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Reduced height alleles (*Rht*) and Hagberg falling number of wheat

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ABSTRACT

Near-isogenic lines varying for alleles for reduced height (*Rht*) and photoperiod insensitivity (*Ppd-D1*) in cv. Mercia (2005/6–2010/11; *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c*+*Ppd-D1a*, *Rht-D1c*, *Rht12*) and cvs Maris Huntsman and Maris Widgeon (2007/8–2010/11; *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht-B1b*+*Rht-D1b*, *Rht-D1b*+*Rht-B1c*) were compared at one field site, but within different systems ('organic', O, 2005/6–2007/8 v. 'intensive', I, 2005/6–2010/11). Further experiments at the site (2006/7–2008/9) compared 64 lines of a doubled-haploid (DH) population [Savannah (*Rht-D1b*) × Renesansa (*Rht-8c*+*Ppd-D1a*)]. Gibberellin (GA) insensitive dwarfing alleles (*Rht-B1b*; *Rht-B1c*; *Rht-D1b*; *Rht-D1c*) could reduce α-amylase activity and/or increase Hagberg falling number (HFN) but effects depended greatly on system, background and season. Only *Rht-B1c* increased grain dormancy despite producing plants taller than *Rht-D1c*. The GA-sensitive *Rht8c*+*Ppd-D1a* in Mercia was associated with reduced HFN but analysis of the DH population suggested this was more closely linked with *Ppd-D1a*, rather than *Rht8c*. The GA-sensitive severe-dwarfing allele *Rht12* was associated with reduced HFN. Instability in HFN over season tended to increase with degree of dwarfing. There was a negative association between mean grain weight and HFN that was in addition to effects of *Rht* and *Ppd-D1* allele.

1. Introduction

Hagberg falling number (HFN) is a quality criterion of bread-making wheat because of its negative association with α-amylase activity (Perten, 1964). Doughs formed from flour with excessive α-amylase are sticky and difficult to process, and when baked, produce discoloured loaves that are poorly structured (Chamberlain et al., 1982). Immoderate levels of α-amylase are most commonly produced in pre-harvest sprouting (PHS) or as late-maturity α-amylase (LMA) (Lunn et al., 2001). Pre-harvest sprouting follows a loss of grain dormancy and subsequent germination whilst in the ear, often in response to wet conditions occurring between grain ripeness and harvest (Barnard, 2001), and also as might occur in lodged crops. Late-maturity α-amylase occurs in the absence of visible sprouting (Mares and Mrva, 2008). Low HFN or high α-amylase activity in the absence of visible sprouting has been variously associated with: low temperatures and/or high soil moisture during the linear phase of grain filling (Gooding, 2010; Gooding et al., 2003); slow grain drying rate; abrupt temperature changes during grain filling; large grain size and mass; low specific weights, and grain cavity characteristics (Clarke et al., 2004; Evers et al., 1995; Farrell and Kettlewell, 2008, 2009; Kindred et al., 2005; Mares and Mrva, 2008). There are strong genotype × environment (Gooding, 2010), and genotype × agronomy (Kindred et al., 2005) interactions on HFN.

Reduced height (*Rht*) alleles (Gale and Youssefian, 1985) are incorporated in wheat breeding programmes to produce semi-dwarf wheats (Flintham et al., 1997a). The gibberellin (GA)-insensitive alleles *Rht-B1b* and *Rht-D1b* (from Norin 10, syn. *Rht1* and *Rht2*), and the GA-sensitive allele *Rht8c* (from Akakomugi, often linked with the photoperiod-insensitivity allele *Ppd-D1a*) individually: reduce height by 10–15%; reduce lodging in fertile and humid conditions; and increase harvest index when added to excessively tall backgrounds (Flintham et al., 1997a; Gooding et al., 2012). *Rht* alleles that confer reduced GA sensitivity have reduced grain α-amylase activity and increased HFN (Flintham et al., 1997b; Gooding et al., 1999). Gibberellin activity and sensitivity is implicated in PHS and in the production of LMA (Flintham et al., 1997b; Mares and Mrva, 2008). The benefit of GA-insensitivity for HFN has

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Abbreviations: DF, degrees of freedom; DH, doubled haploid; GA, gibberellic acid; HFN, Hagberg falling number; I, intensive growing system; LMA, late-maturity alpha-amylase; NIL-isogenic line, near; O, organic growing system; PHS, pre-harvest sprouting; *Ppd*, photoperiod response allele; QTL, quantitative trait loci; REML, residual maximum likelihood; *Rht*, reduced height allele; SED, standard error of difference.

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been particularly evident for the severe-dwarfing allele *Rht-Blc* (from Tom thumb, syn. *Rht3*) with reduced risk of PHS (Flintham et al., 1997b). *Rht-B1c*, unlike the Norin 10 semi-dwarfing alleles, confers marked inhibition of aleurone activity when challenged with GA (Flintham and Gale, 1982), possibly contributing to increased grain dormancy. A severe-dwarfing allele is also present at the *Rht-D1* locus (*Rht-D1c*, syn. *Rht10*, from Ai-Bian), but we are unaware of the previous work characterizing the effects of this allele on grain dormancy and HFN. Both *Rht-B1c* and *Rht-D1c* in the homozygous state produce plants with statures sub-optimal for yield (Addisu et al., 2010), but it has been suggested that *Rht-B1c* may have utility in the heterozygous state, or by controlling height in particularly tall backgrounds, or even triticale (Flintham et al., 1997b).

The benefit of GA-insensitivity for HFN has raised concerns as to the effects of replacing the Norin 10 alleles with *Rht8c* in breeding programmes (Mares and Mrva, 2008). Here we use near-isogenic lines (NILs) to compare the effects of semi-, and severe-dwarfing alleles at the *Rht-B1* and *Rht-D1* loci with GA-sensitive alleles conferring both semi- (*Rht8c*+*Ppd-D1a* linkage block on chromosome 2D) and severe- (*Rht12*, gamma ray-induced allele from 'Karcagi 522') dwarfing. We also compare 62 doubled-haploid (DH) progeny of cv. Savannah (*Rht-D1b*) × Renesansa (*Rht8c*+*Ppd-D1a*) genotyped with markers for the dwarfing genes and *Ppd-D1a* to assess the effects of the alleles individually and in combination. Allele effects on HFN are assessed for stability over contrasting genetic backgrounds, seasons and systems ('intensive' v. 'organic') and interpreted with reference to mean grain weight, grain specific weight, α-amylase activity, and the acquisition and retention of grain dormancy.

2. Experimental

2.1. Crop husbandry

All experiments were conducted within the same 10 ha site at the Crops Research Unit, Sonning, University of Reading, UK (51°29′N, 0°56′W), on a free-draining sandy loam. The site is split between an area receiving synthetic agrochemicals and fertilizers, managed intensively, and an area managed organically since 2001. Full details of the site, crop establishment and husbandry are available elsewhere (Addisu et al., 2009, 2010; Gooding et al., 2012). Untreated seeds were drilled between 21 September and 4 October at a nominal depth of 50 mm, on 120 mm rows in 2 m wide plots separated by 0.5 m double-width track wheelings. Weather data (Table 1) were recorded at an automated meteorological station at the site. Intensive management of the wheat typically involved: herbicide applications at growth stage (GS, Zadoks et al., 1974) 19 and/or 31–32; and fungicide applications at GS 30–31, 39 and 59. No plant growth regulators were applied. In each year, 100 kg N/ha + 40 kg S/ha was applied as a mixture of ammonium nitrate and ammonium sulphate at GS 30–31. A further 100 kg N/ha was applied as ammonium nitrate between GS 34–39. In the organic area, wheat was established after a three-year clover-rich ley. No agrochemicals or fertilizers were applied to the organic wheat. Replication, plot lengths and seed rate varied with experiment and year (Table 1).

2.2. Near-isogenic lines

Near-isogenic lines (NILs) of wheat varying for major dwarfing alleles were compared in complete randomized blocks, harvested in each year from 2006 to 2011 (Table 1). In all six years, the experiments included seven near-isogenic lines (NILs) in a cv. Mercia background (*rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht8c*+*Ppd-D1a*, *Rht-D1c*, *Rht12*). In the last four years, NILs with taller backgrounds were also included i.e. Maris Widgeon and Maris Huntsman comprising *rht* (tall), *Rht-B1b*, *Rht-D1b*, *Rht-B1c*, *Rht-B1b*+*Rht-D1b*, *Rht-D1b*+*Rht-B1c*. Source of dwarfing alleles and markers used is in Addisu et al. (2009).

2.3. Doubled-haploid population

Sixty-two lines were selected from a recombinant doubled-haploid (DH) population of Savannah (*Rht-D1b*) × Renesansa (*Rht8c*+*Ppd-D1a*) (Simmonds et al., 2006). Savannah had high yield potential in NW Europe, low bread-making quality, and was listed for the UK in 1998. Renesansa had high yield potential in southern

Table 1
Experimental details on intensive (I) and organic (O) areas comparing reduced height (*Rht* alleles).

Growing season	2005/6	2006/7	2007/8	2008/9	2009/10	2010/11
Rainfall (mm)/mean temperature (°C)						
March	45.6/5.3	44.4/7.1	82.6/6.5	31.0/7.8	46.2/6.3	13.8/6.5
April	25.7/9.1	1.8/11.4	59.0/8.1	34.0/10.1	22.0/9.2	2.8/12.2
May	79.7/12.6	92.2/12.4	66.4/13.7	30.8/12.5	12.0/11.2	30.0/12.3
June	11.1/16.4	93.7/16.1	49.4/14.9	40.2/15.3	20.8/16.1	89.8/14.2
July	32.0/20.6	115.6/16.3	77.6/16.5	69.2/16.7	31.6/18.4	41.1/16.2
August	36.2/16.8	40.5/16.3	74.6/16.8	27.4/16.9	108.0/16.1	125.2/15.9
Experiments comparing near-isogenic lines (NILs)						
Systems included	Intensive and organic	Intensive and organic	Intensive and organic	Intensive	Intensive	Intensive
Number of complete blocks per system	4	4	3	5	3	4
NILs included	Mercia	Mercia	Mercia, M. Huntsman, M. Widgeon	Mercia, M. Huntsman, M. Widgeon	Mercia, M. Huntsman, M. Widgeon	Mercia, M. Huntsman, M. Widgeon
Plot lengths (m)	10	10	7.5	7.5	7.5	5
Seeds sown/m^2	300	300	250	300	300	300
Harvest date (day.month)	02.8	10.8	03.9	20.8	06.8	15.8
Experiments comparing doubled-haploid (DH) population						
Systems included		Intensive	Intensive and organic	Intensive		
Number of complete blocks per system		1	2	2		
Plot lengths (m)		5	7.5	5		
Seeds sown/m^2		150	250	250		
Harvest date (day.month)		08.8	03.9	25.8		