

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

Article

Accepted Version

Uppal, R.K. and Gooding, M.J. (2013) Gibberellin-responsive and -insensitive dwarfing alleles on wheat performance in contrasting tillage systems. *Field Crops Research*, 141. pp. 55-62. ISSN 0378-4290 doi: 10.1016/j.fcr.2012.11.001 Available at <https://centaur.reading.ac.uk/29734/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1016/j.fcr.2012.11.001>

Publisher: Elsevier

All outputs in CentAUR are protected by Intellectual Property Rights law, including copyright law. Copyright and IPR is retained by the creators or other copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

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

R.K. Uppal, M.J. Gooding

School of Agriculture, Policy and Development, University of Reading, Earley Gate, P.O. Box 237, Reading, RG6 6AR, UK

ABSTRACT

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

1. Introduction

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

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

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

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

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

2. Materials and Methods

2.1. Experimental site and crop husbandry

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

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

2.2. Design of Experiment

Tillage main plots (50×5m) were randomized in three blocks and divided into ten randomized sub-plots (2.5×10m) sown with different NILs at a rate of 300seeds/m². Conventional tillage main plots were ploughed to 300mm and then power harrowed (Lely Roterra). For the minimum tillage plots there was no primary cultivation but a surface tilth (20-30mm) was achieved with a single shallow pass with the power harrow (Baker *et al.*, 1996).

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

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

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

2.3. Assessments

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

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

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

was detectable was hand-harvested, in three randomly-placed 0.1 m² circular quadrats per sub-plot. At anthesis of the individual NILs (i.e. on different calendar days depending on NIL), the above ground crop was hand-harvested from rows both sides of a randomly-placed 0.5 m rule in three positions per sub-plot. The same sampling strategy was employed for hand-harvests at combine harvest maturity when samples were also portioned between grain and non-grain tissues to derive harvest index (HI). Above ground crop dry matter (AGDM) was determined after drying plants at 80°C for 48h. Crop height was calculated as the average of three assessments per sub-plot made between anthesis and harvest maturity with a rising disc of polystyrene (Peel, 1987).

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

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

2.4. Statistical Analysis

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

(ANOVA) comprised a block structure of Block / Tillage / Line / Year, i.e. as plots of the same treatment were superimposed on each other in the successive years Year was treated as a further split to the Line sub-plots within the Tillage main-plots. The treatment structure was Tillage * Line * Year. For the soil tests, there was insufficient precision when tillage treatments were included as individual levels. This weakness was partially rectified by contrasting With Inversion (CT) against Without Inversion (MT+ZT). To further test effects and interactions of GA-sensitivity, whilst also accounting for linear and quadratic effects of height, an analysis of Residual Maximum Likelihood (REML) was conducted where the fixed effects were Year *Tillage *(Height+Height²) * GA sensitivity, and the random model was as for the ANOVA block structure. For presentation purposes the main effects of background (Mercia or Maris Widgeon) on the quadratic responses of variates to height have been removed by subtracting the background effects on the regression constant to rebase the constant to that of Mercia.

3. Results

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

3.1. Effect of tillage on soil properties

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

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

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

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

3.2. Crop Performance

3.2.1. Effects of height

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

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

3.2.2. Effects of GA response

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

3.2.3. Effects of tillage

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

4. Discussion

4.1. Effect of tillage systems

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

4.2. Effects of height

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

4.3. Effects of GA response

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

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

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

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

Acknowledgements

The authors are grateful to Mr Richard Casebow for technical assistance and Professor John Snape, John Innes Centre for supply of the near-isogenic lines.

References

- Addisu, M., Snape, J.W., Simmonds, J.R., Gooding, M.J., 2009. Reduced height (*Rht*) and photoperiod insensitivity (*Ppd*) allele associations with establishment and early growth of wheat in contrasting production systems. *Euphytica* 166, 249-263.
- Addisu, M., Snape, J.W., Simmonds, J.R., Gooding, M.J., 2010. Effects of reduced height (*Rht*) and photoperiod insensitivity (*Ppd*) alleles on yield of wheat in contrasting production systems. *Euphytica* 172, 169-181.
- Alakukku, L., Ristolainen, A., Salo, T., 2009. Grain yield and nutrient balance of spring cereals in different tillage systems. In: Sustainable Agriculture; Proceedings of ISTRO 18th triennial conference, Izmir, Turkey.
- Anon., 2000. Fertiliser recommendations for agricultural and horticultural crops. MAFF reference book 209, 7th edn. HMSO, London
- Bai, G.H., Das, M.K., Carver, B.F., Xu, X.Y., Krenzer, E.G., 2004. Covariation for microsatellite marker alleles associated with *Rht8* and coleoptile length in winter wheat. *Crop Sci.* 44, 1187-1194.
- Ball, B.C., Lang, R.W., O'Sullivan, M.F., Franklin, M.F., 1989. Cultivation and nitrogen requirements for continuous winter barley on a geysol and a cambisol. *Soil Till. Res.* 13, 333-352.
- Baker, C.J., Saxton, K.E., Ritchie, W. R. 1996. No-tillage Seeding : Science and Practice. CAB International, Wallingford, 258 pp.

328 Baumer, K., Kopke, U., 1989. Effects of nitrogen fertilization. In: Baumer, K., Ehlers, W.
329 (Eds.), Agriculture. Energy Saving by Reduced Soil Tillage. Commission of the
330 European Communities, Report EUR 11258, pp. 145–162.

331 Botwright, T., Rebetzke, G.J., Condon, A.G., Richards, R.A., 2001. The effect of *rht* genotype
332 and temperature on coleoptile growth and dry matter partitioning in young wheat
333 seedlings. *Austral. J. Plant Physiol.* 28, 417–423.

334 Botwright, T., Rebetzke, G.J., Condon, A.G., Richards, R.A., 2005. Influence of gibberellin-
335 sensitive *Rht8* dwarfing gene on leaf epidermal cell dimensions and early vigour in
336 wheat (*Triticum aestivum* L.). *Ann. Bot.* 95, 631-639.

337 Chapman, S.C., Mathews, K.L., Trethowan, R.M., Singh, R.P., 2007. Relationships between
338 height and yield in near-isogenic spring wheats that contrast for major reduced height
339 genes. *Euphytica* 157, 391-397.

340 Christian, D.G., Ball, B.C., 1994. Reduced cultivation and direct drilling for cereals in Great
341 Britain. In: Carter, M.R. (Ed.), Conservation tillage in Temperate Agroecosystems.
342 Lweis Publ., Boca Raton, FL., USA, pp. 117-140.

343 Cox, D.J., 1991. Performance of hard red winter wheat cultivars under conventional-till and
344 no-till systems. *North Dakota Farm Research* 48, 17-20.

345 Davies, B., Finney, B., 2002. Reduced Cultivations for Cereals: Research Development and
346 Advisory Needs under Changing Economic Circumstances. Home Grown Cereals
347 Authority, London (Research Review No. 48)

348 Ellis, M.H., Rebetzke, G.J., Cahndler, P., Bonnett, D., Spielmeyer, W., Richards, R.A., 2004. The
349 effect of different height reducing genes on the early growth of wheat. *Funct. Plant*
350 *Biol.* 31, 583–589.

351 Flintham, J.E., Borner, A.B., Worland, A.J., Gale, M.D., 1997. Optimizing wheat grain yield :
352 effects of *Rht* (gibberellin-insensitive) dwarfing genes. *J. Agric. Sci.* 128, 11-25.

353 Foulkes, M.J., Sylvester-Bradley, R., Worland, A.J., Snape, J.W., 2004. Effects of a
 354 photoperiod–response gene *Ppd-D1* on yield potential and drought resistance in UK
 355 winter wheat. *Euphytica* 135, 63–73.

356 Gooding, M.J., Pinyosinwat, A., Ellis, R.H., 2002. Responses of wheat grain yield and quality
 357 to seed rate. *J. Agric. Sci.* 138, 317-331.

358 Gooding, M.J., Addisu, M., Uppal, R.K., Snape, J.W., Jones, H.E., 2012. Effect of wheat dwarfing
 359 genes on nitrogen use efficiency. *J. Agric. Sci.* 150, 3-22.

360 Hall, E.F., Cholick, F.A., 1989. Cultivar × tillage interaction of hard red spring wheat
 361 cultivars. *Agron. J.* 81, 789-792.

362 Jarvis, R.A., 1968. Soils of the Reading District. Rothamsted Experimental Station,
 363 Harpenden, UK.

364 Kankanen, H., Alakukku, L., Salo, Y., Pitkanen, T., 2011. Growth and yield of different spring
 365 cereal species in zero tillage, compared to conventional tillage. *Eur. J. Agron.* 34, 35-
 366 45.

367 Kirkegaard, J.A., Angus, J.F., Gardner, P.A., Miiller, W., 1994. Reduced growth and yield of
 368 wheat with conservation cropping. I. Field studies in the first year of the cropping
 369 phase. *Austral. J. Agric. Res.* 45, 511-528.

370 Mikkola, H.J., Alakukku, L., Kankanen, H., Jalli, H., Lindroos, M., Huusela-Veistola, E.,
 371 Nuutinen, V., Latti, M., Puustinen, M., Turtola, E., Myllys, M., Regina, K., 2005. Direct
 372 drilling in Finland, a review. In: *Proc. 4th Intern. Scientific and Practical Conference,*
 373 *Ecology and Agricultural Machinery, May 25-26, 2005, St Petersburg, Vol. 2, pp, 141-*
 374 *151*

375 Munkholm, L.J., Schjonning, P., Rasmussen, K.J., Tanderup, K. 2003. Spatial and temporal
 376 effects of direct drilling on soil structure in the seeding environment. *Soil tillage Res.*
 377 71, 163-173.

378 O'Leary, G.J., Connor, D.J., 1997. Stubble retention and tillage in a semi-arid environment: 3.
379 Response of wheat. Field Crop Res. 54, 39-50.

380 Patton, C.J., Crouch, S.R., 1977. Spectrophotometric and kinetics investigation of berthelot
381 reaction for determination of ammonia. Anal. Chem. 49, 464-469.

382 Peel, C.H., 1987. Technical note. A rising disc apparatus for the measurement of turfgrass
383 sward heights. J. Sports Turf Res. Inst. 63, 116-135.

384 Rebetzke, G.J., Richards, R.A., 2000. Gibberellic acid-sensitive dwarfing genes reduce plant
385 height to increase seed number and grain yield of wheat. Austral. J. Agric. Res. 51,
386 235-245.

387 Rebetzke, G.J., Appels, R., Morrison, A.D., Richards, R.A., McDonald, G., Ellis, M.H.,
388 Spielmeyer, W., Bonneti, D.G., 2001. Quantitative trait loci on chromosome 4B for
389 coleoptile length and early vigour in wheat (*Triticum aestivum* L.). Austral. J. Agric.
390 Res. 52, 1221-1234.

391 Rebetzke, G.J., Bruce, S.E., Kirkegaard, J.A., 2005. Longer coleoptiles improve emergence
392 through crop residues to increase seedling number and biomass in wheat (*Triticum*
393 *aestivum* L.). Plant Soil 272, 87-100.

394 Rebetzke, G.J., Ellis, M.H., Bonnett, D.G., Richards, R.A., 2007. Molecular mapping of genes for
395 coleoptile growth in bread wheat (*Triticum aestivum* L.). Theor. Appl. Genet. 114,
396 1173-1183.

397 Riley, H., Borrenson, T., Ekeberg, E., Rydberg, T. 1994. Trends in reduced tillage research
398 and practice in Scandinavia. In: Carter, M.R. (Eds.) Conservation Tillage in Temperate
399 Agroecosystems. Lewis Publishers, Boca Raton, Florida, USA, pp, 23-45.

400 Schillinger, W.F., Donaldson, E., Allan, R.E., Jones, S.S., 1998. Winter wheat seedling
401 emergence from deep sowing depths. Agron. J. 90, 582-586.

402 Siemens, M.C., Wilkins, D.E., Correa, R.F. 2004. Development and evaluation of a residue

403 management wheel for hoe-type no-till drills. Trans of Am Soc Agric Eng. 47, 397-404.

404 Sip, V., Ruzek, P., Chrpova, J., Vavera, R., Kusa, H., 2009. The effect of tillage practice, input
 405 level and environment on the grain yield of winter wheat in the Czech Republic. Field
 406 Crop Res. 113, 131-137.

407 Trethowan, R.M., Mahmood, T., Ali, Z., Oidach, K., Garcia, A.G., 2012. Breeding wheat
 408 cultivars better adapted to conservation agriculture. Field Crop. Res. 132, 76–83.

409 Uppal, R. 2012. Effect of wheat dwarfing alleles on physiology of yield and nitrogen use
 410 efficiency in contrasting tillage systems. PhD Thesis, University of Reading

411 Weisz, R., Bowman, D.T., 1999. Influence of tillage system on soft red winter wheat cultivar
 412 selection. J. Production Agric. 12, 415-418.

413 Worland, A.J., Sayers, E.J., Borner, A., 1994. The genetics and breeding potential of *Rht12*, a
 414 dominant dwarfing gene in wheat. Plant Breed. 113, 187–196.

415 Zadoks, J.C., Chang, T.T., Konzak, C.F., 1974. A decimal code for the growth stages of cereals.
 416 Weed Res. 44, 415–421.

417

Figure Legends

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

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

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

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

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 ₂ 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			

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
Depth (mm)				
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





