

A BREEDING SOLUTION TO IMPROVING SEEDLING ESTABLISHMENT OF WHEAT

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Abstract

Semidwarf wheats have the potential to produce high yields when sown and managed under optimal conditions. However, farm yields often fall below this potential because of poor seedling establishment and low vigour associated with gibberellic acid (GA)-insensitive height-reducing (*Rht*) genes contained in these wheats. Wheats containing *Rht* genes sensitive to GA were intercrossed to develop lines for plant height and coleoptile length assessment. Variation in coleoptile length was poorly related to differences in plant height suggesting these traits were largely under independent genetic control. Furthermore, lines identified as short as current semidwarf varieties produced coleoptiles 10 to 100% greater in length. High heritabilities for coleoptile length and plant height ($h^2 = 0.63-0.89$) indicate that simultaneous selection is possible in maximising genetic gain for both characters. These results suggest selection for shorter height, longer coleoptiles wheats could be accomplished simply in a wheat breeding program targeting improved establishment.

Keywords: Triticum aestivum, L., emergence, early vigour, coleoptile, plant height

Historical comparisons of Australian wheat varieties reveal moderate changes in plant height as a consequence of selection for increased grain yield. Older wheat varieties are tall and prone to lodging in favourable environments, whereas current varieties are shorter, less prone to lodging and have good dry-matter partitioning to the grain. The shorter height of current wheat varieties is due to the use of GA-insensitive height-reducing genes (9). These genes decrease plant height by reducing cell size in leaf and stem tissue (6). Reductions in cell size also reduce coleoptile length and seedling leaf area.

The short coleoptiles of current semidwarf wheats do not adversely affect yield in wetter or irrigated environments. However, short coleoptiles can reduce yield through poor establishment in drier, non-irrigated environments (5). A reduction in coleoptile length leads to poor emergence when seed is sown deep such as when soil moisture near the surface is insufficient for germination, or when planting equipment is improperly adjusted. Shorter coleoptiles also compromise emergence with direct drilling or stubble retention in conservation tillage (3,4), or when soil temperatures are high (8). Poor early vigour as a result of poor emergence or reduced leaf area also reduces weed competitiveness and can result in considerable water loss through soil evaporation to reduce yield.

Studies show that wheat height can be reduced by the use of GA-sensitive genes for plant height (11). These genes reduce plant height to levels equivalent to that of plants containing GA-insensitive *Rht* genes yet are less likely to reduce coleoptile length or seedling leaf area (1, 2, 10). However, no study has yet reported the influence of major genes such as *Rht8* or *Rht9* on coleoptile length. Nor has a study reported the inheritance of plant height and coleoptile length in backgrounds segregating for major and minor GA-sensitive genes for reduced plant height. This study reports on the relationship between coleoptile length and plant height for three wheat populations containing GA-sensitive, height-reducing genes.

Materials and Methods

One four-way (Insignia/Skua/Hartog/Mara - hereafter I/S//H/M) and two biparental (APDO/ Spica and Skua/Shortim - hereafter A/S and S/S, respectively) crosses were made among wheat lines containing major and/or minor GA-sensitive genes for reduced plant height. The F₁ plants were self-pollinated, and up to 400 F₂ seed harvested for GA-sensitivity assessment using a method described previously (9). All GA-sensitive progeny were retained and screened again for GA-sensitivity using F_{3,4} seed. Between 60

and 90 F_{4,5} lines non-segregating for GA-sensitivity were retained from each population. To assess variation in plant height these GA-sensitive lines, the original parents and a set of widely-grown GA-insensitive, semidwarf varieties were sown as hills on two sowing dates in the field and in deep tray_??V?the glasshouse. Lines were replicated three times in each study. Plants were grown with adequate water and nutrients so as to maximise genetic differences in the expression of plant height. Plant height was determined at maturity as the distance from the soil surface to the tip of the spike on the tallest tiller. Coleoptile length was determined by sowing F_{5,6} seed of uniform size at a depth of 20 mm in well-watered, deep trays containing a fertile potting mix. Trays were then placed into darkened growth cabinets at 11, 15, 19 and 23? C and sampled after a period of 200? Cd (base temperature of 0? C). Coleoptile length was recorded as the distance from the seed to where the first leaf broke through the coleoptile sheath.

Plant height and coleoptile length data were analysed after first checking for normality and error variance heterogeneity across environments. Residuals plotted against fitted values revealed a random distribution indicating there was no need for data transformation. Variance components, their standard errors and best linear unbiased predictors were obtained following analysis by the method of restricted maximum likelihood. Statistical significance of variance components was ascertained from log likelihood ratio tests for full and reduced models. Heritability was estimated for each population on a line-mean basis (7).

Results and Discussion

Plant height

Genotypic variation for plant height was large among populations and between lines within each population (Table 1). Average height of the A/S population was significantly ($P < 0.05$) greater than either the S/S or I/S//H/M populations, this difference presumably reflecting the taller heights of the parents, APDO and Spica. The S/S and I/S//H/M populations were not different in height partly because of the presence of Skua in both pedigrees but also because Mara is a short, GA-sensitive wheat (Table 1). Mara contains two GA-sensitive, height-reducing genes, *Rht8* and *Rht9*. These genes appear to act additively to reduce the height of Mara when compared with single *Rht8* wheats (G. Rebetzke unpublished data). Interestingly, the S/S population contains no known major GA-sensitive *Rht* genes yet progeny were on average shorter than those segregating for minor genes in the A/S population, and were at least equivalent in height to lines in I/S//H/M (Table 1). Both Skua and Shortim are widely recognised as being much shorter than expected on the basis of their known *Rht* complement and may contain additional *Rht* genes for reduced plant height.

Table 1. Range and mean for plant height and coleoptile length measured on GA-sensitive wheat lines from three wheat populations. Values represent line means from three environments (plant height) or four temperatures (coleoptile length). Plant heights and coleoptile lengths are given for parents as a footnote¹.

Trait	Population		
	Skua/Shortim ¹	Insignia/Skua//Hartog/Mara ¹	APDO/Spica ¹
Plant height (cm)	?	?	?
Mean	85	84	97
Range	75 - 96**	68 - 107**	87 - 109**

Coleoptile length (mm)	?	?	?
Mean	72	75	74
Range	43 - 95**	48 - 104**	48 - 109**

1 Plant height, coleoptile length for each parent? Skua (66cm,48mm), Shortim (73,53), Insignia (85,88), Hartog (80,42), Mara (67,76), APDO (86,79) and Spica (101,79)

** Differences among lines were statistically significant at the 0.01 probability level

Differences in plant height were highly significant ($P < 0.01$) between lines in all populations (Table 1). The range in plant height was largest for the I/S//H/M population presumably because of segregation for major and minor height-reducing genes. The range was not as large for the S/S population, but a number of short, GA-sensitive lines were identified. Of the three populations, only S/S failed to contain lines as short as the shortest height parent (Table 1). The A/S population produced few desirably short lines although lines less than 95 cm in height could be well suited to more marginal areas of the Australian wheatbelt. All populations contained transgressive lines that were taller than the tallest parent in each cross. A number of GA-sensitive lines were observed to be as short as current GA-insensitive, semidwarf cultivars Janz (68 cm), Amery (72 cm), Stiletto (75 cm) and Hartog (80 cm) grown in the same study (Table 1). These shorter lines were only evident in the S/S and I/S//H/M populations and not for A/S indicating the apparent importance of major GA-sensitive genes for reducing plant height to levels considered useful in Australian wheat breeding programs. However, potential still exists for the use of minor genes to modify or enhance the expression of these major GA-sensitive height genes.

Coleoptile length

Differences in coleoptile length were small and nonsignificant ($P > 0.05$) among populations but large and significant ($P < 0.01$) for lines within populations (Table 1). The largest range in coleoptile length was observed in the A/S and I/S//H/M populations while genotypic variance was greatest for the S/S population (Table 2). Coleoptile lengths were also longest in the A/S and I/S//H/M populations. Both populations contained parents recognised as producing longer coleoptiles: Insignia and Spica being long coleoptile wheats of relatively short stature (8, 10). Almost all GA-sensitive progeny produced longer coleoptiles than GA-insensitive, semidwarf cultivars Hartog (42 mm), Janz (49 mm) and Spear (60 mm) grown in the same study.

Genotypic variance for coleoptile length was large and highly significant ($P < 0.01$) for all three populations (Table 2). Genotype \times temperature interaction was also significant ($P < 0.05$) but was only 26 to 28 % as large as the genotypic variance. Analysis of the genotype \times temperature interaction revealed that lines maintained their ranking across temperatures (data not shown). Non-rank changes indicate that long coleoptile families can be selected at cooler or warmer temperatures, and coleoptile length in GA-sensitive genetic backgrounds is reasonably stable across temperatures. The larger genotypic variance for coleoptile length contributed to high heritabilities in all three populations (Table 2). However, larger residual variances indicated that emphasis should be placed on good local control to reduce error and maximise gain from selection for increased coleoptile length.

Table 2. Variance components (\pm standard errors), and heritability on a line-mean basis for coleoptile length measured on GA-sensitive, inbred lines in three wheat populations grown at four temperatures.

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Statistic	Population		
	Skua/Shortim	Insignia/Skua//Hartog/Mara	APDO/Spica
$\sigma^2_{\text{Genotype}}$	172 ? 43**	160 ? 32**	148 ? 33**
$\sigma^2_{\text{Genotype ? temperature}}$	44 ? 15*	45 ? 12**	40 ? 16*
$?\sigma^2_{\text{Residual}}$	168 ? 14**	127 ? 12**	201 ? 15**
$h^2_{\text{Line-mean}}$	0.87**	0.88**	0.85**

*, ** Estimates were statistically different from zero at the 0.05 and 0.01 probability levels, respectively.

Relationship between plant height and coleoptile length

Plant height and coleoptile length were unrelated when viewed across population means (Table 1). For example, average coleoptile length for A/S was the same as for I/S//H/M yet the A/S population was 15 % taller. Linear regression estimates were obtained for coleoptile length and plant height measured on lines sown in the field in May 1995 (Table 3). Relationships were generally poor for all populations with correlations ranging between 0.14 and 0.32. Furthermore, regression slopes were small such that for every 10 cm decrease in line plant height there was between a 1.7 and 3.8 mm decrease in coleoptile length. Slope was smallest for the population containing known genes for longer coleoptile length from Spica. The poor relationships between plant height and coleoptile length observed in these populations agree well with relationships observed in other wheat populations segregating for GA-sensitive, height genes (e.g. 1, 2, 10). However, they contrast markedly with GA-insensitive, semidwarf wheat populations where both phenotypic and genotypic relationships for plant height and coleoptile length are ubiquitously strong (1, 2, 10). Such a strong interdependency indicates a smaller likelihood of obtaining longer coleoptile families without increasing plant height in GA-insensitive, semidwarf genetic backgrounds. The weak relationship for plant height and coleoptile length in the populations sampled here suggests that genes conditioning the two traits segregate independently when viewed in a GA-sensitive *Rht* genetic background. A recent study in which we evaluated a set of short and tall near-isogenic lines varying for *Rht8* and/or *Rht9* height-reducing genes showed that the shorter isolines (91 vs 120 cm) were significantly ($P < 0.01$) longer for coleoptile length (93 vs 83 mm).

Future breeding efforts should consider introducing genes from long coleoptile wheats such as Bencubbin (109 mm) or Stockade (104 mm) to further increase coleoptile length while maintaining shorter plant height. Given the high heritability for coleoptile length ($h^2 = 0.85-0.88$) and plant height ($h^2 = 0.63-0.73$) long coleoptile, reduced height wheats could be developed readily via a two-stage or simultaneous selection strategy for each character in a breeding program. We are currently adopting this approach for assessing a wide range of GA-sensitive *Rht* genes for use in our breeding program to improve the establishment and vigour of Australian wheats.

Ultimately, the adoption of any new characteristic into a breeding program relies on the attribute providing a yield advantage over existing wheat varieties. Preliminary yield data for wheats sown into favourable seedbeds indicated no yield penalty for long coleoptile, GA-sensitive wheats (Rebetzke and Richards unpublished data 1997). Clearly, extension to conservation tillage systems, or environments favouring deeper sowing would provide longer coleoptile wheats an advantage in plant establishment and subsequent grain yield over shorter coleoptile wheats that emerge poorly.

Table 3. Relationship of coleoptile length (CL) and plant height (PH) for GA-sensitive wheat lines from three populations sown during May in 1995.

Skua/Shortim	Insignia/Skua//Hartog/Mara	APDO/Spica
CL = 39 + 0.37 PH	CL = 38 + 0.38 PH	CL = 55 + 0.17 PH
($r^2 = 0.09^*$)	($r^2 = 0.10^*$)	($r^2 = 0.02$)

* Correlations were statistically significant at the 0.05 probability level.

Conclusions

Lines with GA-sensitive, height-reducing genes have been identified. These genes reduce plant height to those of commercial, semidwarf wheats but do not reduce coleoptile length. Ease of selection for plant height and coleoptile length in populations containing GA-sensitive, height-reducing genes indicates the potential of these genes for the rapid development of long coleoptile wheats in breeding programs targeting the development of wheats with improved emergence for deep sowing and conservation tillage-based farming systems.

Acknowledgments

This work is supported in part by the Grains Research and Development Corporation.

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