

# *Gibberellin-responsive and -insensitive dwarfing alleles on wheat performance in contrasting tillage systems*

Article

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1 Gibberellin-responsive and -insensitive dwarfing alleles on wheat  
2 performance in contrasting tillage systems

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7

8 ABSTRACT

9 Near-isogenic lines (NILs) of winter wheat varying for alleles for reduced height  
10 (*Rht*), gibberellin (GA) response and photoperiod insensitivity (*Ppd-D1a*) in cv. Mercia  
11 background (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*) and  
12 cv. Maris Widgeon (*rht* (tall), *Rht-D1b*, *Rht-B1c*) backgrounds were compared to  
13 investigate main effects and interactions with tillage (plough-based, minimum-, and  
14 zero-tillage) over two years. Both minimum- and zero- tillage were associated with  
15 reduced grain yields allied to reduced harvest index, biomass accumulation,  
16 interception of photosynthetically active radiation (PAR), and plant populations. Grain  
17 yields were optimized at mature crop heights of around 740mm because this provided  
18 the best compromise between harvest index which declined with height, and above  
19 ground biomass which increased with height. Improving biomass with height was due  
20 to improvements in both PAR interception and radiation-use efficiency. Optimum height  
21 for grain yield was unaffected by tillage system or GA-sensitivity. After accounting for  
22 effects of height, GA insensitivity was associated with increased grain yields due to  
23 increased grains per spike, which was more than enough to compensate for poorer  
24 plant establishment and lower mean grain weights compared to the GA-sensitive lines.

25 Although better establishment was possible with GA-sensitive lines, there was no  
26 evidence that this effect interacted with tillage method. We find, therefore, little  
27 evidence to question the current adoption of wheats with reduced sensitivity to GA in  
28 the UK, even as tillage intensity lessens.

29

30 Key words: zero tillage; minimum tillage; rht; gibberellin sensitivity; wheat

31

## 32 **1. Introduction**

33 Wheat dwarfing alleles conferring insensitivity to gibberellic acid (GA), *Rht-B1b* and  
34 *Rht-D1b*, have been widely adopted in wheat breeding programmes to reduce plant  
35 height and lodging, and increase harvest index and thereby grain yield (Chapman *et al.*,  
36 2007; Flintham *et al.*, 1997; Addisu *et al.*, 2010). These alleles, however, reduce  
37 coleoptile length and can also be associated with delayed emergence, smaller leaf areas,  
38 and slower accumulation of dry matter by seedlings (Botwright *et al.*, 2001; Botwright  
39 *et al.*, 2005; Rebetzke *et al.*, 2001; Addisu *et al.*, 2009). The negative effects on  
40 establishment and vigour are particularly pronounced when longer coleoptiles are  
41 required for seedlings to emerge from deep sowing to reach moist soil or when stubble  
42 load is high (Schillinger *et al.*, 1998; Rebetzke *et al.*, 2005).

43 A number of dwarfing alleles have been identified that retain response to  
44 endogenous gibberellin allowing selection for early vigour and coleoptile length  
45 (Rebetzke and Richards, 2000; Ellis *et al.*, 2004). The GA sensitive semi-dwarfing allele,  
46 *Rht8c* can confer grain yield and harvest indices similar to GA insensitive dwarfing  
47 alleles whilst retaining the coleoptile lengths and seedling vigor of taller lines (Rebetzke  
48 and Richards, 2000; Botwright *et al.*, 2005; Addisu *et al.*, 2009; 2010). *Rht8c* also has  
49 close linkage with a photoperiod-insensitive allele (*Ppd-D1a*) which reduces time to  
50 stem extension and flowering, and has also been associated with improved plant  
51 establishment rates in certain conditions (Addisu *et al.*, 2010).

52 Reduced tillage systems have long been used to improve productivity and  
53 sustainability of cropping systems and to reduce the time and cost required for crop  
54 establishment (Trethowan *et al.*, 2012). Despite the acknowledged benefits, reduced  
55 early growth is a common observation across soil types and environments (Kirkegaard  
56 *et al.*, 1994; Weisz and Bowman, 1999). Crop yields are often lower under zero tillage

57 during the initial years of transition from plough-based to reduced tillage systems due  
58 to increase in bulk density and soil strength, and reduced N availability (Ball *et al.*, 1989;  
59 Christian and Ball, 1994; Kirkegaard *et al.*, 1994; Alakukku *et al.*, 2009; Kankanen *et al.*,  
60 2011). It is suggested, therefore, that breeding cultivars to exploit or tolerate the  
61 specific conditions that might occur in the initial years after adoption of reduced tillage  
62 systems could be fruitful (O'Leary & Connor, 1997; Trethowan *et al.*, 2012).  
63 Experiments investigating tillage × genotype effects sometimes (Cox, 1991; Sip *et al.*,  
64 2009) but not always (Hall and Cholick, 1989; Trethowan *et al.*, 2012) find significant  
65 interactions. There is little information on the benefits, or otherwise, of different  
66 dwarfing alleles for reduced tillage systems, although some QTLs identified of value for  
67 zero tillage at some field sites may co-locate with alleles for crop height and coleoptile  
68 length (Trethowan *et al.*, 2012).

69 Here we investigate the tillage × GA response interaction using near-isogenic lines  
70 (NILs) in two wheat backgrounds (Mercia and Maris Widgeon) in an attempt to identify  
71 dwarfing alleles of particular worth to reduced tillage systems. We include three tillage  
72 systems; plough-based conventional- (CT); minimum- (MT); and zero- tillage (ZT) and a  
73 range of alleles that confer different effects on height with GA insensitivity (*Rht-B1b*,  
74 *Rht-D1b*, *Rht-B1c* and *Rht-D1c*) and GA sensitivity (*rht(tall)*, *Rht8c+Ppd-D1a* and *Rht12*).

75

## 76 **2. Materials and Methods**

### 77 2.1. Experimental site and crop husbandry

78 A two-year field experiment (2009/10 and 2010/11) was conducted on a free  
79 draining sandy loam (9% (by volume) clay, particle size <0.2µm; 19% silt, 2-20µm; 72%  
80 sand, 20-2000 µm; pH=6.6) overlying coarse red-brown sand, of the Sonning series  
81 (Jarvis, 1968) at the Crops Research Unit, Sonning, The University of Reading, UK (51°

82 29' N, 0° 56' W, 35m asl). The experiment followed a three year rye grass and chicory  
83 ley, destroyed by spraying 1.8kg/ha glyphosate and then sub soiled to 400mm at 1m  
84 spacing. Weather data were recorded at an automated metrological station at the site  
85 (Table 1). Soil was tested for pH, phosphorous, potassium and magnesium availability  
86 (Anon., 2000) and corrective nutrients applied as appropriate. Crop husbandry details  
87 are available in Table 2.

88

## 89 2.2. Design of Experiment

90 Tillage main plots (50×5m) were randomized in three blocks and divided into ten  
91 randomized sub-plots (2.5×10m) sown with different NILs at a rate of 300seeds/m<sup>2</sup> .  
92 Conventional tillage main plots were ploughed to 300mm and then power harrowed  
93 (Lely Roterra). For the minimum tillage plots there was no primary cultivation but a  
94 surface tilth (20-30mm) was achieved with a single shallow pass with the power  
95 harrow (Baker *et al.*, 1996).

96 Untreated seeds were drilled with a Hege 80 plot seed drill, mounted on a Hege 76  
97 tool carrier in 120mm rows in 1.9m x 10m sub-plots, separated by 0.5m double-width  
98 track wheelings, at a nominal depth of 50 mm for conventional, 30 mm in minimum-  
99 tilled, and roughly into coulter slots in the zero-tilled treatments. The NILs were derived  
100 by backcrossing into the comparatively short (mean 820mm at this site, Gooding *et al.*,  
101 2012) cv. Mercia (Talent/Virtue/Flanders, introduced in 1983) and the taller  
102 (1020mm) cv. Maris Widgeon (Holdfast/ Capelle Desprez, introduced in 1964). The  
103 Mercia NILs comprised: the parent line (*rht*, tall); gibberellin-insensitive semi-dwarf  
104 (*Rht-B1b*, *Rht-D1b* from 'Norin 10') and dwarf (*Rht-B1c* from 'Tom thumb'; *Rht-D1c* from  
105 'Ai-Bian') lines; and gibberellin-sensitive semi-dwarf (*Rht8c+Ppd-D1a* from 'Mara') and  
106 dwarf (*Rht12* from 'Karcagi 522') lines (Worland *et al.* 1994; Foulkes *et al.* 2004). The

107 Maris Widgeon NILs comprised *rht* (tall), *Rht-D1b*, and *Rht-B1c*.

108 Before sowing the experiment a second time, for the 2010/11 growing season, weeds  
109 in stubbles of all plots were controlled by spraying 2.1kg/ha glyphosate. Tillage  
110 methods and NILs were superimposed on the same locations as used in the preceding  
111 year.

112

### 113 2.3. Assessments

114 Soil mineral N and total N, S and C were measured in December, February and  
115 October each year by taking five 72mm diameter × 900mm depth cores per main plot.  
116 Cores were separated into 0-300, 300-600 and 600-900 mm horizons. For total N, C and  
117 S samples were dried at 80°C for 48h. After grinding, 0.10 to 0.20 g samples were  
118 oxidatively combusted and assessed for elemental content with LECO FP-528 and a  
119 LECO SC-144DR (LECO Instruments, UK). For mineral N, soil was shaken with 2M KCl to  
120 extract the mineral-N fractions and a dry matter determination carried out. Then  
121 nitrate-N and ammonium-N were measured colourimetrically by determining the  
122 formation of a diazo compound between nitrite and sulphanilamide. This compound  
123 was then coupled with N-1-Naphthylethylenediamine dihydrochloride to give a red azo  
124 dye and then colour was measured at 540nm (Patton and Crouch, 1977). Results were  
125 reported as mg/l in soil on a dry matter basis and then converted to kg mineral-N per  
126 hectare.

127 For bulk density five 72mm × 1000mm cores were taken from each main plot and  
128 separated into 100 mm depth horizons. Samples were dried at 80°C for 48h and  
129 weighed to derive bulk density as the mass of oven dried soil in a unit volume of the  
130 core.

131 Plant population was counted, and above ground crop biomass before the first node



132 was detectable was hand-harvested, in three randomly-placed 0.1 m<sup>2</sup> circular quadrats  
133 per sub-plot. At anthesis of the individual NILs (i.e. on different calendar days  
134 depending on NIL), the above ground crop was hand-harvested from rows both sides of  
135 a randomly-placed 0.5 m rule in three positions per sub-plot. The same sampling  
136 strategy was employed for hand-harvests at combine harvest maturity when samples  
137 were also portioned between grain and non-grain tissues to derive harvest index (HI).  
138 Above ground crop dry matter (AGDM) was determined after drying plants at 80°C for  
139 48h. Crop height was calculated as the average of three assessments per sub-plot made  
140 between anthesis and harvest maturity with a rising disc of polystyrene (Peel, 1987).

141 Interception of photosynthetically active radiation (PAR) was measured above and  
142 below (10mm above soil level) the canopy at three locations per subplot with a dual  
143 sensor ceptometer (AccuPAR LP-80 Decagon Devices Inc, Pullman, Washington) at  
144 approximately 14-day intervals from seedling emergence until interception started to  
145 decline with crop senescence. A logistic curve was fitted to the % interception x time  
146 curve for each plot to provide fitted daily estimates of % interception. These estimates  
147 were multiplied by the daily radiation recorded at an automatic weather station  
148 adjacent to the experiments. The products were summed to estimate the total radiation  
149 intercepted by each plot during the period of assessment.

150 The central 1.3m of each sub-plot was combine harvested for grain yield assessment.  
151 Grain moisture content was determined by drying a 20 g sample at 80°C for 48h  
152 allowing adjustment to dry matter basis. Mean grain weight was assessed by weighing a  
153 250 grain lot after dividing the sup-plot samples.

154

## 155 2.4. Statistical Analysis

156 Statistical analysis was with routines in GENSTAT 11. The analyses of variance

157 (ANOVA) comprised a block structure of Block / Tillage / Line / Year, i.e. as plots of the  
158 same treatment were superimposed on each other in the successive years Year was  
159 treated as a further split to the Line sub-plots within the Tillage main-plots. The  
160 treatment structure was Tillage \* Line \* Year. For the soil tests, there was insufficient  
161 precision when tillage treatments were included as individual levels. This weakness was  
162 partially rectified by contrasting With Inversion (CT) against Without Inversion  
163 (MT+ZT). To further test effects and interactions of GA-sensitivity, whilst also  
164 accounting for linear and quadratic effects of height, an analysis of Residual Maximum  
165 Likelihood (REML) was conducted where the fixed effects were Year \*Tillage  
166 \*(Height+Height<sup>2</sup>) \* GA sensitivity, and the random model was as for the ANOVA block  
167 structure. For presentation purposes the main effects of background (Mercia or Maris  
168 Widgeon) on the quadratic responses of variates to height have been removed by  
169 subtracting the background effects on the regression constant to rebase the constant to  
170 that of Mercia.

171

### 172 **3. Results**

173 The 2009/10 season was exceptionally wet in winter and then drier from stem  
174 elongation to the end of grain filling (April to July) (Table 1). In 2010/11 there was a  
175 particularly dry spring extending from stem elongation to ear emergence (March to  
176 May).

177

#### 178 **3.1. Effect of tillage on soil properties**

179 For the 2009/10 growing season total N, C, S and ammonium N at the time of sowing  
180 were not significantly affected by tillage system (Table 3). Total N was, however,  
181 significantly higher following conventional tillage because of the increase in nitrate N. In

182 February, all soil nutrients were similar in all tillage systems except that nitrate N was  
183 still lower in the reduced tillage systems. After harvest, total N was significantly higher  
184 in conventional tillage whereas other soil parameters did not differ among tillage  
185 systems.

186 For the 2010/11 growing season in February, total N and nitrate N were significantly  
187 higher in conventional tillage. After harvest, total N, C and S were not affected by tillage  
188 system.

189 Bulk density for the 0-300mm horizon was significantly higher in MT and ZT  
190 compared to CT in both seasons (Table 4). In 2010, soil bulk density was significantly  
191 higher in MT in the 300-600mm horizon whereas at the same depth in 2011, it was  
192 significantly higher in CT.

193

## 194 3.2. Crop Performance

### 195 3.2.1. Effects of height

196 Grain yields were optimized at heights around 740mm (Fig. 1a,b) because this provided  
197 the best compromise between harvest index, which declined with height (Fig. 1c,d), and  
198 above ground biomass which increased with height (Fig. 2c,e). Improving AGDM with  
199 height was due to improvements in both PAR interception (Fig. 2g) and RUE (Fig. 2i).

200 The quadratic grain yield response to height was mostly the result of effects on grains  
201 per spike (Fig. 3e), and hence also grains per unit area (Fig. 3c), rather than on mean  
202 grain weight which increased with height (Fig. 3a). There appeared no response to  
203 height for plant establishment (Fig. 3i), early biomass production (Fig. 2a) nor ears per  
204 plant (Fig. 3g).

205

### 206 3.2.2. Effects of GA response

207 After accounting for effects of height, GA insensitivity was associated with increased  
208 grain yields (Fig. 1a). This derived from increased grains per spike and per unit area  
209 (Fig. 3c,e), which was more than enough to compensate for poorer plant establishment  
210 (Fig. 3i) and lower mean grain weights (Fig. 3a) compared to the GA-sensitive lines. GA-  
211 insensitivity had little effect on AGDM at harvest (Fig. 2e) because benefits for PAR  
212 interception were countered by reduced RUE. Despite effects on plant establishment,  
213 there appeared little effect of GA-response on early biomass production (Fig. 2a), ears  
214 per plant (Fig. 3g) or harvest index (Fig. 1c).

215

### 216 3.2.3. Effects of tillage

217 Both minimum- and zero- tillage were associated with reduced grain yields (Fig. 1b),  
218 allied to reduced harvest index (Fig. 1d) and biomass accumulation (Fig. 2b,d,f).  
219 Reduced biomass accumulation was due to lower amounts of PAR intercepted (Fig. 2h)  
220 rather than effects on RUE (Fig. 2j). Poorer PAR interception resulted from the smaller  
221 plant populations in the reduced-tillage systems (Fig. 3j). Although there was some  
222 compensation for lower plant numbers with increased ears per plant, particularly for ZT  
223 (Fig. 3h), this was insufficient to maintain grain numbers per unit area at the level  
224 achieved in the plough-based system (Fig. 3d). There was no effect of tillage on grains  
225 per spike (Fig. 3f), or mean grain weight (Fig. 3b). There was no evidence of an  
226 interaction between tillage and GA response for any of the variates measured. There  
227 was an interaction between line and tillage for plant establishment (Fig. 3j) and also for  
228 AGDM at anthesis (Fig. 2d). With regards establishment there appeared some  
229 advantage for dwarfism in the ZT, although the opposite occurred under CT (Fig 3j). At  
230 anthesis there was no benefit of height for AGDM after ZT but there was an increase in  
231 AGDM with stature following both MT and ZT.

232

## 233 **4. Discussion**

### 234 4.1. Effect of tillage systems

235 The increased bulk density and lower concentrations of mineral N (principally nitrate) in  
236 the early years of adoption of reduced tillage systems is consistent with previous reports  
237 (Baumer and Kopke., 1989; Riley *et al.*, 1994; Munkholm *et al.*, 2003). These effects of  
238 reduced tillage may have contributed to poor plant establishment and early growth, but  
239 other explanations such as poor seed burial and associated exposure and predation, or  
240 increased disease pressures from surface trash are also potential additional causes (Davies  
241 and Finney, 2002; Siemens *et al.*, 2004; Mikkola *et al.*, 2005). Although poor establishment  
242 in the reduced tillage systems was partly countered by increased numbers of ears per plant,  
243 this was far from fully-compensatory with regards to PAR interception and hence biomass  
244 accumulation and yield. Kirkgaard *et al.* (1994) noted that while reduced early growth is a  
245 consistent effect of direct drilling or stubble retention, subsequent growth and yield will  
246 depend on seasonal conditions. In more humid conditions at this site (Gooding *et al.*, 2002)  
247 it is possible for yields not to be constrained by plant populations similar to those achieved  
248 here by MT. However, the dry springs recorded in the present experiments, particularly as  
249 they were coincident with poor uptake of large nitrogen top-dressings (Uppal, 2012), can  
250 be considered to have significantly limited the ability of the wheat to compensate for poor  
251 establishment after reduced tillage in these seasons. The reason why reduced tillage led to  
252 poorer harvest indices is less clear. It is possible that the sparse populations led to an  
253 increase in late, non-fertile tillers (Gooding *et al.*, 2002).

### 254 4.2. Effects of height

255 For plough-based systems, the benefits of stature for RUE, PAR interception, AGDM and  
256 mean grain weight up to heights of around 1m; and declines in harvest index, grains per  
257 spike and hence also grain yield as heights exceed about 800mm is consistent with previous  
258 experiments with these alleles at this site and elsewhere in the UK (Flintham *et al.*, 1997  
259 Addisu *et al.*, 2010; Gooding *et al.*, 2012). Except for plants per unit area, we find no  
260 evidence that tillage system alters the optimum height for grain yield and its components  
261 when stature is modified by major dwarfing alleles. The interaction between tillage system  
262 and a crop's ultimate height for plant establishment has not been reported previously. We  
263 confirm the penalty for severe dwarfism on plant establishment after plough-based tillage  
264 (Addisu *et al.* 2009), but also find this effect to disappear or reverse in the more challenging  
265 conditions of our MT and ZT systems. The basis for this interaction is unclear. It is possible  
266 that sowing depth is important, i.e. coleoptile length and seedling vigour were possibly less  
267 important in the shallower drilling for the reduced tillage systems.

#### 268 4.3. Effects of GA response

269 We confirm that GA insensitivity can be detrimental to crop establishment (Rebetzke *et*  
270 *al.* 2001; Addisu *et al.* 2009). In other studies this negative effect has been particularly  
271 evident in challenging conditions for establishment e.g.: when longer coleoptiles were  
272 required for deeper planting (Schillinger *et al.*, 1998; Botwright *et al.*, 2001; Rebetzke *et*  
273 *al.*, 2007); when stubble load was large (Rebetzke *et al.*, 2005); or when excessively  
274 warm seed beds compromised emergence (Bai *et al.*, 2004). In contrast, although our  
275 reduced tillage systems did challenge establishment, as evidenced by substantially  
276 reduced plant numbers in MT and ZT, we found no GA sensitivity x tillage interaction. It  
277 is possible that GA sensitivity is particularly beneficial for deep sowing and this was not  
278 a factor in our reduced tillage systems. Similarly, it might be supposed that the benefit

279 for GA sensitivity on plant establishment would have been more likely to lead to higher  
280 grain yields in a spring-sown crop (as in Rebetzke *et al.* 2007) where there was less  
281 time for compensatory ear production from GA-insensitive lines.

282 We confirm that dwarfing with GA-insensitivity can increase grain numbers per  
283 spike and reduce mean grain weight (Fintham *et al.*, 1997). What is more notable here,  
284 however, is that these effects persist even when the influence of height has been  
285 accounted for, i.e. it appears that there are beneficial effects of GA-insensitivity on grain  
286 numbers per spike that are not due to effects on ultimate height *per se*. This is  
287 somewhat at variance with the interpretation of Flintham *et al.* (1997) who argued that  
288 GA insensitivity from major *Rht* alleles was limited to below the collar node. Hence,  
289 effects on grain numbers (specifically, increased fertility of distal florets within  
290 spikelets) were purely a response to assimilate source : sink relations. Before rejecting  
291 this argument, however, some caution is required. In our experiments one of the GA-  
292 sensitive lines (Mercia *Rht8c*) is combined with *Ppd-D1a*, and Maris Widgeon *rht* (tall)  
293 could not be compared with a GA-insensitive line of comparable height.

294 In conclusion, we find no evidence that the optimal ultimate crop height, as  
295 modified by major dwarfing alleles, varies with the tillage systems used here. Although  
296 GA-insensitive alleles were associated with poorer establishment, and lower yields in  
297 the reduced tillage systems were linked to reduced plant populations, benefits of GA-  
298 sensitivity did not interact with establishment method and were insufficient to  
299 compensate for fewer grains per spike. We find, therefore, little evidence to question the  
300 current adoption of wheats with reduced sensitivity to GA in the UK, even as tillage  
301 intensity lessens.

302

303

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307

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417

418 **Figure Legends**

419

420 **Fig. 1.** Effect of final crop height, gibberellin (GA) sensitivity and tillage on the grain yield and  
421 harvest index of near-isogenic wheat lines varying for reduced height alleles. Panels on left compare  
422 GA-insensitive (●, solid line) and sensitive (○, dashed line) alleles averaged over tillage and year.  
423 Numerals 0, 1, 2, 3, 8, 10 and 12 in panel *a* correspond to *rht(tall)*, *Rht-B1b*, *Rht-D1b*, *Rht-B1c*,  
424 *Rht8c+Ppd-D1a*, *Rht-D1c*, and *Rht12* respectively; M=Mercia; W=Maris Widgeon. Alleles in other  
425 panels can be deduced as heights are the same. Panels on right compare lines in different tillage  
426 treatments (plough-based = ■, solid line; minimum tillage = □, dashed line; zero-tillage = +, dotted  
427 line), averaged over year, where only GA-sensitive alleles are labelled. Error bars are single standard  
428 error of difference (SED) for comparing lines (within Tillage on right); error degrees of freedom = 54.  
429 Effects of background (M or W) have been removed (see text for details); main and interacting effects  
430 of GA-sensitivity, Tillage, Linear Height and Quadratic Height only fitted if effect is statistically  
431 significant ( $P<0.05$ ).

432

433

434 **Fig. 2.** Effect of final crop height, gibberellin (GA) sensitivity and tillage on the accumulation of  
435 above ground biomass, interception of photosynthetically active radiation (PAR), and radiation use  
436 efficiency (RUE) of near-isogenic wheat lines varying for reduced height alleles. Panels on left  
437 compare GA-insensitive (●, solid line) and sensitive (○, dashed line) alleles averaged over tillage and  
438 year. Numerals 0, 1, 2, 3, 8, 10 and 12 in panel *a* correspond to *rht(tall)*, *Rht-B1b*, *Rht-D1b*, *Rht-B1c*,  
439 *Rht8c+Ppd-D1a*, *Rht-D1c*, and *Rht12* respectively; M=Mercia; W=Maris Widgeon. Alleles in other  
440 panels can be deduced as heights are the same. Panels on right compare lines in different tillage  
441 treatments (plough-based = ■, solid line; minimum tillage = □, dashed line; zero-tillage = +, dotted  
442 line), averaged over year, where only GA-sensitive alleles are labelled. Error bars are single standard  
443 error of difference (SED) for comparing lines (within Tillage on right); error degrees of freedom = 54.  
444 Effects of background (M or W) have been removed (see text for details); main and interacting effects

445 of GA-sensitivity, Tillage, Linear height and Quadratic height only fitted if effect is statistically  
446 significant ( $P < 0.05$ ).

447

448 **Fig. 3.** Effect of final crop height, gibberellin (GA) sensitivity and tillage on the yield components of  
449 near-isogenic wheat lines varying for reduced height alleles. Panels on left compare GA-insensitive  
450 (●, solid line) and sensitive (○, dashed line) alleles averaged over tillage and year. Numerals 0, 1, 2, 3,  
451 8, 10 and 12 in panel *a* correspond to *rht(tall)*, *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-*  
452 *D1c*, and *Rht12* respectively; M=Mercia; W=Maris Widgeon. Alleles in other panels can be deduced  
453 as heights are the same. Panels on right compare lines in different tillage treatments (plough-based =  
454 ■, solid line; minimum tillage = □, dashed line; zero-tillage = +, dotted line), averaged over year,  
455 where only GA-sensitive alleles are labelled. Error bars are single standard error of difference (SED)  
456 for comparing lines (within Tillage on right); error degrees of freedom = 54. Effects of background  
457 (M or W) have been removed (see text for details); main and interacting effects of GA-sensitivity,  
458 Tillage, Linear height and Quadratic height only fitted if effect is statistically significant ( $P < 0.05$ ).

459

460

1 **Table 1**

2 Monthly weather data during crop growing seasons and mean (41 years for temperature and 51 years for  
3 rainfall) at the Crop Research Unit, Sonning, The University of Reading, UK.

	Temperature (°C)			Rainfall (mm)		
	2009/10	2010/11	Mean	2009/10	2010/11	Mean
Sep	14.4	13.5	14.2	17.0	48.4	55.0
Oct	9.7	10.4	10.8	43.4	60.4	66.1
Nov	10.8	5.4	7.1	145.3	39.8	65.4
Dec	2.9	0.2	4.9	104.4	23.4	62.9
Jan	1.4	3.9	4.4	67.6	83.6	59.2
Feb	3.6	6.5	4.5	61.0	51.2	41.4
Mar	6.3	6.5	6.5	46.2	13.8	48.2
Apr	9.2	12.2	8.7	22.0	2.8	47.4
May	11.2	12.3	12.1	12.0	30.0	49.3
Jun	16.1	14.2	15.1	20.8	89.8	47.9
Jul	18.4	15.7	17.3	31.6	40.0	47.4
Aug	16.1	15.9	16.9	108.0	125.2	57.3

4

5 **Table 2**

6 Husbandry applied during the two growing seasons of the experiment

Treatment	Growth Stage (Zadoks <i>et al.</i> , 1974)	2009/10	2010/11
Herbicide	Pre-drilling	Glyphosate 1.8kg/ha (twice)	Glyphosate 2.1kg/ha
Fertilizer	Pre-drilling	120 Kg K <sub>2</sub> O/ha	-
Herbicide	Pre-drilling	Glyphosate 1.4kg/ha	Glyphosate 0.5kg/ha
Drilling		06.11.2009	10.11.2010
Fertilizer	30-31	100kg N/ha + 40kg S/ha	100kg N/ha + 40kg S/ha
Fungicide	30-31	Epoxiconazole 125g/ha + Quinoxifen 150g/ha + Chlorothalonil 1kg/ha	Epoxiconazole 125g/ha + Chlorothalonil 1 Kg/ha + Metrafenon 150 g/ha
Herbicide	31-32	Metsulfuron methyl 5g/ha + Thifensulfuron methyl 50g/ha	Metsulfuron methyl 5g/ha + Thifensulfuron methyl 50g/ha
Fertilizer	34-39	100kg N/ha	100kg N/ha
Fungicide	39	Epoxiconazole 125g/ha + Azoxystrobin 250g/ha	Epoxiconazole 125g/ha + Azoxystrobin 250g/ha
Fungicide	59	Tebuconazole 250g/ha + Deltamethrin 5g/ha	Tebuconazole 250g/ha
Herbicide	Pre-harvest	-	Glyphosate 1.4kg/ha
Harvested		16.08.2010	22.08.2011

7

8



9 **Table 3**

10 Effect of different tillage systems on soil nutrients

	Total N (mg/kg)	Total C (mg/kg)	Total S (mg/kg)	Available N (kg/ha)	Ammonium N (mg/kg)	Nitrate N (mg/kg)
November 2009						
Zero + Min- tillage	0.58	7.88	0.16	34.6	0.58	2.3
Conventional tillage	0.75	6.45	0.12	49.3	0.61	3.5
<i>P</i>	0.083	0.203	0.379	0.047	0.389	0.050
SED	0.078	0.974	0.047	5.62	0.034	0.47
February 2010						
Zero + Min- tillage	0.68	8.53	0.14	32.5	1.94	0.78
Conventional tillage	0.70	8.34	0.17	33.8	1.55	1.26
<i>P</i>	0.146	0.876	0.263	0.818	0.369	0.064
SED	0.013	1.133	0.021	5.37	0.389	0.206
October 2010						
Zero + Min- tillage	0.88	7.10	0.12	57.3	0.49	4.29
Conventional tillage	0.94	7.37	0.11	61.2	0.56	4.54
<i>P</i>	<0.001	0.637	0.680	0.415	0.489	0.546
SED	0.004	0.531	0.007	4.4	0.098	0.394
February 2011						
Zero + Min- tillage	0.96	7.09	0.14	28.3	0.85	1.52
Conventional tillage	1.08	7.41	0.13	36.8	0.84	2.22
<i>P</i>	0.025	0.693	0.695	0.102	0.886	0.065
SED	0.039	0.767	0.025	4.19	0.067	0.30
October 2011						
Zero + Min- tillage	0.85	7.07	0.011			
Conventional tillage	0.85	6.70	0.012			
<i>P</i>	0.932	0.563	0.526			
SED	0.027	0.602	0.020			

11

12 **Table 4**  
 13 Effect of different tillage systems on soil bulk density in two soil horizons

Tillage	2010		2011	
	0-300	300-600	0-300	300-600
Plough-based	1.49	1.60	1.49	1.73
Minimum	1.57	1.65	1.58	1.65
Zero	1.58	1.61	1.60	1.67
<i>P</i>	0.006	0.027	0.002	0.045
SED	0.014	0.011	0.012	0.022

14





