

Effects of reduced height (*Rht*) and photoperiod insensitivity (*Ppd*) alleles on yield of wheat in contrasting production systems

M. Addisu · J. W. Snape · J. R. Simmonds ·
M. J. Gooding

Received: 2 April 2009 / Accepted: 19 August 2009 / Published online: 21 September 2009
© Springer Science+Business Media B.V. 2009

Abstract Near isogenic lines (NILs) varying for reduced height (*Rht*) and photoperiod insensitivity (*Ppd-D1*) alleles in a cv. Mercia background (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*) were compared for interception of photosynthetically active radiation (PAR), radiation use efficiency (RUE), above-ground biomass (AGB), harvest index (HI), height, weed prevalence, lodging and grain yield, at one field site but within contrasting ('organic' vs. 'conventional') rotational and agronomic contexts, in each of 3 years. In the final year, further NILs (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht-B1b+Rht-D1b*, *Rht-D1b+Rht-B1c*) in Maris Huntsman and Maris Widgeon backgrounds were added together with 64 lines of a doubled haploid (DH) population [Savannah (*Rht-D1b*) × Renesansa (*Rht-8c+Ppd-D1a*)]. There were highly significant genotype × system interactions for grain yield, mostly because differences were greater in the conventional system than in the organic system. Quadratic fits of NIL grain yield against height were

appropriate for both systems when all NILs and years were included. Extreme dwarfing was associated with reduced PAR, RUE, AGB, HI, and increased weed prevalence. Intermediate dwarfing was often associated with improved HI in the conventional system, but not in the organic system. Heights in excess of the optimum for yield were associated particularly with reduced HI and, in the conventional system, lodging. There was no statistical evidence that optimum height for grain yield varied with system although fits peaked at 85 and 96 cm in the conventional and organic systems, respectively. Amongst the DH lines, the marker for *Ppd-D1a* was associated with earlier flowering, and just in the conventional system also with reduced PAR, AGB and grain yield. The marker for *Rht-D1b* was associated with reduced height, and again just in the conventional system, with increased HI and grain yield. The marker for *Rht8c* reduced height, and in the conventional system only, increased HI. When using the System × DH line means as observations grain yield was associated with height and early vegetative growth in the organic system, but not in the conventional system. In the conventional system, PAR interception after anthesis correlated with yield. Savannah was the highest yielding line in the conventional system, producing significantly more grain than several lines that out yielded it in the organic system.

M. Addisu · M. J. Gooding (✉)
Crops Research Unit, Department of Agriculture,
The University of Reading, Earley Gate, P.O. Box 237,
Reading RG6 6AR, UK
e-mail: m.j.gooding@reading.ac.uk

J. W. Snape · J. R. Simmonds
Crop Genetics Department, John Innes Centre, Colney
Lane, Norwich NR4 7UH, Norfolk, UK

Keywords *Rht1* · *Rht2* · *Rht3* · *Rht8* ·
Rht10 · *Rht12* · *Ppd-D1a* · Organic agriculture ·

Radiation use efficiency · Harvest index ·
Yield components

Abbreviations

AGB	Above ground biomass
DH	Doubled haploid
DM	Dry matter
FR:R	Far red: red reflectance ratio
GS	Growth Stage
N	Nitrogen
NIL	Near isogenic line
PAR	Photosynthetically active radiation
REML	Residual maximum likelihood
RUE	Radiation use efficiency

Introduction

Flintham et al. (1997) related the effects of alleles conferring insensitivity to gibberellic acid (GA) on wheat yield to their stem shortening ability. For example, grain yields at excessive crop heights can be reduced because of poor harvest indices (Flintham et al. 1997) and/or increased lodging (Berry et al. 2004). Conversely, poor yields associated with severe dwarfism have been ascribed to poorer biomass accumulation; a consequence of reduced light interception and/or reduced radiation use efficiency (Austin 1999). Flintham et al. (1997) identified a target height range for maximising yield, and demonstrated that effects of reduced height alleles (*Rht*) on grain yield of near isogenic lines (NILs) depended on the stature of their tall (*rht*) backgrounds at particular locations. Thus, the ‘Green Revolution’ genes, *Rht-B1b* and *Rht-D1b*, were most beneficial in comparatively tall backgrounds, and in environments conducive to tall stature (Richards 1992; Flintham et al. 1997; Chapman et al. 2007).

The plots studied by Flintham et al. (1997) received fertilizer and fungicide programmes according to local commercial practice. There is uncertainty as to whether dwarfing genes are as relevant to other production methods, such as in organic systems, where the use of synthetic inputs is curtailed or reduced. Frequent nitrogen deficiency in such systems (Berry et al. 2002) could reduce the risk of lodging, and hence one of the penalties of height. Shortening with

dwarfing genes can favour certain diseases (Simon et al. 2004; Srinivasachary et al. 2008), and reduce competitive ability or tolerance against weeds (Zerner et al. 2008), that might otherwise be controlled with agrochemicals in intensive systems (Austin 1999). Early crop vigour has been identified as particularly useful in organic contexts (Wolfe et al. 2008) and we have already shown that several dwarfing genes can reduce early season growth in such systems (Addisu et al. 2009). Nonetheless, Cosser et al. (1997) did find that near isogenic lines containing *Rht-B1b* and/or *Rht-D1b* increased harvest index and grain yield in an organic system, when compared with a particularly tall background in one season.

Here we describe experiments that used both near-isogenic lines and a doubled haploid population, to determine whether the optimum height of a wheat crop varied between two contrasting production systems (intensive ‘conventional’ vs. ‘organic’) on a single site. To investigate the yield response surface to height we included GA-insensitive alleles conferring both semi- (*Rht-B1b*, *Rht-D1b*), and severe dwarfism (*Rht-B1c*, *Rht-D1c*) in backgrounds that vary in stature. We also included alleles conferring semi- [*Rht8c*, *Ppd-D1a*; Worland et al. (1998)] and severe [*Rht12*; Worland et al. (1994)] dwarfism without greatly affecting GA-sensitivity. *Ppd-D1a* reduces height through conferring photoperiod insensitivity and hence time to jointing in short days. This more rapid development has already been associated with improved early season resource capture, and hence potential benefits for use in organic agriculture (Addisu et al. 2009).

Materials and methods

Field experiments were conducted on a free-draining sandy loam overlying coarse red-brown sand of the Sonning series (Jarvis 1968), in each of three growing seasons (2005/2006, 2006/2007 and 2007/2008) at the Crops Research Unit, Sonning, University of Reading, UK (51°29′N, 0°56′W). Weather data (Table 1) were recorded at an automated weather station at the site. Land had been managed conventionally with robust programmes of synthetic fertilizer and agrochemicals (Table 2), or organically since 2001. Untreated seeds were drilled at a nominal depth of 50 mm, on 120 mm rows in 2 m wide plots

Table 1 Monthly weather data and 45 year means at the experimental site

Months	Rainfall (mm)				Mean temperature (°C)			
	2005/2006	2006/2007	2007/2008	Mean	2005/2006	2006/2007	2007/2008	Mean
September	37.4	50.4	40.1	57.4	15.4	17.3	14.5	14.1
October	56.0	123.6	35.1	66.3	13.4	13.2	11.2	10.7
November	31.9	107.4	68.8	63.6	5.9	7.9	7.7	7.1
December	52.0	82.6	45.6	63.7	4.0	6.7	5.4	5.1
January	13.9	65.8	86.4	59.3	4.4	7.1	6.4	4.3
February	47.2	82.8	19.6	39.9	3.9	6.1	5.4	4.5
March	45.6	44.4	82.6	48.0	5.3	7.1	6.5	6.5
April	25.7	1.8	59.0	49.5	9.1	11.4	8.1	8.6
May	79.7	92.2	66.4	49.1	12.6	12.4	13.7	12.0
June	11.1	93.7	49.4	49.0	16.4	16.1	14.9	15.0
July	32.0	115.6	77.6	45.0	20.6	16.3	16.5	17.2
August	36.2	40.5	74.6	57.6	16.8	16.3	16.8	17.0

separated by 0.5 m double-width track wheelings. A plan and rotational history of the site, together with more detailed descriptions of establishment methods, cultivars, markers and seed quality is given in Addisu et al. (2009).

In each of the 3 years seven near isogenic lines (NILs) with a cv. Mercia background (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*) were sown in 10 m (2005 and 2006) and 7.5 m (2007) long plots, randomized in four (2005, 2006) or three (2007) blocks, on both the organic and conventional areas on the same date, at 300 seeds/m² (2005 and 2006), and 250 seeds/m² (2007). In the final year, further NILs (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht-B1b+Rht-D1b*, *Rht-D1b+Rht-B1c*) in both Maris Huntsman and Maris Widgeon backgrounds were added.

In 2007, a further experiment involved 62 lines, varying in height, selected from a recombinant doubled haploid (DH) population of Savannah × Renesansa. Savannah carried the *Rht1-D1b* allele while Renesansa carried *Rht8c* and *Ppd-D1a* but not *Rht1-D1b*. Together with the parents the 64 lines were sown in an 8 × 8 row + column design for two replicates on both the conventional (7.5 m plots) and organic areas (5 m plots) at 300 seeds/m².

Assessments

Throughout growth in the conventional plots, the proportionate interception of photosynthetically

active radiation (PAR) was derived from ceptometer (AccuPAR LP-80; Decagon Devices Inc, Pullman, Washington) readings above and beneath (10 mm above soil level) the canopy (Addisu et al. 2009). This data set was combined with that for daily radiation receipts, to derive total PAR interception over the life of the crop (Kindred and Gooding 2005). To determine the end of canopy photosynthetic function, the red (660 nm): far red (730 nm) reflectance ratio was recorded with sensors (SKR 1800, Skye Instruments Ltd, Llandrindod Wells, UK) above the canopy from anthesis onwards. The ratio achieved above the canopy was expressed as a percentage of that recorded for bare ground at the same time. ‘Green cover’ was determined by first subtracting this percentage from 100, and then for each plot expressing green cover as a percentage of the maximum for the particular plot from anthesis onwards. This final step was necessary to account for differences between genotypes in colour and ground cover, unrelated to degree of senescence. The reduction in ‘green cover’ over time was fitted with a modified gompertz curve (Gooding et al. 2000), and the end of canopy photosynthetic function taken as when green cover was at 80% of maximum, i.e. at the onset of the rapid phase of senescence.

Time to anthesis (GS 65) was derived visually from daily plot inspections in both conventional and organic plots. Crop height was assessed with a rising disc of polystyrene (Addisu et al. 2009). Final crop height was calculated as the mean of three assessments taken after

Table 2 Husbandry applied to the conventional experiments

Treatment	GS (Zadoks et al. 1974)	2005/2006		2006/2007		2007/2008	
		Near isogenic lines		Near isogenic lines		Doubled haploid lines	
Herbicide	Pre-drilling	Glyphosate 1.8 kg/ha	Glyphosate 1.8 kg/ha	Glyphosate 1.8 kg/ha	Glyphosate 1.8 kg/ha	Glyphosate 1.8 kg/ha	
Insecticide	Pre-drilling	Chlorpyrifos 0.45 kg/ha	Chlorpyrifos 0.45 kg/ha	Chlorpyrifos 0.45 kg/ha	Chlorpyrifos 0.45 kg/ha	Chlorpyrifos 0.45 kg/ha	
Herbicide	19	–	Diflufenican 100 g/ha + Isoproturon 1 kg/ha	Diflufenican 100 g/ha + Isoproturon 1 kg/ha	Diflufenican 100 g/ha + Isoproturon 1 kg/ha	Pendimethalin 1.2 kg/ha + (Carfentrazone-ethyl 20 g/ha + Flupysulfuron-methyl 10 g/ha)	
Nutrition	30–31	100 kg N/ha + 40 kg S/ha	100 kg N/ha + 40 kg S/ha	100 kg N/ha + 40 kg S/ha	100 kg N/ha + 40 kg S/ha	100 kg N/ha + 40 kg S/ha	
Fungicide	30–31	Epoxiconazole 125 g/ha + Quinoxifen 150 g/ha	Epoxiconazole 125 g/ha + Quinoxifen 150 g/ha	Epoxiconazole 125 g/ha + Quinoxifen 150 g/ha	Epoxiconazole 125 g/ha + Quinoxifen 150 g/ha + Chlorothalonil 1 kg/ha	Epoxiconazole 125 g/ha + Quinoxifen 150 g/ha + Chlorothalonil 1 kg/ha	
Herbicide	31–32	Metsulfuron-methyl 3 g/ha + Thifensulfuron-methyl 30 g/ha	–	–	Tribenuron methyl 15 g/ha	Tribenuron methyl 15 g/ha	
Nutrition	34–39	100 kg N/ha	100 kg N/ha	100 kg N/ha	100 kg N/ha	100 kg N/ha	
Fungicide	39	Epoxiconazole 125 g/ha + Azoxystrobin 250 g/ha + Chlorothalonil 1 kg/ha	Epoxiconazole 125 g/ha + Azoxystrobin 250 g/ha + Chlorothalonil 1 kg/ha	Epoxiconazole 125 g/ha + Azoxystrobin 250 g/ha + Chlorothalonil 1 kg/ha	Epoxiconazole 125 g/ha + Azoxystrobin 250 g/ha	Epoxiconazole 125 g/ha + Azoxystrobin 250 g/ha	
Fungicide	59	Tebuconazole 250 g/ha	–	–	Tebuconazole 250 g/ha	Tebuconazole 250 g/ha	
Insecticide	61	Deltamethrin 6.25 g/ha	–	–	–	–	
Herbicide	Pre-harvest	–	Glyphosate 1.44 kg/ha	–	–	–	
Harvested		02.08.2006	10.08.2007	03.09.2008	03.09.2008	28.08.2008	

anthesis. Lodging was assessed by accounting for both angle of lean and proportion of plot affected (Caldicott and Nuttall 1979). In the organic areas, weed biomass was determined by destructively sampling 0.5 m² at anthesis, and again at maturity. Harvest index was derived from destructive sampling and partitioning (Kindred and Gooding 2005) before harvesting grain from the central 1.3 m of each plot with a plot combine.

Statistical analysis

The performance of NILs within each year and system were subjected to six (3 years × 2 systems) separate analyses of variance. To combine the data over years to assess the significance of system and system.genotype, the unbalanced structure was dealt with by using Residual Maximum Likelihood (REML) analysis in Genstat 10, where the fixed model was system + genotype + system.genotype, and the random model was year/system/block/genotype. To investigate relationships with height between the system × dwarfing gene means, quadratic regression was employed with system as a grouping factor. To investigate relationships over different cultivar backgrounds, main effects of background within a system were removed from the yield (but not height) variables by subtracting constant effects from that of Maris Huntsman.

For the doubled haploid lines REML analysis was conducted using presence and absence of markers for *Rht-D1b*, *Rht8c* and *Ppd-D1a*, as fixed effects. The random model was block/(row + column) when restricted to a production system, or otherwise system/block/(row + column).

Results

The 2005/2006 season was drier than the long term average (Table 1). Notwithstanding a wet May, grain filling in June and July was associated with comparatively dry and hot conditions, and hence the earliest harvest (Table 2). The 2006/2007 season was relatively wet throughout, except for an exceptionally dry April. This dry spell coincided with large nitrogen top-dressings (Table 2) and lack of rain may have contributed to very poor nitrogen uptake efficiencies in the conventional area (Addisu 2009). The period of rapid canopy formation and grain filling (March to

July) was comparatively wet in 2007/2008, and further rain in August contributed to delayed harvest (Table 1).

Near isogenic lines

The Mercia NIL with *Rht8c+Ppd-D1a* always flowered in the last week of May. Averaged over season and system, *rht* (tall), *Rht-B1b* and *Rht-D1b* all flowered 9 days after *Rht8c+Ppd-D1a* (SED = 0.22, 98 df). The severe dwarfing alleles or combinations conferred further delays in flowering (13, 15, 18, 15 and 15 after *Rht8c+Ppd-D1a* for *Rht-B1c*, *Rht-D1c*, *Rht12*, *Rht-B1b+Rht-D1b*, *Rht-D1b+Rht-B1c*, respectively). There was no evidence of a System.Dwarfing gene interaction on flowering time.

The yields of wheat varied with season; comparatively high yields achieved in 2008 contrasted with low yields in 2007 (Fig. 1). For grain yield and height at maturity the effects of Background, Dwarfing gene, System.Background, System.Dwarfing gene, and Background.Dwarfing gene were all significant at the $P \leq 0.001$ level.

Mercia

None of the Mercia lines grew taller than 90 cm. Crop heights were significantly reduced by the semi-dwarfing alleles (*Rht-B1b*, *Rht-D1b*, *Rht8c+Ppd-D1a*) by 10–15% (Fig. 1). *Rht-B1c* conferred dwarfing intermediate to the semi-dwarfing alleles and the very severe (*Rht-D1c*, *Rht12*) alleles. However, there was no evidence that adding a major gene for reduced height to the commercially released cultivar increased yield in either system (Fig. 1a–c). Yield differences among Mercia NILs were greater in the conventional system than in the organic system in 2007 and 2008 (Fig. 1b, c). Changes in relative yields of specific alleles between the two systems also contributed to the System.Dwarfing gene interaction. Firstly, *Rht-B1c* performed relatively better in the conventional system than in the organic system, causing the relationship between height and yield to deviate significantly from linearity in 2006 and 2008 (Fig. 1a, c), but only in the conventional system. Secondly, yield of *Rht8c+Ppd-D1a* was significantly less than *rht* (tall) and the other semi-dwarf NILs in just the conventional system in 2007 (Fig. 1b), when it was also associated with poor RUE (Table 3).

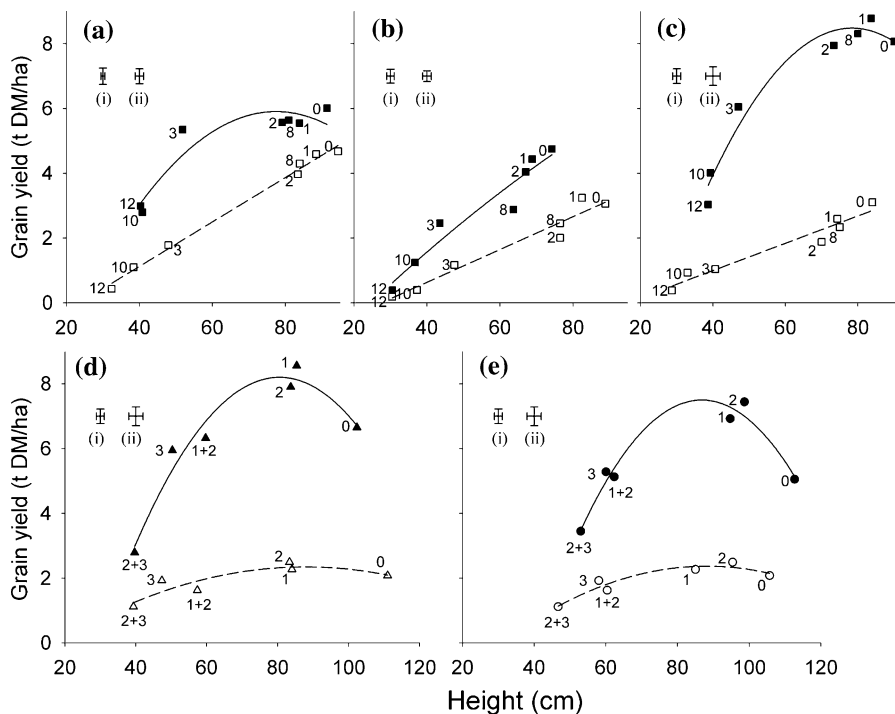


Fig. 1 Relationships between height and grain yield of winter wheat NILs varying in reduced height (*Rht*) genes grown in a conventional (*closed symbols*) and an organic (*open symbols*) production system. 0, 1, 2, 3, 8, 10, 12 correspond to *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*, respectively, in backgrounds of cvs: Mercia harvested in

a 2006, **b** 2007, **c** 2008; **d** Maris Huntsman in 2008; and **e** Maris Widgeon in 2008. *Fitted lines* are linear or quadratic. *Error bars* are SED for comparing NIL means within: (i) conventional, and (ii) organic systems. *df* = 18, 18 and 36 for harvests in 2006, 2007 and 2008, respectively

Although semi-dwarfing alleles failed to increase the yield of Mercia, they did tend to increase harvest index, significantly so in the conventional system of 2006 (Table 4). Where improvements in harvest index did occur, however, they were countered by reductions in above ground biomass. Similarly, *Rht-B1c* in Mercia achieved either greater or comparable harvest indices to that of *rht* (tall) and semi-dwarfs in the conventional system in all years, but reduced above-ground biomass as a result of both reduced PAR interception (in 2005/2006 and 2006/2007) and RUE (in 2006/2007 and 2007/2008) (Table 3). In the organic system, *Rht-B1c* was associated with significantly reduced harvest index (Table 4). This contrasting effect of *Rht-B1c* on harvest index contributed to a significant ($P = 0.013$) System.Dwarfing gene interaction. A similar interaction was evident for *Rht-D1c* in 2006, although in subsequent years, and for *Rht12* in all years, severe dwarfism was associated with reduced harvest index in both systems. These two

shortest Mercia NILs (*Rht-D1c*, *Rht12*) were associated with the lowest biomass, PAR interception and RUE in both systems in all years (Tables 3, 4).

Maris Huntsman and Maris Widgeon

In contrast to Mercia, the heights of Maris Huntsman and Maris Widgeon exceeded 100 cm (Fig. 1d, e). In the conventional system this was associated with significant lodging by anthesis (21 and 6% for Maris Huntsman and Maris Widgeon, respectively). For both cultivars, lodging was controlled, and yield and harvest index increased by the addition of either of the Norin-10 semi-dwarfing alleles (*Rht-B1b* and *Rht-D1b*) (Fig. 1d, e). In the organic system, differences in yield amongst these NILs were much less, although *Rht-B1b* or *Rht-D1b* still appeared to increase yield (but $P > 0.05$). Further dwarfism in Maris Huntsman, either by combining *Rht-B1b* with *Rht-D1b* or by using *Rht-B1c* was associated with

Table 3 Accumulated interception of photosynthetically active radiation (PAR) and radiation use efficiency (RUE) to produce above ground biomass of near isogenic lines differing in major genes for reduced height, in three winter wheat cultivar backgrounds, grown on conventionally managed land

Harvest date	Mercia			Maris Widgeon	Maris Huntsman	REML predicted allele means
	2 Aug. 2006	10 Aug. 2007	3 Sept. 2008	3 Sept. 2008	3 Sept. 2008	
PAR (MJ/m ²)						
<i>rht</i> (tall)	762	720	677	675	686	706
<i>Rht-B1b</i>	746	725	697	724	701	719
<i>Rht-D1b</i>	722	687	679	674	704	693
<i>Rht8c+Ppd- D1a</i>	749	708	690			714
<i>Rht-B1c</i>	625	630	698	662	715	659
<i>Rht-D1c</i>	569	605	660			603
<i>Rht12</i>	539	549	587			552
<i>Rht-B1b+Rht-D1b</i>				696	677	688
<i>Rht-D1b+Rht-B1c</i>				658	686	674
SED	19.7	35.7	19.6	19.6	19.6	23.6 ^a 14.0 ^b
RUE (g/MJ)						
<i>rht</i> (tall)	1.84	1.38	2.33	2.43	1.90	1.79
<i>Rht-B1b</i>	1.59	1.24	2.40	2.72	2.17	1.81
<i>Rht-D1b</i>	1.67	1.20	2.23	2.12	2.36	1.72
<i>Rht8c+Ppd- D1a</i>	1.63	0.87	2.31		1.59	
<i>Rht-B1c</i>	1.84	0.85	1.67	1.82	1.95	1.45
<i>Rht-D1c</i>	1.11	0.49	1.58			1.06
<i>Rht12</i>	1.52	0.25	1.40			1.08
<i>Rht-B1b+Rht-D1b</i>				1.97	1.95	1.47
<i>Rht-D1b+Rht-B1c</i>				1.36	1.59	0.98
SED	0.193	0.130	0.231	0.231	0.231	0.173 ^a 0.103 ^b
<i>df</i>	18	18	36	36	36	95

^a For comparing alleles only present in Maris Huntsman and Maris Widgeon (maximum SED)

^b For comparing alleles present in all three backgrounds (minimum SED)

increased harvest index in the conventional system but the opposite effect in the organic system (Table 5), giving a similar System.Dwarfing gene interaction to that seen with *Rht-B1c* in Mercia. Also consistent with Mercia, the severest dwarfism, achieved here by combining *Rht-D1b* with *Rht-B1c* was associated with reduced harvest index, above ground biomass and radiation use efficiency in both systems and backgrounds (Tables 3, 5).

Analysis combined over backgrounds

In the regression of REML predicted means for yield against height (Fig. 2), there was a very highly

significant ($P < 0.001$) change to the model when both linear and quadratic terms were allowed to vary with System (Fig. 2, $r_{\text{adj}}^2 = 0.91$). As previously described, the interactions with System arose mostly because the effects of height and Dwarfing gene on yield were greater in the higher yielding conditions of the *conventional* system. When the effects of yield potential of the system were removed, i.e. by expressing yields as a percentage of the maximum predicted by the quadratic fits (6.02 t DM/ha at 85 cm for conventional, and 3.52 t DM/ha at 96 cm for organic), there was no statistical justification for fitting separate quadratic responses of yield against height for the two systems ($P = 0.123$ for the

Table 4 Harvest index and above-ground biomass at harvest maturity of near isogenic lines of cv. Mercia differing in major genes for reduced height grown on conventionally (C) and organically (O)-managed land

NIL	Harvest date						NIL × system means		NIL mean
	2 Aug. 06		10 Aug. 07		3 Sept. 08		C	O	
	C	O	C	O	C	O			
Harvest index (%)									
<i>rht</i> (tall)	42.9	37.4	47.6	37.8	51.3	40.4	47.1	38.6	42.8
<i>Rht-B1b</i>	46.8	43.2	50.0	37.5	52.5	39.2	49.7	40.3	45.0
<i>Rht-D1b</i>	46.5	35.4	49.1	37.9	52.4	40.6	49.3	37.9	43.6
<i>Rht8c+Ppd-D1a</i>	46.3	39.2	46.8	39.0	52.3	37.9	48.3	39.0	43.6
<i>Rht-B1c</i>	46.6	30.7	46.2	33.2	51.7	39.1	48.0	34.1	41.1
<i>Rht-D1c</i>	44.4	28.8	42.1	23.3	38.6	31.3	42.2	27.7	34.9
<i>Rht12</i>	36.8	20.0	27.3	23.0	36.8	32.8	33.5	24.8	29.2
SED	1.48	3.99	1.92	2.57	3.86	3.41	1.90 ^a		1.35
Biomass (t DM/ha)									
<i>rht</i> (tall)	14.0	12.6	10.0	8.1	15.7	7.4	13.3	9.5	11.4
<i>Rht-B1b</i>	11.9	10.7	8.8	8.6	16.7	6.9	12.4	8.8	10.6
<i>Rht-D1b</i>	12.0	11.6	8.2	5.3	15.2	4.6	11.8	7.3	9.5
<i>Rht8c+Ppd-D1a</i>	12.2	11.2	6.2	6.2	15.9	6.1	11.3	7.9	9.6
<i>Rht-B1c</i>	11.5	6.0	5.3	3.6	11.7	2.6	9.6	4.1	6.8
<i>Rht-D1c</i>	6.3	4.1	3.0	1.7	10.4	3.0	6.5	2.8	4.7
<i>Rht12</i>	8.3	2.1	1.4	0.9	8.2	1.2	6.1	1.3	3.7
SED	1.39	1.36	0.76	0.86	1.69	1.39	0.78 ^a		0.55
<i>df</i>	18	18	18	18	36	36	120 ^a		120

^a For the NIL × system interaction

change). In this latter analysis: the common line estimates for constant, linear and quadratic effects were -105 (SE = 15.1), 4.53 (SE = 0.451), and -0.025 (SE = 0.00312), respectively; the variance accounted for among the 38 genotype × system means was 87% ($r_{adj.}^2$); and the height at fitted maximum yield was 91 cm.

There was no evidence that the mode of action of the dwarfing gene influenced the relationship between height and yield. The alleles producing the shortest plants produced similarly poor yields irrespective of whether the allele conferred GA insensitivity (*Rht-D1c*) or not (*Rht12*). The additive effects of *Rht8c+Ppd-D1a* (GA-sensitive) in Mercia produced plants of similar stature and yield to *Rht-D1b* (GA-insensitive).

Despite the similarities in optimum height for yields in the two systems, there were factors that might have been expected to contribute to more of an

interaction. As well as lodging only occurring in the conventional system, weeds were mostly found in the organic system, where they proliferated in plots of the severe dwarf genotypes (Fig. 3), accumulating 5 t DM/ha in *Rht12*.

Performance of doubled haploid lines

The REML analysis including the allele specific markers for *Ppd-D1a*, *Rht-D1b* and *Rht8c* as fixed effects revealed significant associations (Table 6). *Ppd-D1a* was associated with reduced time to flowering of 7 days (SED = 0.68; $df > 200$) irrespective of system. In the conventional system *Ppd-D1a* was associated with reduced interception of PAR, above-ground biomass and grain yield. In the organic system, the reverse effects of *Ppd-D1a* on biomass and grain yield were apparent. The marker for *Rht-D1b* was associated with a slight delay in

Table 5 Harvest index and above-ground biomass at harvest maturity of near isogenic lines of cv. Maris Huntsman and Maris Widgeon differing in major genes for reduced height

grown on conventionally (C) and organically (O)-managed land, harvested 3 Sept. 2008

	Maris Huntsman			Maris Widgeon			Allele mean
	C	O	NIL mean	C	O	NIL mean	
Harvest index (%)							
<i>rht</i> (tall)	42.0	42.3	42.1	38.9	31.9	35.4	38.8
<i>Rht-B1b</i>	44.6	42.0	43.3	45.6	34.7	40.2	41.7
<i>Rht-D1b</i>	55.6	41.7	48.7	45.0	33.4	39.2	43.9
<i>Rht-B1b+Rht-D1b</i>	46.5	37.7	42.1	39.2	32.5	35.8	39.0
<i>Rht-B1c</i>	49.3	38.0	43.6	38.6	34.6	36.6	40.1
<i>Rht-D1b+Rht-B1c</i>	31.7	34.8	33.3	33.0	28.9	31.0	32.1
SED	3.86	3.41	3.08	3.86	3.41	3.08	2.18
Biomass (t DM/ha)							
<i>rht</i> (tall)	16.3	6.5	11.4	13.1	6.6	9.9	10.6
<i>Rht-B1b</i>	19.6	7.6	13.6	15.2	6.6	10.9	12.2
<i>Rht-D1b</i>	14.2	8.9	11.5	16.6	7.2	11.9	11.7
<i>Rht-B1b+Rht-D1b</i>	13.7	3.9	8.8	13.2	5.2	9.2	9.0
<i>Rht-B1c</i>	12.1	5.3	8.7	13.9	5.4	9.7	9.2
<i>Rht-D1b+Rht-B1c</i>	8.9	2.7	5.8	11.1	4.0	7.5	6.7
SED	1.69	1.39	1.27	1.69	1.39	1.27	0.90
<i>df</i>	36	36	36	36	36	36	55

flowering (2 days; SED = 0.56) and a reduction in height, irrespective of system (Table 6). In the conventional system, *Rht-D1b* was associated with increased grain yield through improved harvest indices, rather than increased above ground biomass. *Rht-D1b* was not associated with increased harvest index, or grain yield in the organic system. The marker for *Rht8c* was associated with slightly earlier flowering (2 days; SED = 0.67) and reduced height irrespective of system. In the conventional system *Rht8c* was associated with increased harvest index but reduced biomass production. Grain yield appeared unaffected by *Rht8c* in either system.

In the analysis using individual DH lines as fixed effects, there were very highly significant ($P < 0.001$) effects of line on final crop height, grain yield, harvest index, and above-ground crop biomass (Fig. 4) in both systems. Significant cross-overs in performance of lines in the two systems were evident. The highest yielding line in the conventional area was Savannah (Fig. 4), but this was far from the case in the organic area.

Associations between height and grain yield were much weaker in the DH population than they were

amongst the NILs. The range of heights was slightly less than in the NIL comparisons, but many more factors were contributing to the variation in yield. For grain yield there was statistical justification for allowing the quadratic response to height to vary with system ($P = 0.05$), but this was mostly due the response in the organic area (Fig. 4a). In the conventional area there was no association between height and grain yield, any such relationship possibly being masked by other confounding influences such as date of flowering and senescence. For instance, in the conventional area, grain yield was significantly associated with post-anthesis PAR interception [correlation coefficient (r) = 0.57; $df = 62$; $P < 0.001$]. In addition to height, the yield of the DH lines in the organic area was significantly associated with assessments of establishment and early growth that were associated with the presence of *Ppd-D1a* (Addisu et al. 2009). For example, there was a significant correlation ($r = 0.58$; $df = 62$; $P < 0.001$) between grain yield and a score associated with plant population, and early ground cover, dry matter accumulation, and above ground nitrogen (PC1 in Addisu et al. 2009). There was

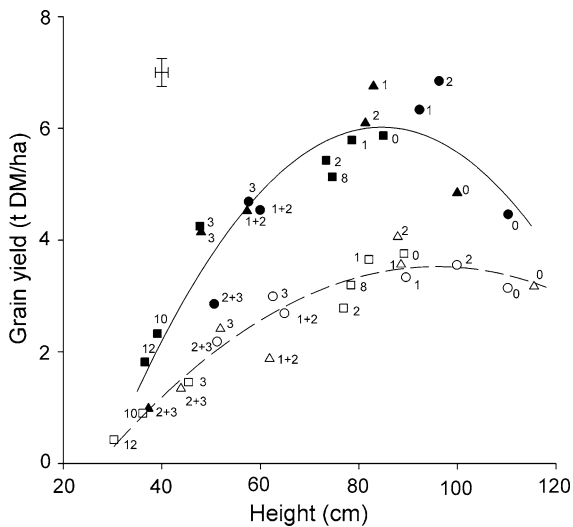


Fig. 2 Relationships between height and grain yield of winter wheat near-isogenic lines varying in reduced height (*Rht*) genes grown in a conventional (*closed symbols*) and an organic (*open symbols*) production system. 0, 1, 2, 3, 8, 10, 12 correspond to *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*, respectively, in backgrounds of cvs Mercia (*open square, filled square*), Maris Widgeon (*open circle, filled circle*), and Maris Huntsman (*open triangle, filled triangle*). *Fitted lines* are quadratic. Points are predicted means from a REML analysis of genotypes compared in replicated experiments over 3 years, with main effects of background within system removed (see text for details). *Error bars* are average SEDs for comparing NIL means within systems (166 *df*)

no such correlation between early growth and yield in the conventional area ($r = 0.02$; $P = 0.88$).

For harvest index, the fitted quadratic response to height was the same in each system, declining as heights exceeded 80 cm (Fig. 4b). Above ground biomass increased with height in both systems, more so in the organic system than in the conventional system. In neither system was there any evidence that this response deviated from linearity over the ranges observed (Fig. 4c).

Discussion

The fitted peak yields in the NIL experiment of 7 and 4 t/ha at 15% moisture for conventional and organic systems, respectively, are not unrepresentative of UK yields, especially considering that the regression constants for the different backgrounds were rebased to that of Maris Huntsman.

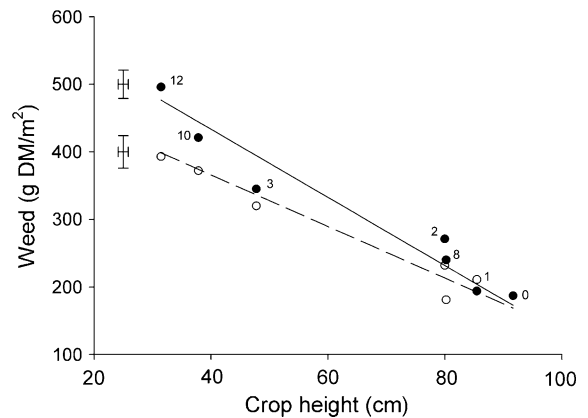


Fig. 3 Relationships with height of weed dry matter at anthesis (*open circle*) and maturity (*filled circle*) of winter wheat NILs of cv. Mercia varying in reduced height (*Rht*) genes grown in an *organic* production system. 0, 1, 2, 3, 8, 10, 12 correspond to *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c+Ppd-D1a*, *Rht-D1c*, *Rht12*, respectively. Points are means from genotypes compared in replicated experiments in 2006 and 2007. *Error bars* are one SED for comparing NILs within systems (42 *df*)

Despite including a wider range of gibberellin insensitive dwarfing alleles than Flintham et al. (1997), and the inclusion of two gibberellin sensitive dwarfing alleles, our results are consistent in showing optimal heights for grain yield in conventional production systems in NW Europe is broadly between 80 and 100 cm. We demonstrate and confirm that excessive dwarfism for yield can be associated with reduced PAR, RUE, AGB, HI, and in the organic system with increased weed prevalence (Flintham et al. 1997; Cosser et al. 1997; Austin 1999). Excessive height for yield can be particularly associated with reduced HI (Flintham et al. 1997) and, in conventional systems, lodging (Berry et al. 2004). Our results are also consistent with others in showing that the value of semi-dwarfing genes is greater in taller backgrounds (Richards 1992; Flintham et al. 1997).

Taken together with the DH results, there is a suggestion that the ideal height for a wheat crop could be slightly higher in an organic system than in a conventional system, but this can not be supported statistically. We could not reproduce the statistical yield benefit of adding *Rht-B1b* or *Rht-D1b* to Maris Widgeon grown organically reported by Cosser et al. (1997), possibly because of the greater weed

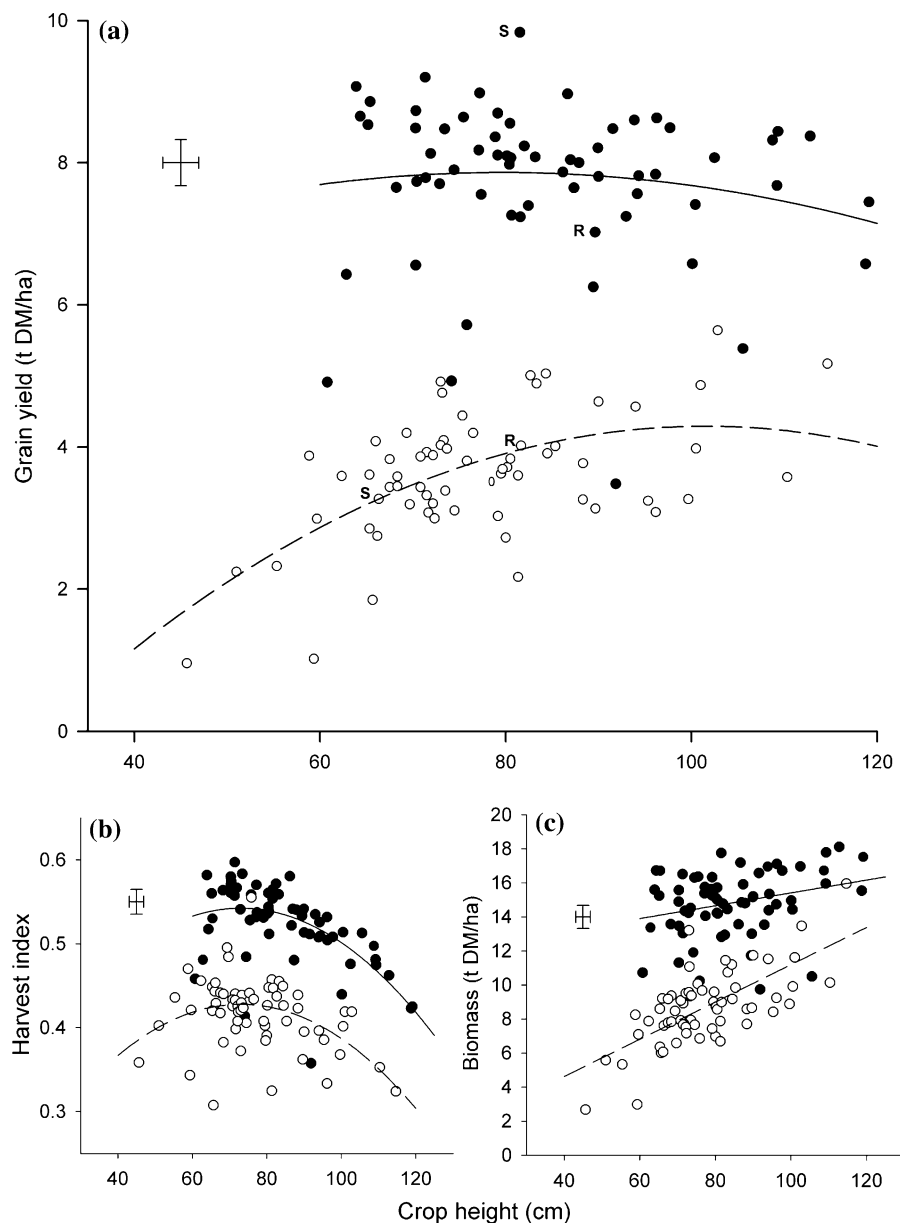
Table 6 Means for presence and absence of markers for photoperiod insensitivity and reduced height amongst doubled haploid lines of Savannah × Renesansa harvested in 2008 for yields and partitioning of dry matter, cumulative interception of photosynthetically active radiation (PAR) and radiation use efficiency (RUE) when grown conventionally or organically. *df* > 100

Marker	Conventional		Organic		SED
	–	+	–	+	
Final crop height (cm)					
<i>Ppd-D1a</i>	82.6	87.5	74.4	81.6	2.25
<i>Rht-D1b</i>	92.6	77.7	84.1	71.7	2.18
<i>Rht8c</i>	90.5	79.4	81.4	74.9	2.25
Grain yield (t DM/ha)					
<i>Ppd-D1a</i>	8.03	7.58	3.53	3.71	0.240
<i>Rht-D1b</i>	7.40	8.05	3.73	3.68	0.222
<i>Rht8c</i>	7.85	7.70	3.53	3.78	0.240
Harvest index (%)					
<i>Ppd-D1a</i>	52.2	52.9	42.5	41.4	1.38
<i>Rht-D1b</i>	50.5	54.3	42.0	42.3	1.30
<i>Rht8c</i>	51.0	54.3	41.2	42.6	1.38
Biomass (t DM/ha)					
<i>Ppd-D1a</i>	15.4	14.3	8.2	9.1	0.54
<i>Rht-D1b</i>	14.6	14.9	8.9	8.8	0.52
<i>Rht8c</i>	15.4	14.1	8.6	9.0	0.54
PAR (MJ/m ²)					
<i>Ppd-D1a</i>	594	566			15.0
<i>Rht-D1b</i>	570	589			12.3
<i>Rht8c</i>	590	570			14.8
RUE (g/MJ)					
<i>Ppd-D1a</i>	2.58	2.53			0.071
<i>Rht-D1b</i>	2.55	2.58			0.060
<i>Rht8c</i>	2.60	2.51			0.071

pressures found in the present study. Similar to Cosser et al. (1997), however, we have no evidence that use or otherwise of major semi-dwarfing genes to aid performance in conventional systems would be detrimental to grain yield if the same selections were grown in an organic system. This conclusion is reached despite influences that might have been expected to lead to more of a distinction in target heights between the two systems: high weed pressures in the organic system, and significant lodging in the conventional system. We also find that benefits of intermediate dwarfism for improved harvest index in the conventional system are not reliably expressed in the organic system. It is possible that competition from weeds and/or reduced late-season nutrient availability (Wolfe et al. 2008; Baresel et al. 2008) could reduce grain numbers and/or mean grain weight and hence reduce efficiency of dry matter partitioning to the grain in the organic system.

Although we do not report crossovers in performance based on *Rht* inclusion, the DH experiment demonstrates that crossovers do occur. It seems that the presence or absence of *Ppd-D1a* can contribute to these crossovers. The relationship between the duration of canopy life, hence light interception post-anthesis, and grain yield is well known (Verma et al. 2004). The negative association between the marker for *Ppd-D1a* on time to senescence, AGB and grain yield in the conventional system is consistent with this relationship. Similarly, the earlier maturation of *Rht8c+Ppd-D1a* in Mercia may have contributed to the reduced yield seen for this line in the conventional system of 2007. Foulkes et al. (2004), also found *Ppd-D1a* to reduce AGB in the UK. In the organic system, however, *Ppd-D1a* appeared to increase yields, possibly associated with increased early resource capture. The positive associations between *Ppd-D1a*, early season growth, and grain

Fig. 4 Relationships between height and wheat grain yield, harvest index and above-ground crop biomass for double haploid progeny of Savannah (S) × Renesansa (R) grown in a conventional (*closed symbols*) and an organic (*open symbols*) production system. Error bars are SED for comparing DH line means within systems (125 df)



yield in the organic system is consistent with the view that early vigour is particularly important in this context (Wolfe et al. 2008), i.e. in situations where resources such as nitrogen are likely to be initially plentiful after a legume-rich ley, but then become deficient later in the season (Baresel et al. 2008; Addisu 2009).

Acknowledgments The authors are grateful to the Felix Trust for providing a scholarship for M. Addisu, RJ Casebow

and RE Kiff for technical support, and to Dr HE Jones for useful comments made on this manuscript.

References

- Addisu M (2009) Effects of green revolution and other dwarfing genes in contrasting wheat production systems. PhD thesis, The University of Reading
- Addisu M, Snape JW, Simmonds JR, Gooding MJ (2009) Reduced height (Rht) and photoperiod insensitivity (Ppd)

- allele associations with establishment and early growth of wheat in contrasting production systems. *Euphytica* 166:249–267
- Austin RB (1999) Yield of wheat in the United Kingdom: recent advances and prospects. *Crop Sci* 39:1604–1610
- Baresel JP, Zimmermann G, Reents HJ (2008) Effects of genotype and environment on N uptake and N partition in organically grown winter wheat (*Triticum aestivum* L.) in Germany. *Euphytica* 163:347–354
- Berry PM, Sylvester-Bradley R, Philipps L (2002) Is the productivity of organic farms restricted by supply of available nitrogen? *Soil Use Manage* 18:248–255
- Berry PM, Sterling M, Spink JH, Baker CJ, Sylvester-Bradley R, Mooney SJ, Tams AR, Ennos AR (2004) Understanding and reducing lodging in cereals. *Adv Agron* 84:217–271
- Caldicott JJB, Nuttall AM (1979) A method for the assessment of lodging in cereal crops. *J Nat Inst Agric Bot* 15:88–91
- Chapman SC, Mathews KL, Trethowan RM, Singh RP (2007) Relationships between height and yield in near-isogenic spring wheats that contrast for major reduced height genes. *Euphytica* 157:391–397
- Cosser ND, Gooding MJ, Davies WP, Thompson AJ, Froud-Williams RJ (1997) Cultivar and Rht gene influences on the competitive ability, yield and the breadmaking quality of organically grown winter wheat. In: Gooding MJ, Shewry PR (eds) *Aspects of applied biology* 50. Optimising cereal inputs: its scientific basis. Association of Applied Biologists, Warwick, pp 39–51
- Flintham JE, Borner A, Worland AJ, Gale MD (1997) Optimizing wheat grain yield: effects of Rht (gibberellin-insensitive) dwarfing genes. *J Agric Sci* 128:11–25
- Foulkes MJ, Sylvester-Bradley R, Worland AJ, Snape JW (2004) Effects of a photoperiod-response gene Ppd-D1 on yield potential and drought resistance in UK winter wheat. *Euphytica* 135:63–73
- Gooding MJ, Dimmock JPRE, France J, Jones SA (2000) Green leaf area decline of wheat flag leaves: the influence of fungicides and relationships with mean grain weight and grain yield. *Ann Appl Biol* 136:77–84
- Jarvis RA (1968) *Soils of the reading district*. Rothamsted Experimental Station, Harpenden, UK
- Kindred DR, Gooding MJ (2005) Heterosis for yield and its physiological determinants in wheat. *Euphytica* 142: 149–159
- Richards RA (1992) The effect of dwarfing genes in spring wheat in dry environments. 1. Agronomic characteristics. *Aust J Agric Res* 43:517–527
- Simon MR, Worland AJ, Struik PC (2004) Influence of plant height and heading date on the expression of the resistance to *Septoria tritici* blotch in near isogenic lines of wheat. *Crop Sci* 44:2078–2085
- Srinivasachary GN, Steed A, Simmonds J, Leverington-Waite M, Wang Y, Snape J, Nicholson P (2008) Susceptibility to fusarium head blight is associated with the *Rht-D1b* semi-dwarfing allele in wheat. *Theor Appl Genet* 116:1145–1153
- Verma V, Foulkes MJ, Worland AJ, Sylvester-Bradley R, Caligari PDS, Snape JW (2004) Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica* 135:255–263
- Wolfe MS, Baresel JP, Desclaux D, Goldringer I, Hoad S, Kovacs G, Loschenberger F, Miedaner T, Ostergard H, van Bueren ETL (2008) Developments in breeding cereals for organic agriculture. *Euphytica* 163:323–346
- Worland AJ, Sayers EJ, Borner A (1994) The genetics and breeding potential of *Rht12*, a dominant dwarfing gene in wheat. *Plant Breed* 113:187–196
- Worland AJ, Korzun V, Roder MS, Ganai MW, Law CN (1998) Genetic analysis of the dwarfing gene *Rht8* in wheat. Part II. The distribution and adaptive significance of allelic variants at the *Rht8* locus of wheat as revealed by microsatellite screening. *Theor Appl Genet* 96:1110–1120
- Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. *Weed Res* 44:415–421
- Zerner MC, Gill GS, Vandeleur RK (2008) Effect of height on the competitive ability of wheat with oats. *Agron J* 100:1729–1734