016x - 0.31$; $R^2 = 0.84$. Average root thickness plotted against root biomass per plant (○) 1st *y*-axis: $y = 0.011x - 0.25$; $R^2 = 0.83$

of total root biomass for cv. Hustler (Barraclough and Leigh 1984) may correspond to 0.20–0.69 t ha^{-1} of root biomass in the top 10 cm of soil. The estimates of root biomass made in this study therefore appear to be plausible although it must be emphasised that varietal differences in the distribution of roots with depth, as observed by Ford et al. (2002), could significantly alter the range of estimates of total root biomass indicated by this study. It seems safe to conclude that there is large genetic variation for root biomass in the surface layer of soil. Supporting evidence for this is difficult to find because no other studies can be found that have investigated genetic differences in root biomass of mature wheat.

Interestingly, the variation in root biomass was strongly correlated with the mean root thickness and did not correlate with the total root length in the top 10 cm of soil. This indicates that genetic variation in the surface root biomass is mainly caused by variation in the degree of secondary thickening around the upper parts of the roots rather than the number of primary root axes or root branching.

Each 10 mm increase in root plate spread was associated with an increase in the root biomass in the top 10 cm of soil of 0.28 t ha^{-1}. The root biomass in the top 10 cm can be estimated by extrapolating the relationship between root plate spread and root biomass (Fig. 4). Extrapolating from the maximum measured root plate spread of 46 mm to the ideotype target of 56.5 gives 1.03 t ha^{-1}. This estimate must be used with caution because the relationship between the spread of the root plate and root biomass must be confirmed in other experiments and because of the degree of the extrapolation. Nonetheless, this root mass is 0.4 t ha^{-1} greater than the root mass in the top 10 cm of most well-anchored crops observed in this study. For lodging-proof crops, the total root biomass may need to be as much as 1.3 t ha^{-1} greater than the most well-anchored crop assuming 30% root biomass in the top 10 cm of soil.

The root biomass in the top 10 cm of soil and the stem biomass of a lodging-proof crop (0.7 m, 8 t ha^{-1}) has been estimated at 9 t ha^{-1}. Direct measurements of biomass indicate that current crops have a stem and surface root biomass of 7.6 t ha^{-1} (Sylvester-Bradley et al. 1998; Barraclough and Leigh 1984). Estimates of biomass from measurements of lodging characteristics and relationships presented in this paper indicate that the most lodging-resistant cultivars may have a stem and surface root biomass of 8.2 t ha^{-1}. It therefore seems likely that breeders must develop germplasm with about 0.8–1.4 t ha^{-1} extra biomass in the stem and surface roots to make crops lodging-proof. According to the development of the lodging characters (Crook et al. 1994), it is estimated that more than 70% of this extra biomass would be accumulated before the emergence of the flag leaf. The remainder of the additional biomass requirement is likely to compete with the developing grain florets and production of water-soluble stem reserves. This is likely to reduce yield potential and indicates that some lodging may need to be accepted to ensure that the ideotype has the greatest yield potential. An ideotype with a lodging return period of 1 year in 10 is estimated to require 1.3 t ha^{-1} less stem and root biomass which would make its nongrain biomass requirements similar to existing crops. Further work could investigate the potential reduction in grain yield from partitioning more biomass to support tissues. If this can be quantified then it should be possible to define an optimum lodging risk at which reduction in yield, caused either directly by lodging or indirectly by changes in dry matter partitioning, is minimised.

The methods described above may also be used as the basis for estimating how alterations in grain yield and height may affect the biomass required for a lodging-proof state. Increasing height has been shown to increase the leverage exerted at the base of a shoot by 4.7 N mm cm^{-1} irrespective of crop yield (Berry et al. 2004). The diameter of the bottom internode and the root plate spread must increase by 0.36 and 3.7 mm, respectively, to support each 10 cm increase in height. Based on these dimensions, it can be shown that increasing height from 0.5–1.1 m increases the biomass requirements by 0.23 t cm^{-1} (Fig. 5).

The increase in biomass required to support heavier yields depends upon whether yield improvements arise from increases in shoot number or from increasing ear weight. Historically, both components of yield have been improved (Austin et al. 1989; Shearman et al. 2005). Increasing yield by increasing the size of the ear (i.e., more grains per

ear and larger grains) increases shoot leverage by 28 N mm t^{-1} and increases the leverage exerted on the anchorage system by 70 N mm (Berry et al. 2004). The diameter of the bottom internode and the root plate spread must increase by 0.20 and 1.9 mm, respectively, to support each tonne increase in yield. Increasing yield from 8 to 16 t ha^{-1} by increasing the size of the ear increases the stem and root biomass requirements for a 0.7-m tall crop by 0.43 t of biomass per t of grain yield (Fig. 5). Increasing yield by increasing shoots m^{-2} has no effect on the leverage exerted by individual shoots. It can be shown that the leverage exerted on the anchorage system increases by 78 N mm t^{-1} if it is assumed that shoot number per plant increases in direct proportion to yield. Increasing yield from 8–16 t ha^{-1} in this way would necessitate an increases in the stem and root biomass of 1.16 t of biomass per t of grain yield. This is mainly due to the greater stem biomass required for the extra shoots.

The surface root and stem biomass required for a lodging-proof state increase as yields become heavier. UK wheat yields have increased at a rate of 1 t ha^{-1} per decade (Austin 1999). If future yield improvements of 1 t ha^{-1} per decade were to occur entirely though increasing the size of the ear without any changes in crop height, then stem diameter must be increased by 0.2 mm per decade and root plate spread by 1.9 mm per decade to prevent an increase in lodging risk. These equate to improvements of about 5% per decade. The necessary increase in stem strength may also be effected by increasing stem diameter by 0.1 mm per decade and material strength by 1 MPa per decade (a 3% increase per decade). Yield improvement resulting from greater number of shoots would require a similar rate of improvement in root plate spread, but would not necessitate an increase in the strength of the stem because individual shoot size remains the same. However, the increase in shoot density is likely to cause a reduction in stem strength, which must be countered by breeding for stronger stems. It is important to note that yield improvement brought about via greater shoots requires a much greater investment in biomass to maintain lodging resistance than yield improvement brought about from increases in ear size.

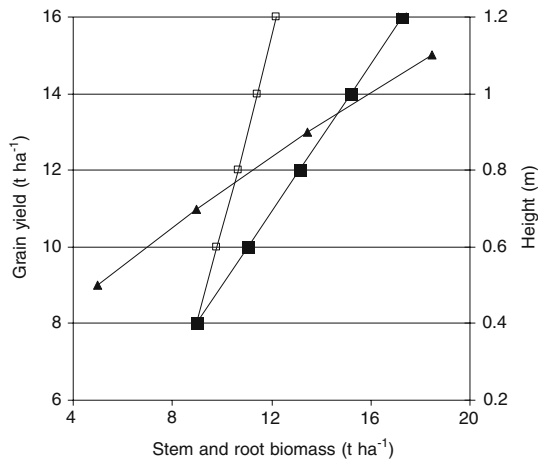

Fig. 5 Stem biomass and root biomass (in top 10 cm of soil) requirements of lodging-proof wheat crops (▲) with different heights each yielding 8 t ha^{-1} and (□) with different yields achieved by altering ear size, each with a height of 0.7 m, and (■) with different yields achieved by altering shoot number, each with a height of 0.7 m

These calculations indicate that the maximum harvest index (grain dry weight/total above ground dry weight) compatible with a lodging-proof state is 0.42 for a crop yielding 8 t ha^{-1} (at 15% moisture), rising to 0.50 for a crop yielding 16 t ha^{-1}. This assumes a ratio of chaff to grain dry weight of 0.2 and yield improvements arise from increasing ear size rather than shoot number. If yield improvements arise from increasing shoots, then the harvest index of a 16 t ha^{-1} crop is about 0.40. These estimates of harvest index are significantly less than the theoretical upper limit for wheat grown in NW Europe of 0.62 that was suggested by Austin et al. (1980). Clearly total biomass must be increased for both yield and lodging resistance to be improved. For example, to maintain a lodging-proof state the total crop dry weight must increase by at least 1.28 t ha^{-1} for each tonne increase in fresh grain (15% moisture). Evidence that UK plant breeders have begun to increase total biomass has been reported by Shearman et al. (2005). This indicates that increasing both yield and lodging resistance is feasible.

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