



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

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## ARTICLE INFO

### Article history:

Received 9 August 2012

Received in revised form 1 November 2012

Accepted 2 November 2012

### Keywords:

Zero tillage  
Minimum tillage  
Rht  
Gibberellin sensitivity  
Wheat

## 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 740 mm 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. Although better establishment was possible with GA-sensitive lines, there was no evidence that this effect interacted with tillage method. 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.

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## 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, 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 vigour 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.

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**Table 1**  
Monthly weather data during crop growing seasons and mean (41 years for temperature and 51 years for 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
September	14.4	13.5	14.2	17.0	48.4	55.0
October	9.7	10.4	10.8	43.4	60.4	66.1
November	10.8	5.4	7.1	145.3	39.8	65.4
December	2.9	0.2	4.9	104.4	23.4	62.9
January	1.4	3.9	4.4	67.6	83.6	59.2
February	3.6	6.5	4.5	61.0	51.2	41.4
March	6.3	6.5	6.5	46.2	13.8	48.2
April	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
June	16.1	14.2	15.1	20.8	89.8	47.9
July	18.4	15.7	17.3	31.6	40.0	47.4
August	16.1	15.9	16.9	108.0	125.2	57.3

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  $\times$  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 < 0.2  $\mu$ m; 19% silt, 2–20  $\mu$ m; 72% sand, 20–2000  $\mu$ m; 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, 35 m asl). The experiment followed a three year rye grass and chicory ley, destroyed by spraying 1.8 kg/ha glyphosate and then sub soiled to 400 mm 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 m  $\times$  5 m) were randomized in three blocks and divided into ten randomized sub-plots (2.5 m  $\times$  10 m) sown with different NILs at a rate of 300 seeds/m<sup>2</sup>. Conventional tillage main plots were ploughed to 300 mm and then power harrowed (Lely Roterra). For the minimum tillage plots there was no primary cultivation but a surface tilth (20–30 mm) 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 120 mm rows in 1.9 m  $\times$  10 m sub-plots, separated by 0.5 m double-width track wheelings, at a nominal depth of 50 mm for conventional, 30 mm in minimum-tilled, and roughly into coulters slots in the zero-tilled treatments. The NILs were derived by backcrossing into the comparatively short (mean 820 mm at this site, Gooding et al., 2012) cv. Mercia (Talent/Virtue/Flanders, introduced in 1983) and the taller (1020 mm)

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 2.1 kg/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 72 mm diameter  $\times$  900 mm 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 48 h. After grinding, 0.10–0.20 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 2 M 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 540 nm (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 72 mm  $\times$  1000 mm cores were taken from each main plot and separated into 100 mm depth horizons. Samples were dried at 80 °C for 48 h 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 m<sup>2</sup> 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 48 h. 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 (10 mm 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  $\times$  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 1.3 m 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 48 h allowing adjustment to dry matter basis. Mean grain weight was assessed by weighing a 250 grain lot after dividing the sup-plot samples.

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