Genotypic increases in coleoptile length improves stand establishment, vigour and grain yield of deep-sown wheat

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Abstract

Timely sowing is critical for achieving high grain yields in winter cereals. However, inadequate seed-zone moisture for germination commonly delays sowing to reduce biomass and subsequent yield in semi-arid environments. Sowing deep to reach soil moisture is often avoided by growers of *Rht-B1b* and *Rht-D1b* semi-dwarf wheat as these wheat show poor emergence when sown deep. Their reduced cell elongation associated with insensitivity to endogenous gibberellins, results in shorter coleoptiles and smaller early leaf area. Alternative dwarfing genes responsive to endogenous gibberellins (e.g. *Rht8*) are available for use in wheat breeding. These reduce plant height without affecting coleoptile length and offer potential to select longer coleoptile wheat for deep sowing. Nine semidwarf (*Rht8*, *Rht-B1b*, and *Rht-D1b*) and seven tall (*rht*) wheat genotypes were sown at depths of 50, 80 and 110 mm at three locations in 2 or 3 years. Coleoptile lengths measured in a growth cabinet at four temperatures (11, 15, 19 and 23 °C) were strongly correlated with coleoptile length ($r_p = 0.77\text{--}0.79^{**}$) and plant number ($r_p = 0.49\text{--}0.79^{**}$) in deep-sown plots in the field. Furthermore, differences in coleoptile length were genetically correlated with greater numbers of emerged seedlings ($r_g = 0.97^{**}$), shallower crown depth (-0.58^{**}), greater seedling leaf area (0.59^{**}) and seedling biomass (0.44^{**}). Wheat containing the *Rht-B1b* or *Rht-D1b* dwarfing genes produced significantly ($P < 0.01$) shorter coleoptiles (97 mm) than both *Rht8* (118 mm) and tall (117 mm) wheat. In turn, compared with emergence from 50 mm depth, the *Rht-B1b* and *Rht-D1b* wheat produced significantly fewer seedlings at 110 mm sowing depth (-62%) than either *Rht8* (-41%) or tall (-37%) wheat. Effects of deep sowing early in the season were maintained with reductions in spike number and biomass at both anthesis and maturity. Kernel number was also reduced with deep sowing leading to reductions in grain yield. Over all entries, genotypic increases in plant number were associated with increases in fertile spike ($r_g = 0.61^{**}$) and kernel number (0.21^{**}), total biomass (0.26^{**}) and grain yield (0.28^{**}). Reduction in spike number and grain yield with deep sowing was smallest for the *Rht8* (-18 and -10%) and *rht* (-15 and -7%) wheat, and largest for the *Rht-B1b/D1b* (-39 and -16%) wheat. Plant height and coleoptile length were independent among *Rht8* and tall wheat genotypes. This study demonstrates the importance of good seedling emergence in achieving high wheat yields, and the potential use of alternative dwarfing genes such as *Rht8* in development of long coleoptile, reduced height wheat suitable for deep sowing.

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1. Introduction

A lack of adequate autumn rainfall can delay sowing of wheat crops in environments where irrigation is unavailable.

Delayed sowing after the optimum date is commonly associated with reductions in aerial biomass and grain yield (Photiades and Hadjichristodoulou, 1984; Coventry et al., 1993; Mahdi et al., 1998). Resulting yield reductions can be large with reported losses of between 140 and 330 kg ha⁻¹ week⁻¹ sowing delay for Australian wheat crops (Doyle and Marcellos, 1974; Shackley and Anderson,

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1995). Given Australian average wheat yields are *ca.* 2 t ha⁻¹, delays in sowing can represent substantial yield losses of between 7 and 17% per week. While the potential exists for earlier sowing of longer-season varieties (Penrose, 1993; Gomez-Macpherson and Richards, 1995), short coleoptiles limit this potential as earlier sowing typically coincides with warm conditions where seed-zone moisture for germination is often inadequate or dries rapidly.

Although there may be insufficient moisture for seed germination near the soil surface, adequate moisture for germination may still occur at depth particularly after a long fallow, or summer rainfall. Deep sowing should allow growers to use soil moisture lying below the drying topsoil, and is an option considered by growers in Australia and elsewhere (Donald and Puckridge, 1975; Photiades and Hadjichristodoulou, 1984; Mahdi et al., 1998; Schillinger et al., 1998). Deeper sowing also assists in reducing removal of seed by birds and rodents (Brown et al., 2003), and in avoiding phytotoxicity associated with some pre-emergent herbicides (O'Sullivan et al., 1985). Although deep sowing allows growers to sow their wheat crops closer to the optimum sowing time, emergence from depth commonly results in fewer, later emerging plants (Gan et al., 1992). Deep-sown seedlings have smaller relative growth rates and slower leaf area development to reduce plant biomass (Hadjichristodoulou et al., 1977; Huang and Taylor, 1993). Resulting smaller leaf area early in the season reduces competitiveness of wheat crops against weeds (Coleman et al., 2001), and increases water loss through evaporation from the soil surface, reducing crop water-use efficiency, biomass and grain yield (López-Castañeda and Richards, 1994). Later emerging plants have smaller biomass at anthesis, fewer spikes and lower final biomass and grain yield (Gan et al., 1992; Mahdi et al., 1998).

Development of wheat varieties with the capacity to emerge from deep sowing would benefit growers in arid regions. Numerous studies (e.g. Fick and Qualset, 1976; Whan, 1976a; Reithmuller, 1990; Schillinger et al., 1998; Takeda and Takahashi, 1999; Matsui et al., 2002) have demonstrated a positive association between coleoptile length and increased plant number with deep sowing. Shorter coleoptiles and poor emergence have commonly been associated with presence of the *Rht-B1b* and *Rht-D1b* dwarfing genes (Fick and Qualset, 1976; Allan, 1989; Schillinger et al., 1998; Takeda and Takahashi, 1999; Matsui et al., 2002). Both *Rht-B1b* and *Rht-D1b* genes decrease sensitivity of vegetative tissues to endogenous gibberellins to slow cell elongation and reduce cell size (Keyes et al., 1989; Hoogendoorn et al., 1990). Reductions in cell size contribute to reduced plant height but also reductions in leaf size, subcrown internode and coleoptile lengths (Fick and Qualset, 1976; Whan, 1976b; Allan, 1989; Rebetzke et al., 2001; Matsui et al., 2002). Many of the alternative, gibberellin-sensitive dwarfing genes (e.g. *Rht4*, 8, 9, 12 and 13) reduce plant height without affecting coleoptile length (Ellis et al., 2004). The correlation between plant

height and coleoptile length was small in populations varying for *Rht8* and *Rht9*, indicating the potential for selection of long coleoptile, reduced height wheat using these dwarfing genes (Rebetzke et al., 1999; Rebetzke and Richards, 2000). Indeed, Schillinger et al. (1998) demonstrated the potential of *Rht8* in the development of semidwarf, long coleoptile wheat targeted at sowing depths exceeding 160 mm.

The primary aim of this paper was to investigate the influence of genotypic changes in coleoptile length on plant number, early growth and grain yield for deep-sown wheat evaluated over multiple environments. A secondary aim explored the potential utility of GA-sensitive dwarfing genes for genetic improvement of seedling emergence and early growth in wheat.

2. Materials and methods

2.1. Genotypes

Sixteen genotypes representing wheat with GA-insensitive (*Rht-B1b* and *Rht-D1b*) and GA-sensitive (*Rht8*) dwarfing genes and tall, non-dwarf (*rht*) genotypes were used. Six *Rht8* semi-dwarfs were obtained from a cross between the GA-sensitive, semidwarf (*Rht8*) variety Mara and tall (*rht*) variety Halberd. Wheat varieties Halberd, Heron and five tall progeny from a four-way cross (Insignia/Skual/Hartog/Mara) were used to represent tall wheat. Semidwarf varieties Janz (*Rht-B1b*), and Hartog and Spear (*Rht-D1b*) were included as GA-insensitive controls. Presence of the *Rht8* dwarfing gene was determined after Rebetzke and Richards (2000) by genotyping alleles at the *gwm261* microsatellite marker locus chromosomally linked to *Rht8* (Korzun et al., 1998). This marker is informative in Mara-derived progeny (Ellis et al., 2005). Similarly, presence of the *Rht-B1b* and *Rht-D1b* dwarfing genes was determined in all lines using single nucleotide polymorphism markers for these alleles after Ellis et al. (2002). Lines were selected on the basis of differences in dwarfing genes but similarity in flowering time, with no consideration given to yield potential or other agronomic characteristics.

2.2. Agronomic evaluation

Seed of all 16 lines were obtained from the same environment to avoid confounding of effects of seed source (maternal environment) with differences in seedling growth. Mean seed size ranged between 36 and 40 mg across lines with the exception of variety Spear which averaged 46 mg in size. Seed of all entries were sown into 6.0-m long, 0.17-m spaced, 10-row plots at Moombooldool and Condobolin NSW in 1998–2000 (Table 1). Sowings were also made at Ginninderra ACT in 1998 and 1999. Entries were sown at two sowing depths (50 and 110 mm) except for Moombooldool and Ginninderra 1998 and 1999 where an

Table 1

Pre-sowing and growing season rainfall (mm) for each location in the 3 years (1998–2000) experiments were grown

Environment	Sowing date	May	June	July	August	September	October	November
1998								
Condobolin	27 May	56	48	75	82	79	48	51
Moombooldool Wagga	25 May	16	59	77	40	85	40	34
1999								
Condobolin	15 June	7	27	53	42	23	122	17
Moombooldool Wagga	18 June	45	28	35	48	45	101	25
2000								
Condobolin	23 May	95	18	15	59	13	64	63
Moombooldool	26 May	64	38	31	73	22	60	67

additional 80 mm sowing depth was included. The 50 mm depth was chosen as optimal following the work of Reithmuller (1990), who suggested that shallower sowing risks reduced seedling emergence due to soil drying. Post-emergence assessment of sowing depth confirmed the accuracy of the target sowing depths except at Moombooldool in 1998 where alternate rows in the 110 mm sowing were sown at 140 mm depth. Sowing rate was 200, 180 and 160 seed m⁻² for Ginninderra, Moombooldool and Condobolin, respectively. All sowings followed a defined fallow period usually commencing with pasture removal by herbicide application in August–September of the previous year. Nutrients were supplied at sowing with a complete fertilizer (Starter 15[®]—15% N:12% P:12% S) at 103 kg ha⁻¹, and plots were reliant on pre- and growing-season rainfall (Table 1). Sowings were maintained free of weeds and diseases with the application of appropriate herbicide and fungicide control measures.

For each plot, plant height was determined at maturity as the distance from the soil surface to the top of the ear (awns excluded) of the tallest spikes. Spikes were sampled from each plot at anthesis and maturity using a 1.36 m × 0.40 m quadrat, air-dried at 70 °C for 3 days and weighed before and after threshing. Spikes were counted for both harvests, and harvest index calculated as the ratio of grain to total above-ground biomass for the maturity harvest. Plots were end-trimmed to ca. 5.4 m and the outside border rows removed before machine harvesting. Harvested portions of each plot were located ca. 0.8 m from adjacent plots to remove potential shading and other competition effects between neighboring genotypes. Kangaroo damage at Ginninderra prevented any plot harvesting at this location. For all harvested sites, kernel weight was determined for a 200-grain sample from each plot, and kernel number (m⁻²) calculated from plot yields. The experimental design at each location was a split-plot design containing two replications. Whole plots comprised the different sowing depths while lines were allocated at random within each depth.

2.3. Seedling emergence counts

Every 1–2 days after sowing, seedling emergence counts were made of lines representative of each height class

(HM14bS (*Rht8*), HM16S (*Rht8*), Hartog (*Rht-D1b*) and Halberd (*rht*)) at each depth in Condobolin and Moombooldool in 1998, and Ginninderra and Moombooldool in 1999. This was achieved by counting numbers of seedlings in four, 50 cm rows in each plot. A Gompertz curve was fitted to the seedling emergence data for individual plots of all treatments. In the non-linear model, seedling emergence was the response variable (*Y*) and thermal time (*X*) was the explanatory variable with the form of the fitted curve being:

$$Y = A + C \exp^{(-\exp(-B(X-M)))}$$

As there is no emergence at time = 0, *A* (the lower asymptote) was set at 0. It was assumed that the base temperature for germination and early growth of wheat was 0 °C and was the same for all genotypes (Angus et al., 1981). The value at the upper asymptote was *C*, *M* was the *X*-axis value corresponding to the midpoint (i.e. at 50% of maximum seedling emergence) of the growth response curve, and *B* was the slope of the line at this midpoint. The lag period from sowing until the first seedlings emerged was obtained from the second derivative of the Gompertz equation with respect to *X*. Air temperatures during the period from sowing to emergence were recorded in an adjacent Stevensons screen. Temperatures obtained for Condobolin in 1998 and Ginninderra in 1999 indicated correlations of air and soil temperatures at 100 mm soil depth of 0.94 and 0.91 (*P* < 0.01), respectively.

2.4. Coleoptile length and early vigour measurements

Ten randomly sampled plants were excavated at ca. DC1.4 (four mainstem leaves) from plots at each sowing depth (50, 80, 110 and 140 mm) at Moombooldool in 1998. Individual plants were cut at the seed and measurements made of coleoptile length and crown depth, numbers of mainstem leaves, primary and coleoptile tillers, and widths and lengths of all mainstem leaves. Plant leaf area was determined using a planimeter (Delta-T[®]), and then all above- and below-ground tissue (excluding roots) dried at 70 °C for 3 days before weighing. In a separate experiment, good quality seeds free of any visible damage and weighing between 40 and 42 mg were obtained for all genotypes.

Seeds were sown at a depth of 20 mm into wooden seedling trays (600 mm × 300 mm × 120 mm) containing a fertile, compost-based potting mix before being placed into darkened growth cabinets set at constant temperatures of 11, 15, 19 and 23 °C. Each tray contained four replicates of all lines arranged in a randomised complete block design. Seedlings were removed from the dark at *ca.* 200 degree-days (assuming a base temperature of 0 °C) and coleoptile lengths measured.

2.5. Statistical analysis

Data were analysed statistically after first checking for normality and error variance homogeneity across environments. Residual plots revealed a random distribution indicating no need for data transformation (data not shown). Combined analyses of variance and covariance over environments were performed using the multivariate analysis of variance option MANOVA of the SAS Generalised Linear Models procedure GLM (SAS, 1990). Variance and covariance components for treatment effects were estimated by equating appropriate mean squares and cross-products to their expectation. Environments were deemed random and entries and sowing depths fixed effects in the linear model. Protected least significant differences (L.S.D.) were calculated for multiple comparisons although *a priori* single degree-of-freedom contrasts were made for testing 50 mm versus 110 mm sowing depth effects in each environment.

For the seedling emergence Gompertz analysis, adjusted coefficients of determination (R^2) across all plots ranged from 0.90 to 0.99 with an average of 0.98 indicating the adequacy of the Gompertz model in explaining variation in seedling emergence across thermal time at all depths in each environment. Regression parameters estimated from the emergence data for each combination of site, year, block, entry, and sowing depth were collated and analyzed using SAS GLM (SAS, 1990). Statistical significance is reported at $P = 0.05$ unless otherwise stated.

3. Results

3.1. Field environments

The sites and seasons over which experiments were conducted provided a contrasting set of field environments from which genotypic response to sowing depth could be assessed. Some pre-sowing rainfall was obtained in all environments with the exception of 1999 where a lack of adequate May rainfall delayed sowing up to 1 month at both Moombooldool and Condobolin (Table 1). In-crop rainfall varied from 232 mm at Condobolin in 2000 to 335 mm at Moombooldool in 1998. Across all years, rainfall amount and distribution were similar for Condobolin and Moombooldool. In general, the 1998 growing

season was characterized by more rainfall which increased biomass and grain yield relative to other seasons (Table 2).

3.2. Average effects of sowing depth

Inspection of plots at the onset of seedling emergence confirmed target sowing depths were achieved at most sites and seasons (data not shown). One exception was Moombooldool in 1998 where the 110 mm sowing depth resulted in alternating rows of 110 and 140 mm sowing depths (Table 3). Furthermore, greater variance in sowing depth was observed at deeper sowings than for shallow sowings. For example, excavation of individual plants at Moombooldool in 1998 revealed that realized sowing depths ranged between 50 and 62 mm and 94 and 123 mm for target depths of 50 and 110 mm, respectively. Sowing beyond a depth of 50 mm was commonly associated with significant reductions in the number of emerged seedlings (Tables 2 and 3). Averaged across all environments, there were *ca.* 65% more seedlings at 50 mm than when sown at a depth of 110 mm (*cf.* 136 and 83 plants m^{-2}). This reduction with deep sowing was reasonably consistent across environments except at Condobolin in 2000 where there was a greater reduction (>40%) of seedlings emerging from 110 mm. Seedling numbers at Moombooldool in 1998 were 150, 132, 111 and 83 plants m^{-2} for 50, 80, 110 and 140 mm, respectively (Table 3), indicating a strong, linear reduction ($r_p = -0.99$, $P < 0.01$) in plant number with increasing sowing depth.

Effect of sowing depth on early growth of seedlings was examined in detail at Moombooldool in 1998. Deeper sowing had a large effect on early seedling growth and was associated with significantly ($P < 0.01$) fewer coleoptile and primary tillers per plant, and fewer, narrower yet longer leaves to reduce seedling leaf area and plant biomass (Table 3). These reductions, together with fewer plants, resulted in large and significantly linear reductions in tiller number, leaf area and biomass per m^2 . Greater crown depth with deep sowing resulted in a greater proportion of total plant biomass (excluding roots) allocated below the soil surface. For example, at 50 mm sowing depth, crowns were positioned close to the soil surface and all non-root, plant biomass was located at, or above, the soil surface. This contrasts with significantly deeper crown placement and a corresponding reduction in allocation to above-ground biomass for the 110 mm (75%) and 140 mm (34%) sowing depths, respectively.

Responses to sowing depth extended beyond early plant growth to influence later vegetative and reproductive growth (Table 2). For example, an increase in sowing depth from 50 to 110 mm was associated with a significant ($P < 0.01$) reduction in anthesis spike number (396–309 spikes m^{-2}) and anthesis biomass (835–690 g m^{-2}). Although fewer spikes were produced with deep sowing, resulting spikes were significantly ($P < 0.01$) larger in size

Table 2

Environment means for agronomic characteristics measured on wheat genotypes sown at two depths and at two sites over 3 years

Environment	Sowing depth (mm)	Number of plants (m ⁻²)	Plant height (cm)	Number of grain (m ⁻²)	100-grain (mg)	Number of spikes (m ⁻²)	Spikes per plant (n)	Grains per spike (n)	Grain yield (t ha ⁻¹)	Total biomass (t ha ⁻¹)	Biomass per plant (g)	Harvest index
1998												
Condobolin	50	119	99	11375	3.70	289	2.43	39	4.22	11.2	9.7	0.38
	110	79 ^{*,a}	95 [*]	10535 [*]	3.73	242 ^{**}	3.06 [*]	44 ^{**}	3.90 [*]	10.3 [*]	14.2 ^{**}	0.38
Moombooldool	50	152	97	11221	3.54	385	2.51	29	3.94	11.2	7.3	0.35
	110	106 ^{**}	91 ^{**}	9206 ^{**}	3.60	265 ^{**}	2.35	35 ^{**}	3.29 ^{**}	8.9 ^{**}	8.5 [*]	0.37 [*]
1999												
Condobolin	50	128	68	5818	3.35	247	1.92	24	1.91	5.4	4.3	0.35
	110	73 ^{**}	69	5303 [*]	3.29	207 ^{**}	3.24 ^{**}	26 [*]	1.73 [*]	4.7 ^{**}	7.4 ^{**}	0.37 [*]
Moombooldool	50	142	84	8034	3.69	299	2.10	27	2.93	7.6	5.4	0.38
	110	92 ^{**}	81 [*]	7349 [*]	3.62	233 ^{**}	2.53 ^{**}	32 ^{**}	2.64 ^{**}	6.4 ^{**}	7.3 ^{**}	0.41 ^{**}
2000												
Condobolin	50	129	83	ne	ne	ne	ne	ne	2.53	ne	ne	ne
	110	46 ^{**}	80 [*]	ne	ne	ne	ne	ne	2.07 ^{**}	ne	ne	ne
Moombooldool	50	143	95	9929	3.87	ne	ne	ne	3.79	10.4	7.3	0.37
	110	100 ^{**}	93	7349 ^{**}	4.05 ^{**}	ne	ne	ne	3.49 ^{**}	8.8 ^{**}	9.2 ^{**}	0.40 ^{**}
L.S.D. ($P = 0.05$) ^b		10	4	671	0.11	27	0.39	3	0.22	0.8	1.0	0.02

ne, Not estimated; symbols (*, **) indicates differences between means at 50 and 110 mm sowing depths for $P = 0.05$ and 0.01 , respectively.^a A priori single d.f. contrasts within each environment.^b Least significant difference for comparisons between sowing depths in all environments.

Table 3

Mean seedling response to sowing depth for 16 wheat genotypes at Moombooldool, NSW in 1998

Sowing depth (mm)	Number of plants (m^{-2})	Number of mainstem leaves (n)	Crown depth (mm)	Leaf 1 width (mm)	Leaf 1 length (mm)	Coleoptile tiller frequency (%)	Number of tillers/plant ^a (n)	Plant leaf area ^a (cm^2)	Above-ground biomass/plant ^a (g)	Below-ground biomass/plant ^{a, b} (g)
50	150	3.8	25	3.2	102	17.4	0.62 (94)	14.7 (2261)	0.13 (20.1)	0.00 (0.00)
80	132	3.7	33	3.0	113	1.2	0.53 (75)	14.3 (1968)	0.13 (17.2)	0.00 (0.43)
110	111	3.6	43	2.9	113	0.6	0.39 (44)	12.7 (1444)	0.07 (7.63)	0.01 (1.22)
140	83	3.5	47	2.8	114	0.0	0.36 (30)	11.9 (1031)	0.05 (4.18)	0.02 (1.32)
L.S.D. ($P = 0.05$) ^c	12	0.1	7	0.1	7	4.4	0.08 (11)	1.2 (252)	0.01 (2.48)	0.01 (0.35)

Plants from all genotypes and sowing depths were sampled when the average number of mainstem leaves for all genotypes in the 50 mm sowing depth was 3.8.

^a Values in parenthesis are estimates per unit area.^b Biomass per plant excluding roots.^c Least significant difference for differences between means at each sowing depth.

Table 4

Environmental (r_e) and genotypic (r_g) correlations between number of emerged seedlings and different agronomic characteristics measured on 16 wheat genotypes sown at two or three depths in 3 years and two sites

Parameter	Number of grains (m^{-2})	Grain weight (mg)	Number of spikes (m^{-2})	Spikes per plant (n)	Grains per spike (n)	Grain yield ($t\ ha^{-1}$)	Total biomass ($t\ ha^{-1}$)	Biomass per plant (g)	Harvest index	Plant height (cm)
r_e	0.38**	0.13	0.82**	−0.73**	−0.28*	0.38*	0.35*	−0.45**	−0.34*	0.24*
r_g	0.21*	0.28*	0.61**	−0.46**	−0.54**	0.28*	0.26*	−0.41**	−0.21*	0.15

Symbols (*, **) denotes correlation is significantly different from zero at $P = 0.05$ and 0.01 , respectively.

(cf. 2.09 and 2.23 g spike⁻¹) (data not shown). Where estimates were obtained, deeper sowing was associated with fewer spikes m⁻² but more grains per spike (Table 2). Kernel number per unit area was also reduced to decrease grain yield in all environments in spite of more fertile spikes per plant. Similarly, total biomass decreased despite higher values for harvest index. Kernel weight was generally unchanged by sowing depth (Table 2). Morphological and agronomic changes with deep sowing were reasonably consistent across sites and years although deeper sowing at Condobolin in 2000 resulted in a significantly greater reduction in seedling number and grain yield than for other environments.

Environmental correlations (r_e) were obtained to assess the effect of changes in seedling number on covariation in a range of agronomic traits (Table 4). Fewer seedlings with deeper sowing in each environment was associated with significant ($P < 0.01$) reductions in spike and kernel number m⁻². Fewer plants contributed to smaller biomass and grain yield, despite reductions in plant height and greater harvest index (Table 4). Reduction in numbers of plants m⁻² was partly compensated for by greater numbers of fertile spikes per plant, more grains per spike and greater biomass per plant. Change in plant number with sowing depth had no effect on kernel weight.

3.3. Effects of genotypes

3.3.1. Seedling emergence

Good seedling emergence was observed for all genotypes in the shallow, 50 mm sowing depth in each environment with only small yet significant differences in stand establishment between lines. For example, when averaged across all environments, lines HM14bS (*Rht8*), Halberd (*rht*), Hartog (*Rht-D1b*) and Spear (*Rht-D1b*) produced 131, 146, 143 and 145 plants m⁻², respectively, when sown at 50 mm. To account for these minor differences, emergence with deeper sowing was expressed relative to emergence with shallow sowing for key agronomic traits in Fig. 1.

Seedling emergence and early growth was measured at four sowing depths at Moombooldool in 1998 (Tables 5 and 6). There were large and significant genotypic differences in emergence at the deeper sowing depths. For example, relative to the 50 mm sowing depth, reduction in numbers of plants m⁻² for 140 mm depth were -14% (Halberd), -78% (Hartog), -34% (HM14bS), -59% (Janz) and -43% (Spear). For the dwarfing gene groups, increases in sowing depth were associated with linear ($r^2 = 0.95\text{--}0.99$, $P < 0.01$) reductions in the number of emerged seedlings. This reduction was greatest for the GA-insensitive, *Rht-B1b/D1b* group ($b = -9.7 \pm 0.5$ plants m⁻² mm⁻¹) with less

Fig. 1. Change (%) in different agronomic characteristics with deep-sowing at 110 mm expressed relative to the shallow 50 mm sowing depth. Bars represent (left to right) *Rht8*, *Rht-B1b/D1b*, *rht* wheat.

Table 5

Parameter value estimates obtained from Gompertz, non-linear regression of seedling emergence and accumulated thermal time for four wheat genotypes grown at four environments (Condobolin and Moombooldool in 1998, and Ginninderra and Moombooldool in 1999) at three sowing depths (50, 80 and 110 mm)

Sowing depth (mm)	Entry	Number of plants (m^{-2})	Lag ($^{\circ}Cd$)	B ($no^{\circ}Cd^{-1}$)	C (n)	M ($^{\circ}Cd$)
50	Halberd	158	131	0.512	153	148
	Hartog	157	134	0.462	154	149
	HM14bS	141	132	0.462	153	144
	HM16S	151	130	0.494	163	146
80	Halberd	136	149	0.090	143	162
	Hartog	103	156	0.124	96	173
	HM14bS	129	146	0.128	126	162
	HM16S	129	148	0.119	128	167
110	Halberd	83	163	0.105	84	181
	Hartog	50	173	0.098	48	184
	HM14bS	100	164	0.057	100	182
	HM16S	90	160	0.106	104	177
L.S.D. ($P = 0.05$) ^a		16 ^b , 21 ^c	6	0.028	20	5
L.S.D. ($P = 0.05$) ^d		20 ^e , 21 ^f	6	0.032	20	5

Lag is the time at which 5% of seedlings emerge, C is the value at the upper asymptote (maximum number of seedlings), M is the x-axis value corresponding to the midpoint (i.e. at 50% of maximum seedling emergence) of the curve, and B is the slope of the line at this midpoint.

^a For mean comparisons within depths.

^b L.S.D. for comparisons of numbers of plants m^{-2} within 50 and 110 mm sowing depth.

^c L.S.D. for comparisons of numbers of plants m^{-2} within 80 mm sowing depth.

^d For mean comparisons between depths.

^e L.S.D. for comparisons of numbers of plants m^{-2} between 50 and 110 mm sowing depth.

^f L.S.D. for comparisons of numbers of plants m^{-2} between 80 and 50 or 110 mm sowing depth.

than 40% of seedlings emerging with deep sowing. The *Rht8* ($b = -7.4 \pm 0.5$) and tall ($b = -6.6 \pm 0.4$) wheat emerged similarly, with deep sowing, producing 59 and 63%, respectively, of the numbers at 50 mm sowing depth.

Gompertz analysis was used to examine non-linear trends in seedling emergence over time for three sowing depths in four environments. Data was expressed on a thermal time basis. Large and significant differences were obtained for all estimated parameters (Table 5). Deeper sowing was associated with fewer seedlings and a slower rate and longer duration of seedling emergence, and this was consistent across environments (data not shown). Deeper sowing was associated with significantly delayed initial emergence ('lag') by ca. 40 and 55 $^{\circ}Cd$ for the 80 and 110 mm sowing depths, respectively (Table 5). In turn, time to 50% emergence (M) was significantly delayed by 19 and 34 $^{\circ}Cd$, for the 80 and 110 mm depths, respectively. Rate of seedling emergence (B) was significantly faster in the 50 mm sowing depth and was not different for the 80 and 110 mm depths. Reduction in seedling number at 80 and 110 mm depths was greatest for the GA-insensitive Hartog (−34 and −68%, respectively) (Table 5). The GA-sensitive wheat Halberd (−47% at 110 mm), HM16S (−40%) and HM14bS (−29%) were less affected by deep sowing. Genotype $\times$ site and genotype $\times$ year interactions were not significantly different from zero for any component of the Gompertz equation of seedling appearance (data not shown). Duration and rate of seedling emergence were similarly affected for all lines with deep sowing. The variety Hartog was the slowest to emerge at all depths while there was little difference in time to emergence for the other

wheat. For example, deeper sowing of HM14bS was associated with a 32 $^{\circ}Cd$ delay in initial seedling emergence whereas for Hartog the delay was significantly greater (39 $^{\circ}Cd$).

3.3.2. Early growth

Deeper sowing at Moombooldool in 1998 was associated with greater coleoptile and subcrown internode (SCI) lengths, and deeper crown placement (Table 6). At 140 mm depth, coleoptile lengths varied from 105 to 131 mm for the *Rht8* wheat, 88 to 120 mm for the *Rht-B1b/D1b* wheat, and 106 to 132 mm for the tall wheat. Across all entries, genetic increases in coleoptile length were associated with genotypically greater numbers of emerged plants, a longer SCI and shallower crown, longer and marginally wider leaves, and greater tiller number, leaf area and plant biomass (Table 6). With deep sowing, coleoptile length was greatest for the *Rht8* and tall wheat, while SCI was greatest and crown depth shallowest for the tall wheat. Change in leaf and tiller number per plant with deeper sowing was similar for all dwarfing gene classes whereas leaf one width and length responded markedly with deep sowing for the *Rht8* and tall wheat. Increases in leaf length compensated for narrower leaf width to maintain mainstem leaf area with deep sowing for the *Rht8* wheat. However, a reduction in tiller number resulted in significant reductions in plant biomass with deep sowing. Reduction in plant leaf area and biomass with deep sowing was greatest for the *Rht-B1b/D1b* wheat. Further, emergence of fewer seedlings at all depths exceeding 50 mm resulted in an even greater reduction in leaf area and biomass m^{-2} .

Table 6

Seedling characteristics for wheat genotypes representing different dwarfing gene classes when sown at four depths at Moombooldool, NSW in 1998

Dwarfing gene class	Sowing depth (mm)	Number of plants (m ⁻²)	Coleoptile length (mm)	Subcrown internode length (mm)	Crown depth (mm)	Number of mainstem leaves (<i>n</i>)	Leaf 1 width (mm)	Leaf 1 length (mm)	Number of tillers per plant ^a	Leaf area per plant ^a (cm ²)	Biomass per plant ^a (g)
<i>Rht8</i>	50	155	56	34	21	3.9	3.3	107	1.9 (289)	15.7 (2437)	0.14 (21.0)
	80	145	93	65	27	3.9	3.3	122	1.7 (240)	16.7 (2421)	0.14 (20.3)
	110	115	112	79	42	3.7	3.0	124	1.2 (142)	14.7 (1685)	0.07 (8.2)
	140	91	118	84	47	3.6	2.9	123	1.0 (90) (**)	14.2 (1277) ns (**)	0.06 (5.0) (**)
<i>Rht-B1b/D1b</i>	50	146	52	34	21	3.9	2.9	91	1.8 (259)	14.0 (2064)	0.13 (18.7)
	80	101	81	64	32	3.8	2.8	95	1.7 (174)	13.1 (1323)	0.13 (13.4)
	110	90	93	79	45	3.6	2.9	94	1.2 (108)	11.5 (1035)	0.06 (5.4)
	140	54	97	88	50	3.5	2.9	98	1.0 (58) (**)	10.9 (596) * (**)	0.04 (2.7) (**)
<i>rht</i>	50	153	56	34	22	3.7	3.4	101	1.9 (286)	17.9 (2739)	0.15 (22.6)
	80	138	96	73	27	3.7	3.2	113	1.5 (215)	16.1 (2202)	0.14 (19.1)
	110	114	110	87	37	3.7	3.1	113	1.3 (167)	15.0 (1716)	0.07 (8.5)
	140	96	117	94	42	3.4	2.9	113	1.2 (105) (**)	13.6 (1306) * (**)	0.05 (4.4) (**)
L.S.D. (<i>P</i> = 0.05) ^b		21	8	9	8	0.2	0.2	9	0.4 (68)	3.0 (530)	0.02 (3.4)
<i>r_g</i> (x. coleoptile length) ^c		0.97**	–	0.58*	–0.58*	0.05 ns	0.18*	0.74**	–0.59* (0.64**)	0.35* (0.59**)	– ^d , (0.44*)

The genetic correlation between coleoptile length and each seedling characteristic is estimated across all 16 genotypes at all sowing depths. Values for some characteristics are given on an individual plant and per unit area (in parenthesis) basis. (*, **) Indicate statistically significant differences in means across depths at *P* = 0.05 and 0.01, respectively.

^a Values in parenthesis are estimates per unit area.

^b Least significant difference for comparisons between sowing depths and dwarfing gene classes.

^c Genetic correlation between each characteristic and coleoptile length for all 16 genotypes; *, ** indicate genetic correlation is statistically different from zero at *P* = 0.05 and 0.01, respectively.

^d Genotypic variance was negative and so genetic correlation not estimated.

Genotypic differences in coleoptile length for the 140 mm sowing depth at Moombooldool in 1998 were strongly correlated with coleoptile length measured at 11 ($r_p = 0.78^{**}$), 15 (0.79^{**}), 19 (0.79^{**}) and 23 °C (0.77^{**}) in trays in darkened growth cabinets (Table 7). Mean coleoptile length in the growth cabinet was averaged across all four temperatures and was positively and linearly correlated with numbers of emerged seedlings for the 110 mm sowing depth at all sites and years ($r_p = 0.49$ – 0.79 , $P < 0.01$) (Table 7). These correlations were smallest for the 50 mm sowing depth and intermediate in size for the 80 mm sowing depths (Table 7).

3.3.3. Plant height

Plant height varied considerably among entries (Table 8). Much of the height difference was attributable to contrasts between the tall and the semidwarf *Rht-B1b/D1b* and *Rht8* dwarfing gene wheat. There was little difference in the average heights of the GA-sensitive and insensitive dwarfing gene groups with both averaging a height reduction of ca. 17 cm (18%) compared to the mean height of the tall group. At 50 mm sowing depth, the shortest entry was the GA-sensitive (*Rht8*) breeding line HM10S (72 cm) while the next shortest entry was the GA-insensitive (*Rht-B1b*) variety Janz (76 cm). The tallest entry was ISHM10 (101 cm), although this entry was not significantly different from the tall varieties Heron (98 cm) and Halberd (100 cm). Large background variability was observed for height within dwarfing gene groups. The largest range occurred among the GA-sensitive (72–87 cm) and the smallest for the GA-insensitive (76–87 cm) genotypes. While genotypic variation in plant height and coleoptile length measured in growth cabinets was large, the correlations between the two were small and non-significant ($P > 0.05$) varying between -0.19

Table 7

Phenotypic correlations for mean coleoptile length measured at four temperatures in a growth cabinet and number of emerged seedlings at different sowing depths assessed in field environments

Environment	Number of plants (m^{-2})		
	50 mm	80 mm	110 mm
1998			
Condobolin	−0.03 ns	0.59*	0.52*
Ginninderra	−0.26 ns	−0.19 ns	0.49*
Moombooldool	0.32 ns	0.58*	0.72**, ^a
1999			
Condobolin	0.50*	0.40 [†]	0.76**
Ginninderra	0.33 ns	0.56*	0.72**
Moombooldool	0.01 ns	0.41 [†]	0.68*
2000			
Condobolin	−0.21 ns	– ^b	0.70**
Moombooldool	−0.09 ns	–	0.79**

Symbols ([†], *, **) indicates correlation is significantly different from zero at $P = 0.10$, 0.05 and 0.01, respectively.

^a The correlation for coleoptile length and number of emerged seedlings at 140 mm depth was 0.74^{**} .

^b (–) Not estimated.

Table 8

Mean values of agronomic traits for different *Rht* dwarfing gene groups and the lowest- and highest-yielding genotype within each group when sown at an optimum 50 mm sowing depth at two sites over 3 years

<i>Rht</i> class/ genotype	Number of plants (m^{-2})	Plant height (cm)	Number of grains (m^{-2})	100-grain weight (mg)	Number of spikes (m^{-2})	Spikes per plant (n)	Grains per spike (n)	Grain yield (t ha^{-1})	Total biomass (t ha^{-1})	Biomass per plant (g)	Harvest index
<i>Rht8</i>											
Lowest ('HM15S')	138	83	8948	3.59	290	2.39	30.9	3.10	8.63	6.27	0.38
Highest ('HM14BS')	134	86	8425	3.58	306	2.28	28.2	2.90	8.35	5.55	0.37
	148*	82**	8819*	3.79**	268*	2.62*	33.3*	3.28**	8.26ns	6.17*	0.41**
<i>Rht-B1b/D1b</i>											
Lowest ('Hartog')	143	85	10456	3.66	319	2.83	31.6	3.61	9.82	7.03	0.39
Highest ('Spear')	144	85	10053	3.71	291	2.66	33.0	3.46	9.33	6.57	0.40
	145	87	10343*	3.84**	336*	2.95*	30.1*	3.76**	10.50**	7.33*	0.37**
<i>Rht</i>											
Lowest ('ISHM7')	135	99	8659	3.63	310	2.70	28.3	3.01	9.21	6.91	0.35
Highest ('Halberd')	134	101	7396	3.62	341	2.47	21.7	2.49	9.44	7.29	0.30
	147**	100	9625**	3.88**	303*	2.90**	32.1*	3.57**	10.51**	7.34ns	0.36**
L.S.D. ($P = 0.05$) ^a	8	2	402	0.05	29	0.29	2.0	0.11	0.56	0.60	0.01

(*, **) Indicates a statistically significant difference at $P = 0.05$ and 0.01 for the low- and high-yielding genotype in each *Rht* dwarfing gene class.

^a Least significant difference for comparisons between mean *Rht* dwarfing gene classes.

and 0.23 across sites and years (data not shown). When restricted to the six *Rht8* wheat only, the correlations between plant height and coleoptile length were again small and non-significant ($P > 0.05$) ranging between -0.30 and 0.09 .

3.3.4. Grain yield and yield components

Genotypic correlations were obtained across all genotypes to assess the effect of genetic changes in seedling number on agronomic traits (Table 4). Across all sowing depths, sites and seasons, genotypes with greater seedling emergence produced larger grain and more fertile spikes m^{-2} to increase kernel number and yield. Greater grain yield reflected increases in total biomass despite the reduction in harvest index with greater seedling number. Genotypes producing fewer emerged seedlings with deep sowing partly compensated by increasing the number of fertile spikes produced per plant, and increasing spike fertility to increase numbers of kernels per spike. More and larger spikes resulted in greater biomass per plant.

Comparisons among dwarfing gene classes indicated large mean differences in grain yield and associated traits when evaluated at the optimum 50 mm sowing depth (Table 8). At this depth, the *Rht-B1b/D1b* group produced significantly more biomass, fertile spikes, kernel number and yield than the *Rht8* and tall wheat. The greater yields of the *Rht-B1b/D1b* wheat likely reflect their selection as commercial varieties. This contrasts with the lower grain yields of the *Rht8* wheat where no previous selection has been made for grain yield. Therefore, the influence of deep sowing on grain yield and components for each dwarfing gene class was expressed relative to shallow sowing in Fig. 1.

The smallest reduction in plant number with deep sowing to 110 mm was for the tall (*rht*) and semidwarf *Rht8* wheat (Fig. 1). Genotypic variation was large and significant ($P < 0.01$) for anthesis dry matter (data not shown), and maturity estimates of grain yield and yield components (Table 8). Change in anthesis biomass with deep sowing was greatest for the *Rht-B1b/D1b* wheat ($755\text{--}577 \text{ g m}^{-2}$ ca. -24%) and not different for the *Rht8* ($857\text{--}726 \text{ g m}^{-2}$ ca. -15%) and tall, *rht* ($892\text{--}765 \text{ g m}^{-2}$ ca. -14%) wheat. These values reflected reductions in spike number with deep sowing for *Rht-B1b/D1b* ($374\text{--}265 \text{ spikes m}^{-2}$), *Rht8* (380 to 319) and *rht* ($435\text{--}342$) groups. In turn, increase in spike size with deep sowing was greatest for the *Rht-B1b/D1b* genotypes.

4. Discussion

Crop establishment and early growth are among the more critical growth phases in winter cereals. Indeed, surveys of Australian wheat growers have indicated variable sowing depth leading to poor crop establishment as a major concern when planning for sowing (Reithmuller, 1990). Many factors can contribute to deep sowing including the deep

placement of seed to reach moisture for germination, poor depth control on seeders, and sowing into poorly prepared seed-beds. Further, stubble and large soil-clods can increase the distance over which the coleoptile must elongate to emerge (Rebetzke et al., 2005; Gooding et al., 2006) when shallow sowing into a seed bed has been achieved.

4.1. Effect of deep sowing on grain yield

In the current study, effects of deep sowing were evident soon after sowing with delayed emergence and establishment of fewer plants. Deep sowing reduced early leaf area development and slowed biomass production. Slower leaf area development is associated with increased evaporation losses from the soil surface thereby reducing crop water-use efficiency (López-Castañeda and Richards, 1994).

Many of the changes in seedling growth were linear with changes in sowing depth, persisting through to anthesis and beyond to affect grain yield. Negative affects of early plant growth on yield were exacerbated by reduced plant numbers with deep sowing. Reductions in biomass and grain yield were evident for depths exceeding 50 mm and greatest at the deepest sowing depth of 110 mm. These reductions were repeatable across years and sites, and are consistent with reports of deep sowing elsewhere (Hadjichristodoulou et al., 1977; Photiades and Hadjichristodoulou, 1984; Reithmuller, 1990; Gan et al., 1992; Mahdi et al., 1998; Alam, 2002).

Reduced plant stands with deep sowing is commonly found to reduce spike number m^{-2} , thereby reducing kernel number, total biomass and grain yield (e.g. Photiades and Hadjichristodoulou, 1984; Mahdi et al., 1998). Although yields are reduced, the fewer plants with deep sowing achieve greater harvest index and biomass per plant, more fertile spikes, and more grains per spike. This compensation was evident from anthesis onward and may reflect reduced competition allowing access to more resources (e.g. water, nutrients and light) (Photiades and Hadjichristodoulou, 1984). However, the potential for greater weed problems with poor establishment in farmers' fields may reduce the capacity for plants to compensate with more fertile spikes when deep sown.

4.2. Overcoming poor establishment with greater coleoptile length

Few studies have reported the genotypic relationship between coleoptile length and seedling emergence, and subsequent effects on early growth, biomass and grain yield. Genotypic differences in coleoptile length were strongly, positively correlated with numbers of emerged seedlings with deep sowing in all environments. These associations were strongest at the 110 and 140 mm sowing depths, intermediate in size for the 80 mm sowing depth and smallest for the shallow, 50 mm sowing depth. Longer coleoptiles improved the ability to emerge from depth.

Genotypically longer coleoptile wheat also emerged sooner, produced more plants and had greater early vigour particularly with deep sowing. These plants also produced longer sub-crown internodes and therefore shallower crowns. Greater numbers of emerged seedlings resulted in more tillers, total leaf area and biomass per unit area for the longer coleoptile wheat. Subsequent growth resulted in larger plants containing more spikes at anthesis. In turn, longer coleoptile plants produced more fertile spikes to increase kernel number, kernel weight, biomass and yield. There was some compensation in shorter coleoptile wheat where the smaller numbers of plants produced were larger, and had more fertile spikes which contained more grains.

Schillinger et al. (1998) observed that coleoptile length and seedling emergence were strongly correlated ($r_p = 0.79–0.84$) across genotypes when sowing depth exceeded 160 mm. Similarly, the correlation between plant number and coleoptile length for 10 wheat growing in ploughed and unploughed soils was greatest for deep sowing ($r = 0.65–0.77$, $P < 0.05$) below 90–110 mm and smallest for sowing depths less than 50 mm (Alam, 2002). In the same study, grain yield was positively correlated ($r = 0.57–0.86$) with seedling number across genotypes in a range of cultivated systems. Similar positive associations have been reported for wheat elsewhere (e.g. Whan, 1976a; Matsui et al., 2002) and confirm the need for selection of longer coleoptiles for deep sowing. This is already being undertaken using *Rht8* to reduce plant height in the USA (Schillinger et al., 1998).

Genotypic differences in coleoptile length were positively correlated between field and controlled environments. Further, there was little evidence of genotype $\times$ temperature interaction for coleoptile length measured across temperatures ranging between 11 and 23 °C, consistent with previous studies (e.g. Rebetzke et al., 1999, 2001). Repeatability of coleoptile length is important in selection and it is especially useful if selection for a trait in a controlled environment (allowing selection at any time of the year and under controlled conditions) provides a correlated response in the field. Large variability in seed depth arising from non-uniform seed placement demonstrates the need for better sowing equipment if screening directly for coleoptile length in the field. This variability may partly account for the unexplained variation in the relationship between coleoptile length and sowing depth. Another factor contributing to seedling emergence was the potential for some wheat to elongate internodes below the crown. For example, the *Rht-B1b* genotype Janz elongated as many as three internodes to reach the soil surface when sown at 140 mm (data not shown). However, the frequency of seedlings showing this ability was low, indicating the trait to be of low penetrance and therefore likely to be difficult to select. Nonetheless, Gooding et al. (2006) indicate the potential of internode elongation in emergence from soft, sandy soils of short coleoptile wheat varieties.

4.3. Influence of dwarfing genes on coleoptile length and establishment

The shortest coleoptiles were generally associated with presence of the *Rht-B1b* and *Rht-D1b*, GA-insensitive dwarfing genes. While the coleoptile of Janz was among the shortest in this study, this wheat produces among the longest coleoptile of Australian commercial semidwarf wheat (Bonnett et al., 2001; Alam, 2002). The longer coleoptile length of Spear was consistent with previous reports (Bonnett et al., 2001) although its greater length (and higher seedling numbers) may also be partly attributable to its 10% larger kernel weight. Larger seed contributes to longer coleoptiles and greater emergence with deep sowing (Hadjichristodoulou et al., 1977; Gan et al., 1992). Nonetheless, while wheat with GA-insensitive dwarfing genes were associated with fewer emerged seedlings from depth, by maturity they recovered from poor emergence, producing large plants with more fertile spikes. This ability to recover presumably reflects the inherently high yield potential for which these commercial varieties had been selected and has been observed with deep sowing elsewhere (Alam, 2002). However, as with our study, increased tillering failed to fully compensate for fewer emerged plants.

The shorter coleoptiles of current *Rht-B1b* and *Rht-D1b* semidwarf varieties have been associated with reduced yield when sown deep. Reithmuller (1990) reported significant yield reductions when sowing depth exceeded 39 mm. The semidwarf, short coleoptile (length 64 mm) variety Kulin showed yield reductions of 13 kg ha⁻¹ mm⁻¹ while the tall, long coleoptile (length 102 mm) variety Gutha showed yield reduction of 7 kg ha⁻¹ mm⁻¹ for each increase in sowing depth below 39 mm. Numerous authors have reported that coleoptile length and reduced plant emergence are decreased by the presence of the *Rht-B1b* and *Rht-D1b* dwarfing genes (Fick and Qualset, 1976; Allan, 1989; Schillinger et al., 1998; Takeda and Takahashi, 1999; Ellis et al., 2004). Indeed, increasing the frequency of GA-insensitive dwarfing genes in the development of near-isogenic single- and double-dwarfs lines is linearly associated with reduced coleoptile length and seedling emergence with deep sowing (e.g. Allan, 1989; Takeda and Takahashi, 1999).

The GA-insensitive dwarfing genes decrease cell elongation to reduce leaf, subcrown internode and coleoptile size (Keyes et al., 1989; Hoogendoorn et al., 1990). The GA-responsive dwarfing genes, including *Rht8*, allow the benefits of decreased plant height (reduced lodging, increased harvest index and grain yield) whilst enabling selection for greater coleoptile length (e.g. Rebetzke and Richards, 2000). As for tall wheat, plant height and coleoptile length are uncorrelated in populations varying for the presence of *Rht8* (Rebetzke et al., 1999; Rebetzke and Richards, 2000). This was also true for this sowing depth study where the shortest *Rht8* wheat, HM10S, had one of the longest coleoptiles. Further, high single-plant and family-mean heritabilities (Rebetzke et al., 1999) and a preponder-

ance of additive gene action (Rebetzke et al., 2004) suggests it should be simple to select for increased coleoptile length in non-*rht*, tall or *Rht8*, semidwarf genetic backgrounds.

5. Conclusions

This study has demonstrated deep sowing reduces plant number and early vigour to reduce tiller and spike number, biomass and grain yield. Genotypically greater coleoptile length provides some opportunity for maintaining plant number and achieving high grain yields with deep sowing. Although there is limited scope in breeding of long coleoptile wheat in genetic backgrounds containing *Rht-B1b* and *Rht-D1b* dwarfing genes, GA-sensitive dwarfing genes such as *Rht8* offer the potential for selection of longer coleoptile, reduced height wheat for deep sowing. These novel dwarfing genes have had little use to date in commercial breeding programs but show agronomic promise in the development of high-yielding, reduced height wheat with long coleoptiles.

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