Semi-dwarfing (Rht-B1b) improves nitrogen-use efficiency in wheat, but not at economically optimal levels of nitrogen availability

Semi-dwarfing (*Rht-B1b*) improves nitrogen-use efficiency in wheat, but not at economically optimal levels of nitrogen availability

S. LODDO[1] and M.J. GOODING[2]

[1]Department of Environmental Agronomy and Crop Sciences, University of Padova, Agripolis, Viale dell'Università, 16, 35020 Legnaro, Padova, Italy.
[2] Crops Research Unit, University of Reading, Early Gate, P.O. Box 237, Reading RG6 6AR,U.K.

A UK field experiment compared a complete factorial combination of three backgrounds (cvs Mercia, Maris Huntsman and Maris Widgeon), three alleles at the *Rht-B1* locus as Near Isogenic Lines (NILs: *rht-B1a* (tall), *Rht-B1b* (semi-dwarf), *Rht-B1c* (severe dwarf)) and four nitrogen (N) fertilizer application rates (0, 100, 200 and 350 kg N/ha). Linear+exponential functions were fitted to grain yield (*GY*) and nitrogen-use efficiency (*NUE*; *GY*/available N) responses to N rate. Averaged over N rate and background *Rht-B1b* conferred significantly (P<0.05) greater *GY*, *NUE*, N uptake efficiency (*NUpE*; N in above ground crop / available N) and N utilization efficiency ($NUtE_g$; *GY* / N in above ground crop) compared with *rht-B1a* and *Rht-B1c*. However the economically optimal N rate (N_{opt}) for N:grain price ratios of 3.5:1 to 10:1 were also greater for *Rht-B1b*, and because *NUE*, *NUpE* and *NUtE* all declined with N rate, *Rht-Blb* failed to increase *NUE* or its components at N_{opt}. The adoption of semi-dwarf lines in temperate and humid regions, and the greater N rates that such adoption justifies economically, greatly increases land-use efficiency, but not necessarily, *NUE*.

Keywords: wheat, fertilisation, nitrogen-use efficiency, *Rht*, dwarfing alleles.

Introduction

Inefficient use of nitrogen fertiliser is economically and energetically wasteful and impacts negatively on the environment such as via groundwater contamination with leachate, and atmospheric pollution (Byners 1990). There is, therefore, urgency to enhance N use efficiency (*NUE*) of crops; defined by Moll et al. (1982), as the ability of plants to produce harvestable dry biomass (grain yield; *GY*) per unit of available N. *NUE* has two components: N uptake efficiency (*NUpE*), the ability to recover available N in crop biomass; and N utilization efficiency (*NUtE*), the ability to produce *GY* per unit N recovered in crop biomass (Moll et al. 1982). *NUE* at constant N availabilities varies amongst wheat varieties and has been improved by wheat breeders, particularly as dry matter harvest index (*DMHI*; *GY /* above ground crop DM) increased (Ortiz-Monasterio et al. 1997; Barraclough et al. 2010). The adoption of major alleles for reducing height (*Rht*) has been notably successful in these regards (Gooding et al. 2012). However, modern shorter varieties also justify, economically, a greater use of N fertilizer, and Sylvester-Bradley and Kindred (2009) argue that *NUE* of varieties should be compared at a range of N availabilities. Here we compare three reduced height alleles in different genetic backgrounds at a range of N rates so as to evaluate *NUE* at constant and economically justified nitrogen fertilizer rates (N_{opt}).

Table 1. Nitrogen (kg/ha) treatments applied during stem extension

Total N applied	23 March (1 node)	28 April (2 nodes)	14 May (flag leaf emerg.)
0	-	-	-
100	50	-	50
200	50	100	50
350	50	250	50

Materials and Methods

A field experiment was set up on a free-draining sandy loam soil, during the 2009-2010 growing season, at the Crop Research Unit, University of Reading, UK (51˚29'N, 0˚56'W). Nine near isogenic lines (NILs) were included as a factorial combination of three background varieties (Maris Huntsman, Maris Widgeon and Mercia) and three alleles of the *Rht-B1* locus: *rht-B1a* (tall), *Rht-B1b* (semi-dwarf, syn. *Rht1*) and *Rht-B1c* (severe-dwarf, syn. *Rht3*). On 22 October, 300 untreated seeds/m^2 were drilled into 120 mm rows in 2 x 6 m sub-plots, separated by a 500 mm double track wheeling. Seed bed preparation, crop protection and nutrition other than for N was as per local commercial practice (Addisu et al. 2010). Main plots, randomised in three complete blocks, comprised the nine background x allele combinations; each contained four randomised sub-plots allocated one of four N rates applied as granular ammonium nitrate (Table 1). For the five months encompassing stem extension and grain filling, rainfall was low compared to the long term average (46, 22, 12, 21, 32 for March to July respectively), whilst mean air temperatures were close to normal for the site (6.3, 9.1, 11.2, 16.1 and 18.4^{o}C respectively). Crop height was measured five days before harvest with a polystyrene rising disc (Addisu et al. 2009). During the week before harvest, above ground whole crop rows either side of three randomly placed 0.5 m lengths (total area equivalent of 0.36 m^2) were collected from each subplot. Samples were partitioned into grains, chaff and straw. After oven drying, dry weight of each component was estimated and N content assessed with the Dumas combustion method (LECO FP-328, LECO, Stockport, UK). Plot combine harvesting on 9 August 2010 was with a 1.4 m cutter bar such that effective separation of subplots was 0.8 m to reduce edge effects. After oven drying a sample for 72 h at 65 ˚C, *GY* was corrected to dry matter (DM) basis. Information from sample areas was used to calculate *DMHI* and nitrogen harvest index (*NHI*, nitrogen in grain/nitrogen in above ground crop biomass). *NUpE*, *NUtE* and *NUE* were calculated as in Moll et al. (1982).

Appropriate split plot analyses of variance included a treatment structure of Background*Allele*pol(N rate;2) (GENSTAT 13; VSN International, Hemel Hempstead, UK). *GY* and *NUE* response to N rate deviated significantly from linearity (P<0.001 for deviations), and for *GY* there was also some evidence that including a quadratic effect was insufficient (P=0.066 for deviations). The exponential plus linear model ($A+B.r^{Nrate}+C.Nrate$) with constant value of r (0.99), that had previously been found to be appropriate for many sites and seasons in the UK (Foulkes et al. 1998) was, therefore, used (Fig. 1A). Soil available N was taken as the N in the above ground crop biomass at harvest for the zero N treatment (Sylvester-Bradley and Kindred 2009). As genotypes did not differ significantly for this measure (*rht-B1a*, *Rht-B1b*, *Rht-B1c* = 70, 80, 72 kg N/ha respectively; S.E.D. = 8.6; d.f. = 16) the grand mean of 74 kg N/ha was used. N_{opt} was calculated (Foulkes et al. 1998) for four

N:grain price ratios between 3.5:1 and 10:1, i.e. broadly indicative of the range observed in the UK since 2000 (Sylvester-Bradley and Kindred 2009) .

Results and Discussion

For *GY* effects of Background (*P*=0.046), Allele (*P*=0.002), N rate (*P*<0.001), and Allele x N rate (*P*<0.001) were significant (Fig. 1A). There was no Background x Allele interaction (*P*=0.78) nor three factor interaction (*P*=0.38) so all data are presented as Allele x N rate combinations, averaged over background.

Table 2. Effect of *Rht-* allele and nitrogen fertilizer application rate on final crop height, above ground crop biomass, and harvest index of winter wheat. Values are means of three genotypic backgrounds.

N rate	Height (mm)			Above ground crop biomass (t DM/ha)			Dry matter harvest index (%)		
	B1a	*B1b*	*B1c*	*B1a*	*B1b*	*B1c*	*B1a*	*B1b*	*B1c*
0	910	720	420	8.6	9.3	7.6	44.6	49.0	52.8
100	1020	830	460	14.4	14.8	12.0	45.4	47.9	51.7
200	1020	840	480	16.2	18.2	13.9	45.2	47.0	50.4
350	1000	830	470	16.8	18.6	14.1	45.3	49.8	49.8
S.E.D. (54 d.f.)*			11.0			0.65			1.14
Mean	990	810	460	14.0	15.2	11.9	45.1	48.4	51.2
S.E.D. (16 d.f.)**			11.5			0.58			0.73

*for comparing N rates within alleles; **for comparing allele means

Dwarfing alleles reduced crop height (Table 2) within expectations (Flintham et al. 1997), i.e. the semi-dwarfing *Rht-Blb* by 18% and the severe dwarfing *Rht-B1c* by 54%. As in previous studies *Rht-B1b* gave the highest *GY* because it produced much more above ground biomass than *Rht-B1c* and a greater *DMHI* than *rht-B1a* (Flintham et al. 1997; Addisu et al. 2010). The *GY* of *Rht-B1b* was the most responsive to N (Fig. 1A) partly because of a combination of comparatively high biomass yield and *DMHI* at the highest N rate (Table 2).

The results presented (Fig. 1B-C) here are consistent with previous work at this site showing semi-dwarfing alleles to increase *NUE*, *NUpE* and *NUtE* at a constant nitrogen fertilizer application rate (200 kg ha^{-1}, Gooding et al. 2012). However, we demonstrate that this advantage of *Rht-B1b* disappears if alleles are compared at N_{opt}. At none of the N:grain price ratios did the *NUE* at N_{opt} of *Rht-B1b* exceed that of *rht-B1a*. Similar results were obtained when comparing commercial elite lines released between 1977 and 2007 (Sylvester-Bradley and Kindred 2009): more modern, shorter varieties had higher *NUE* at 200 kg N/ha, but as they had greater yield responses to nitrogen fertilizer, they justified heavier N fertilisation, and at N_{opt} gave *NUE* similar to older genotypes.

A criticism of our work is its reliance on a single field experiment. However, the decline in *NUE*, *NUpE* and *NUtE* with *N* rate (Fig. 1B-C) is not unexpected (Sylvester-Bradley and Kindred 2009), nor is the increased nitrogen responsiveness of semi-dwarf lines (Anderson et al. 1991). We demonstrate that these combined effects can negate benefits of semi-dwarfing alleles for *NUE* when economic considerations are included. It is obvious that land-use efficiency (yield/ha) is greatly increased with the adoption of semi-dwarf lines and the higher fertilization rates that they justify, but improved *NUE* in such circumstances is less likely.

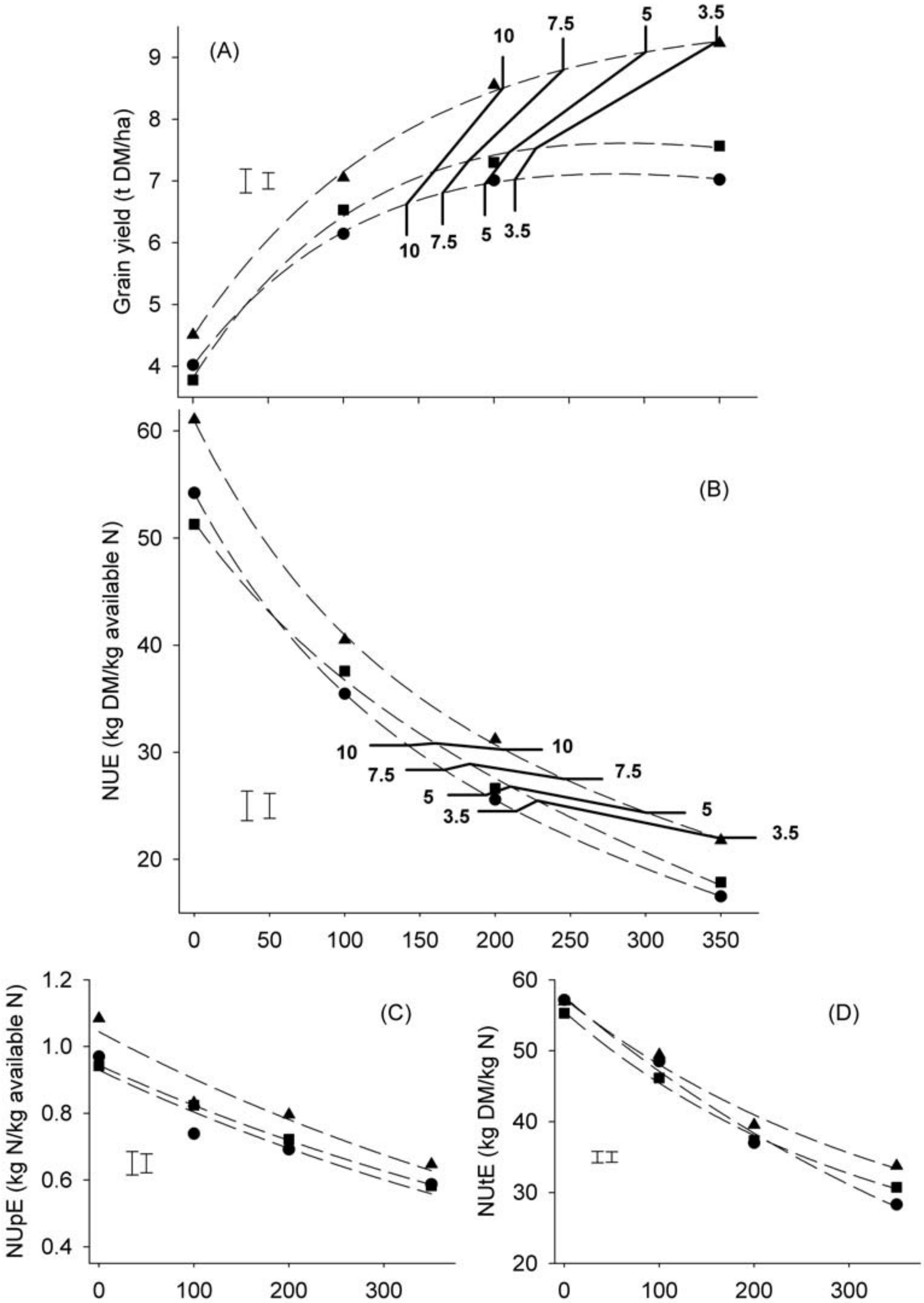

Figure 1. The effect of allele (■=*rht-B1a*, ▲=*Rht-B1b*, ●=*Rht-B1c*) and nitrogen fertilizer application rate on: A, grain yield; B, nitrogen-use efficiency (NUE, grain yield/available N); C, nitrogen uptake efficiency (NUpE; N in above ground crop/available N); and D, nitrogen utilization efficiency (NUtE; grain yield/N in above ground crop). Solid lines in A and B link points at the economically optimal levels of nitrogen application rates

for the different N:Grain (85% DM) price ratios signified by the associated numerals. Error bars are one S.E.D. for (left) comparing alleles at the same N rate, and (right) for comparing N rates with the same allele (54 d.f.)

Acknowledgements

The authors are grateful R.J. Casebow for technical support and to "Fondazione Ing. Aldo Gini" for funding a study grant to S. Loddo.

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**:249-267.

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.

Anderson, W.K., Seymour, M., D'Antuono, M.F. 1991. Evidence for differences between cultivars in responsiveness of wheat to applied nitrogen. Aus. J. Agric. Res **42**:363-377.

Barraclough, P., Howarth, Jones, J., Lopez-Bellido, R., Parmar, S., Shepherd, C.E., Hawkesford, M.J., 2010. Nitrogen efficiency of wheat: Genotypic and environmental variation and prospects for improvement. Eur. J. Agron. **33**:1-11.

Byners, B.H. 1990. Environmental effects of N fertilizer use – An overview. Fert. Res. **26:**209-215.

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

Foulkes, M.J., Sylvester-Bradley, R., Scott, R.K. 1998. Evidence for differences between winter wheat cultivars in acquisition of soil mineral nitrogen and uptake and utilization of applied fertilizer nitrogen. J. Agric. Sci. **130**:29-44.

Gooding, M.J., Addisu, M., Uppal, R.K., Snape, J., Jones H.E. 2012. Effect of wheat dwarfing genes on nitrogen use efficiency. J. Agric. Sci. **150** In Press.

Moll, R.H., Kamprath, E.J., Jackson, W.A. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agron. J. **74**:562–564.

Ortiz-Monasterio, J.I., Sayre, K.D., Rajaram, S., McMahon, M. 1997. Genetic progress in wheat yield and nitrogen-use efficiency under four nitrogen rates. Crop Sci. **37:**892-898.

Sylvester-Bradley, R., Kindred, D.R. 2009. Analysing nitrogen response of cereals to prioritize routes to the improvement of nitrogen use efficiency. J. Exp. Bot. **60**:1939-1951.