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Identification of genetic markers for lodging resistance in wheat

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Abstract

Wheat breeders have traditionally increased lodging resistance by shortening crop height; however the scope for further reducing crop height appears to be limited because more extreme dwarfing genes have been shown to be incompatible with high yields. Lodging either occurs through buckling of the stem base (stem lodging) or through overturning of the root anchorage system (root lodging). Lodging resistance could therefore be increased by strengthening the stem base and anchorage system. However these traits are not currently assessed by breeders because they are too time consuming to measure. This project therefore aimed to provide UK breeders with new molecular tools to help them breed new wheat varieties with greater lodging resistance by increasing stem and anchorage strength.

Two breeding populations from Nickerson-Advanta were analysed across three seasons. There was significant genetic variation within plant breeder's germplasm for the traits which determine stem strength and anchorage strength, and for height. Genetic markers were found for several of the key traits that, with further development and validation, could be used to facilitate trait selection. Some of the genetic markers for increasing lodging resistance were associated with lower yields. It was shown that by selecting the correct combination of genetic markers it would be possible to increase lodging resistance by the equivalent of three varietal lodging resistance scores (standing powers) without reducing yield. A different combination of genetic markers would increase yield without increasing lodging risk.

The project identified several height genes within UK elite wheat varieties in addition to the 'standard' semi-dwarf genes. If reliable genetic markers can be identified for these height genes then plant breeders could select the most appropriate parents for crossing in order to produce new varieties of optimal height. The project also discovered that some height genes are more responsive to plant growth regulators (PGRs) than others which should pave the way for predicting varietal responses to PGRs and so allowing them to be targeted more accurately.

One of the genetic markers which identified a major yield gene was shown to increase both grain and straw yields by about 0.5 t/ha each, and did not affect rooting at depth. This discovery indicates that breeders can improve yield and stem strength simultaneously. Straw is also an increasingly valuable co-product for biomass and potentially for liquid biofuel production.

Project Summary

Introduction

The process by which the shoots of small grain cereals are displaced from their vertical stance is known as lodging. This can reduce yield by up to 80% and causes several knock-on effects including reduced grain quality, greater drying costs and slower harvest. Great strides were made during the 1950's and 60's to reduce lodging risk by the introduction of semi-dwarf varieties. The yield of these varieties was greater than the traditional varieties for two reasons; 1) reduced stem growth rates allowed more resources to be partitioned to the developing grain and 2) they could respond to greater amounts of fertilisers because they were less susceptible to lodging. The continued improvement in lodging resistance has been made with the use of plant growth regulators (PGRs) which are used on about 90% of UK winter wheat.

Dwarfing genes and PGRs have been very effective tools for reducing lodging risk and maintaining steady improvements in yield, but they have not eradicated lodging. There is evidence that plant breeders and farmers will not be able to rely on these tools for further reductions in lodging in order to counter the increased risk resulting from higher yields. For example, scope for continuing to reduce lodging risk by further shortening crops will be limited because the more extreme dwarfing genes appear to be incompatible with high yields. It has been observed that the minimum height for high yields in both UK and German wheats is between 0.7 and 1.0 m. This minimum height has already been achieved in some varieties. As a result of this, improving lodging resistance is a very high priority for all plant breeding programmes in the UK and it is clear that alternative methods of preventing lodging other than shortening crops must be found in order to maintain improvements in yield potential.

Lodging either occurs through buckling of the stem base (stem lodging) or through overturning of the root anchorage system (root lodging). Lodging risk could, therefore be reduced by strengthening the stem base and anchorage system. Recent work described in HGCA Project Report No 305 demonstrated that there is considerable genetic variation for the strength of the stem base and anchorage system between modern wheat varieties which could be exploited by plant breeders. Stem and anchorage strength are not currently assessed in breeding programmes, partly

because their importance in lodging has only recently become apparent, but also because they are very time consuming traits to measure accurately. As a result there has been no significant improvement in stem and anchorage strengths in current varieties (HGCA Project Report No 305). The identification of genetic markers associated with these biophysical properties would therefore help plant breeders to select for lodging resistance. The overall strength of the stem base is determined by the stem diameter, stem wall width and the material strength of the stem wall. The strength of the anchorage system is determined by the depth and spread of the root plate. It is important to find genetic markers for each of these sub-traits because they may be under independent genetic control.

In addition to the areas of work outlined above which form the main objectives of the original proposal the project also tested the hypothesis that differences in canopy size at GS31 between breeding lines are associated with stem strength measured at, or after, flowering. If this hypothesis could be proven then measurements of canopy size in spring could be used by plant breeders as a method for rapidly screening for stem strength.

Project extension – associated effects of a genetic marker for yield

Work carried out within the project during 2004-5 and 2005-6 identified a genetic marker that was linked with increasing grain yield, ear size and height, and with decreasing the spread of the root plate and the wall width of the lower internodes. It is possible that this 'yield gene' causes the reduction in root plate spread and wall width directly by partitioning less biomass to these tissues in preference to the upper shoot and ear. If this is true then this could severely constrain plant breeders' attempts to increase yield and lodging resistance simultaneously. Therefore understanding the associated effects of this yield gene on the partitioning of biomass between the grain and non-grain components is of great importance. Furthermore the reduction in the spread of the root plate may indicate that this yield gene is also associated with a reduction in rooting at depth and therefore drought tolerance.

HGCA funded an extension to the project to test the hypothesis that the high yield gene reduces the amount of biomass partitioned to the stem base and roots and this in turn reduces the spread of the root plate, rooting at depth and the width of the

stem wall. If this hypothesis is proven, then this will indicate that yield and the other traits are influenced by the same gene via changes in biomass partitioning.

Aim and objectives

Project aim

Enable Nickerson-Advanta, and other UK breeders in the longer term, to produce new wheat varieties with stronger stems and anchorage in order to make them more resistant against lodging.

Specific objectives

SO1 - Identify two breeding populations with a range of stem and anchorage strength.

SO2 - Measure stem and anchorage strength and their underlying sub traits in the two breeding populations, as well as other important agronomic traits.

SO3 – Construct genetic maps for the two breeding populations.

SO4 - Identify genetic markers for stem and anchorage strength.

SO5 - Compare the genetic markers across years, locations and populations and determine whether there are any correlations with other agronomic traits.

SO6 - Test whether differences in canopy size at GS31 between varieties are associated with differences in stem strength measured at flowering or after.

Extension objectives

SO1 Understand the mechanism by which a yield gene increases yield.

SO2 Investigate whether the yield gene can be separated from effects on lodging traits.

SO3 Investigate whether the yield gene affects rooting at depth.

Materials and Methods

Field experiments

Experiment 1 – Variety screen 2003-4

The objective of this experiment was to assess the genetic variation of existing elite winter wheat varieties for the traits affecting stem strength and anchorage strength. This information was required to help choose contrasting sets of varieties that when crossed would be likely to give rise to breeding populations that segregated for the traits in question. The field trial was carried out in 2003-04 at ADAS Rosemaund (silt clay loam). Twenty nine winter wheat varieties were arranged in a randomized block design with two replicates (plot size of 12m x 2m).

Experiment 2 – Mapping population 2004-7

Two breeding populations (doubled haploid mapping populations) from crosses between elite winter wheat varieties that contrasted for stem and anchorage strength were investigated. The Rialto x Savannah (RiSa) cross included 126 DH breeding lines and the Solstice x Xi19 (SoXi) cross included 120 DH breeding lines. The DH breeding lines were arranged in a resolvable incomplete block design known as an Alpha Design. Each treatment was replicated twice in plots measuring 12m x 2m. A 6m length of each plot was treated with a plant growth regulator (PGR) programme. Each breeding population was grown in three seasons and the sites alternated between ADAS Boxworth (clay) and ADAS Rosemaund (silt clay loam).

Measurements

In all experiments grain yield was determined using a small plot combine, specific weight and grain moisture were measured using a Dickey John, and the percentage of each plot that was stem and root lodged was recorded. Plant number was measured between GS11 and GS13. The date when 50% of the ears had fully emerged was recorded. The plant characters associated with lodging were measured between GS69 (end of flowering) and GS85 (soft dough stage). Plants were always selected from the non-PGR half of each plot, except at Boxworth in 2007 when severe lodging in the plot halves without PGR meant that the plants had to be taken from the PGR treated halves. The lodging associated plant characters that were measured included; bottom two internodes - overall strength, diameter, wall width and material strength; the root system - spread and depth of the root plate; the main shoot - overall height, height

to centre of gravity, natural frequency (rate of shoot oscillation) and ear area. The number of shoots per plant was also recorded. Additional measurements were recorded on a subset of lines including the light intercepted by the canopy at GS31, leaf erectness and shoot number at GS31, the number of crown roots per plant, the root biomass in the top 10 cm, root length, root thickness and the dry weight of each internode. Root length and root thickness were measured using a winRHIZO scanner (Regent instruments, inc.).

To carry out the project extension, 10 breeding lines were chosen from the Rialto x Savannah breeding population with the genetic marker for increased yield and 10 breeding lines were chosen without this genetic marker. Care was taken to ensure that the two subsets of lines did not differ systematically for any other genetic markers. The following measurements were recorded on this subset of lines in 2007 at ADAS Boxworth; the dry weights of the grain, straw and chaff, and the root length and thickness at soil depths of 40-60 cm, 60-80 cm and 80-100 cm.

Calculations and statistics

A previously validated model of lodging was used to calculate the lodging risk of each breeding line from measurements of the characteristics associated with lodging.

Lodging risk was calculated in terms of the minimum wind speed required to cause lodging, which was termed the failure wind speed. The data was adjusted to account for any developmental changes that occurred during the sampling period. REML was 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.

Genetic map production and genetic marker analysis

Genetic marker maps were produced using microsatellite and DArT genetic markers on the two DH breeding populations. The extent to which variation in each trait was associated with each genetic marker was then assessed using analysis of variance and composite interval mapping with QTL Cartographer version 2.5.

Results

Genetic variation in lodging risk

Over three seasons the breeding lines had a very wide range of average values for the traits associated with lodging and other agronomic traits (Table 1). These differences were highly statistically significant. Between seasons there was often a change in rankings between the breeding lines for the traits, but this variation was usually small compared with the genetic differences across seasons. A model of lodging was used to estimate the effect on lodging risk of altering each trait by the range observed between breeding lines. Lodging risk was estimated in terms of equivalent changes to the varietal lodging resistance score (Standing Power) described in the HGCA Recommended List. This showed that improving a trait by the range observed between breeding lines could increase the lodging resistance score by several points, which is very significant given that the current scale runs from 1 (very lodging susceptible) to 9 (lodging resistant). Plant breeders should focus on manipulating plant height, the spread and depth of the root plate, stem diameter, the material strength of the stem wall and overall stem strength to effect the greatest increases in lodging resistance.

It is clear from Table 1 that extremely large improvements in lodging resistance could be made if the most lodging resistant traits that have been observed could be combined together in one variety. An investigation into the correlations between traits indicated that this should be possible because relatively few of the traits were strongly correlated with each other. Shorter breeding lines tended to be lower yielding which could act as a constraint for improving lodging resistance by further shortening crops. Shorter breeding 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 overall stem strength. The material strength of the stem wall was negatively correlated with the diameter and wall width of the stem, which could constrain the breeder's ability to improve overall stem strength. Despite this correlation the diameter of the stem was positively correlated with overall stem strength which indicates that this trait will be a useful selection criterion for overall stem strength. 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.

Table 1. Trait values for breeding lines averaged across 3 seasons and the estimated effect of changing each trait by the range observed between breeding lines on the lodging resistance score.

| Trait | Rialto x Savannah breeding population | | Solstice x Xi19 breeding population | |
|---|---------------------------------------|---|-------------------------------------|---|
| | Range between breeding lines | Effect of range on Lodging resistance score | Range between breeding lines | Effect of range on Lodging resistance score |
| [†] bottom internode | | | | |
| Height to ear tip (mm) | 695 - 1080 | -4.3 | 817 - 1062 | -2.7 |
| Height at centre of gravity (mm) | 359 - 571 | -2.3 | 451 - 602 | -1.5 |
| Natural frequency (Hz) | 0.71 - 1.50 | +2.9 | 0.84 - 1.48 | +2.0 |
| Ear length (mm) | 11.0 - 16.8 | -2.5 | 11.7 - 17.7 | -2.4 |
| Shoot number per plant | 3.08 - 3.97 | -1.8 | 3.06 - 4.18 | -2.0 |
| Root plate spread (mm) | 34.6 - 46.6 | +5.3 | 37.7 - 49.5 | +4.4 |
| Root plate depth (mm) | 39.2 - 60.8 | +6.9 | 45.5 - 57.3 | +3.2 |
| [†] Stem diameter (mm) | 3.50 - 4.45 | +5.4 | 3.75 - 4.32 | +2.5 |
| [†] Stem wall width (mm) | 0.54 - 0.83 | +1.4 | 0.53 - 0.79 | +1.3 |
| [†] Stem material strength (Mpa) | 32.0 - 63.6 | +5.1 | 34.1 - 54.4 | +3.4 |
| [†] Overall stem strength (Nmm) | 140 - 259 | +4.6 | 154 - 258 | +4.0 |
| Stem failure wind speed (m/s) | 10.3 - 20.0 | +9.7 | 11.0 - 17.1 | +6.1 |
| Root failure wind speed (m/s) | 5.2 - 10.7 | +11.0 | 5.6 - 9.7 | +8.2 |
| Grain yield (t/ha) | 7.68-10.05 | - | 8.57- 10.22 | - |
| Specific weight (kg/hl) | 74.3 - 80.7 | - | 73.1 - 79.8 | - |
| Thousand grain weight (g) | 40.0 - 57.2 | - | 41.4 - 52.1 | - |
| Natural Lodging (%) | 0 - 75 | - | 0 - 78 | - |
| Plants/m ² | 142 - 196 | - | 139 - 192 | - |
| Ear emergence (June date) | -1 to 7 | - | 0 to 7 | - |

NB the range in some traits is estimated to affect the Lodging Resistance Score by more than the entire current 1 to 9 scale.

The Lodging resistance scores described in the HGCA Recommended Lists are estimated from field observations of a mixture of stem and root lodging and are expressed on a 1 (very susceptible) to 9 (resistant) scale. In practice varieties with a standing power of 3 or less are usually too susceptible to lodging to be grown commercially. Xi19 represents one of the most lodging susceptible varieties that are currently grown with a lodging resistance score of 5 (adjusted to 4 in the 2008-9 recommended List) and Solstice represents one of the most lodging resistant varieties with a lodging resistant score of 8. These two varieties were grown in all of the field experiments within this project and they act as useful benchmarks against which to compare the lodging resistance of the breeding lines. Calculations of lodging resistance score from measurements of the lodging-associated traits using a model of lodging showed that a significant number of breeding lines had stem and root lodging resistance scores that were 3 or more points greater than Solstice. The highly lodging resistant lines usually had strong stem bases and strong anchorage systems. The height of the lodging resistant lines ranged from short (70 cm) to the height of typical

varieties (80-90 cm). Yields were either similar to Solstice or up to 0.8 t/ha less. It therefore seems plausible that significant improvements can be made to lodging resistance without losing yield potential or having to select for very short varieties. Increasing yield and lodging resistance together may pose a greater challenge.

The project quantified the dimensions that a wheat plant would require to avoid lodging in all but the most extreme wind and rain conditions that would occur once every 25 years. The 'Lodging-proof ideotype' was published in the plant breeding journal *Euphytica* (Berry, P.M., Sylvester-Bradley, R. and Berry, S. (2007). Ideotype design for lodging-proof wheat. *Euphytica* **154**, 165-179). The analysis of the lodging associated traits in the breeding populations indicated that it would be possible to achieve the lodging-proof ideotype for stem lodging, but not for root lodging. Breeding lines with a wider root plate must be found to achieve the lodging-proof ideotype for root lodging.

Breeding lines with large canopies at GS31 tended to have weak stems during grain filling. This correlation was weak, but was consistent with strong correlations between early canopy size and stem strength that have been observed for single variety trials with a range of sowing dates and seed rates. Breeding lines with large canopies at GS31 also tended to have a greater final height. Breeding lines with erect leaves at GS31 tended to have a weaker bottom internode and a wider root plate during grain filling and a greater grain yield. In general the correlations between spring-time assessments and traits measured during grain filling were weak, but they were consistent across two seasons and both breeding populations. Spring-time assessments of canopy size and leaf posture may therefore provide crude indications of some lodging –associated traits such as overall stem strength, height and the width of the root plate.

Genetic markers

Genetic maps were constructed for the two breeding populations. Each genetic map contained more than 400 genetic markers which was a sufficient density for accurately associating traits with particular chromosomal regions. The project identified genetic markers that were associated with the overall strength, thickness and wall width of the stem, the spread and depth of the root plate, crop height, grain yield and specific weight. The genetic markers for heavier yield were often associated with traits which increased lodging risk, such as a greater height or a smaller root plate. This discovery

may help to explain why plant breeders have found it difficult to increase yield and lodging resistance together. The also project showed that several of the genetic markers for lodging resistance were not related to yield, e.g. some of the genetic markers for height. This discovery offers the prospect for combining genetic markers for increased yield with other genetic markers for increased lodging resistance to increase yield by 0.7 t/ha without increasing lodging risk. A different combination of genetic markers could be used to increase the varietal lodging resistance score by 3 points without affecting yield. This is equivalent to changing the lodging resistance of a variety from low to high.

The project identified several height genes that exist within UK elite wheat varieties which are in addition to the 'standard' semi-dwarf genes (*Rht1* and *Rht2*). These height genes had individual effects on height of 4 cm to 7 cm and all genes for increased height together increased height by 26 cm. Importantly, it was found that some of the genes that increased height were associated with greater yield and some were not. This means that the height genes could be mixed and matched to help increase yield without increasing lodging risk as described above. It was also shown that some genes for increased height were much more responsive to shortening by plant growth regulators (PGRs) than others. Breeding lines with the 'PGR responsive' height genes underwent an average height reduction of 122 mm in response to a PGR programme, whereas breeding lines without the 'PGR responsive' genes underwent a height reduction of only 60 mm. Reducing height by 60 mm and 122 mm is equivalent to increasing the lodging resistance score by 1-1.5 and 2-3 points respectively. This discovery may explain why some varieties appear to be more responsive to PGRs than others. If the different height genes can be identified in current varieties then this offers the prospect of targeting PGRs at specific varieties depending on which height genes they possess.

Project extension

The main aim of the project extension was to better understand the physiological mechanism by which a yield gene discovered during the first two years of the project increased yield. Ten breeding lines were chosen with and without the yield gene and detailed measurements were made on these. Measurements in 2007 showed that the subset of 20 breeding lines was generally representative of the whole population. The subset of lines with the yield gene yielded 0.68 t/ha more, were 3 cm taller, had larger ears, and a narrower and shallower root plate.

The overall above ground biomass of the breeding lines with the yield gene was 1.16 t/ha greater than the breeding lines without the yield gene (Table 2). The stem biomass of the high yielding breeding lines was 5.55 t/ha compared with 5.04 t/ha for the low yielding breeding lines. There was little difference in chaff weight and the harvest index (ratio of grain biomass to total biomass) between the breeding lines with and without the yield gene (Table 2). These results are significant because they illustrate that plant breeders can increase both grain yield and straw yield, and a gene that controls this has been identified.

The root length density declined from an average of 0.607 cm/cm³ between 40 and 60cm soil depth to 0.533 cm/cm³ between 80 cm and 100 cm soil depth. No consistent differences were observed between the high and low yielding breeding lines for the root length density at the 40-60 cm, 60-80 cm and 80-100 cm soil horizons. Between 40 and 100 cm soil depth the high yielding lines had a root length density of 0.561 cm/cm³ compared with 0.545 cm/cm³ for the low yielding lines and this difference was not statistically significant (Table 2). Analyses were also carried out for the length of root with a thickness greater than, or less than, 1 mm which also showed no differences between the high and low yielding breeding lines. Between 40 and 100 cm soil depth the roots of the high yielding breeding lines were slightly thicker than the low yielding breeding lines with an average thickness of 0.348 mm compared with 0.337 mm (Figure 2), but again this difference was not statistically significant.

Table 2. Average traits values for subset of breeding lines with and without the yield gene

| Trait | Breeding lines WITHOUT yield gene | Breeding lines WITH yield gene | SED (37 df) |
|---|-----------------------------------|--------------------------------|-------------|
| | | | |
| Total biomass (t/ha) | 12.12 | 13.28 | 0.510 * |
| Straw biomass (t/ha) | 5.04 | 5.55 | 0.364 |
| Chaff biomass (t/ha) | 1.08 | 1.15 | 0.069 |
| Harvest index | 0.500 | 0.500 | 0.013 |
| Chaff: ear index | 0.146 | 0.140 | 0.005 |
| Root length density (cm/cm ³) | 0.545 | 0.561 | 0.0548 |
| Root thickness (mm) | 0.337 | 0.348 | 0.0231 |

Root traits measured between 40 and 100cm soil depth

*P<0.05, ** P<0.01

Implications for the farming industry

This project has demonstrated that very large genetic variation exists within plant breeder's germplasm for the traits which determine stem strength and anchorage strength, and for height. Genetic markers were found for several of the key traits that, with further development and validation, could be used to facilitate trait selection. Some of the genetic markers for increasing lodging resistance were associated with lower yields. It was shown that it would be possible to increase lodging resistance by the equivalent of three varietal lodging resistance scores (standing powers) without reducing yield by selecting the correct combination of genetic markers. Trait combinations were also identified for increasing yield without increasing lodging risk.

Several breeding lines were identified which had a very high lodging resistance of up to 3 variety lodging resistance scores greater than the most resistant varieties currently grown. These could be used as parents for crosses to produce new varieties with high lodging resistance.

Genetic markers for increased yield were also identified. One of these 'yield genes' was shown to increase both grain yield and straw biomass. This is a significant finding because until the late 1980s breeders increased grain yield without altering total biomass by increasing the proportion of total biomass partitioned to the grain at the expense of straw. There is evidence that after the late 1980s breeders began to increase the total amount of biomass. This was an important breakthrough because at the time it was believed that varieties were approaching the theoretical maximum for the proportion of total biomass that could be allocated to grain without weakening the supporting stem. The discovery of a gene that controls the increase in total biomass, together with an understanding of how it works, will help to achieve further increases in yield potential. Improvements in total biomass may also mean that stem strength and yield can be improved together. Straw is also an increasingly valuable bi-product as a feedstuff for bioenergy systems.

The project identified several height genes within UK elite wheat varieties in addition to the 'standard' semi-dwarf genes (*Rht1* and *Rht2*). If reliable genetic markers can be identified for these height genes then plant breeders could select the most appropriate parents for crossing in order to produce new varieties with an optimum height. The

discovery that some height genes are more responsive to PGRs than others should pave the way for predicting which varieties will respond most to different types of PGR and allow PGRs to be targeted more accurately.

Further work

Develop reliable genetic markers for the height genes which work in different varieties and environments. These genetic markers can then be used by plant breeders to choose the most appropriate parents for crossing, efficient selection of breeding lines with the most desirable combinations of height genes (e.g those which are associated with high yield), and for identifying which varieties respond most to PGRs allowing a more targeted use of these chemicals.

Further investigate the physiological mechanisms by which the 'yield genes' identified within this project increase yield and investigate any associated effects on other traits. This understanding would be needed to select the most appropriate crop management for maximising the yield improvements. For example if the yield improvements were shown to be caused by a longer grain filling period then greater emphasis must be placed on protecting the green canopy for as long as possible. This understanding may also be used to help identify other yield genes.

The genetic markers which affected height and stem strength/anchorage strength traits should be further investigated to understand whether the same gene affects all traits or whether the traits are controlled by different genes which are located very close together on the same chromosome. These genetic markers should be further investigated in other breeding populations to test how reliable they are.