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Genotypic variation in the uptake, partitioning and remobilisation of nitrogen during grain-filling in wheat☆

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ABSTRACT

Twenty elite varieties of wheat (*Triticum aestivum* L.), primarily winter wheat, were grown with low and high supplies of nitrogen (N) in a field experiment at Rothamsted, southern England, in the season 2004–05. The aim was to quantify genetic variation in the uptake, partitioning and remobilisation of N in individual plant organs at extreme rates of N supply. The biggest contibutor to variation in plant and crop performance was 'N-rate' followed by 'growth stage' and then 'genotype'. At both N-rates, there was significant genetic variation in crop performance (grain yield, grain %N, total N-uptake and post-anthesis N-uptake), and in N contents of individual organs at anthesis and maturity, and in N remobilised from individual vegetative organs to the grain during grain-fill. Nitrogen was remobilised from all vegetative organs with very high levels of efficiency by all varieties (80–85%). Stem-N was a major N pool at anthesis probably due to the amounts of soluble N compounds in transit in the vascular system at this time. Despite the genetic variation in N-related plant parameters including stem-N, there were no strong correlations with grain yield and grain %N at a given N-rate. This was probably due to the narrow gene pool employed in this single-season study.

1. Introduction

The yield and quality of wheat grain strongly depend on the availability and uptake of nitrogen (N). High yields of high quality grain can only be achieved with high uptakes of N (Barraclough et al., 2010). A continuing challenge for intensive agriculture is to improve N use efficiency so that yields can be improved or maintained with reduced N inputs. This can be achieved by better recovery of soil and fertiliser-N and by better internal use of N by the plant. In plants, N is needed to grow a leaf canopy for intercepting radiation and for photosynthesis in green tissues. The N requirement for an optimal canopy of winter wheat (for 95% light interception) is 3 g N/m^2 green area (Sylvester-Bradley and Kindred, 2009), whilst maximum rates of photosynthesis in C_3 cereals occur at leaf N concentrations above 2 g N/m^2 green leaf (Sinclair and Horie, 1989). When N supplies are abundant, wheat plants are able to accumulate and store luxury amounts of N (not needed for current growth requirements). This is achieved by producing infertile tillers and by storing N as nitrate, amino acids, amides and soluble proteins in various organs, tissues and organelles of fertile shoots (Millard, 1988). These storage pools have an important function in high input situations where they can improve N uptake efficiency when supplies are abundant (usually pre-anthesis), and buffer dwindling root uptake (usually post-anthesis). It's plausible that stored N could ameliorate the effects of the putative 'self-destruct' hypothesis of Sinclair and De Wit (1975) in which they surmised leaf N remobilised to grain was responsible for inducing leaf senescence and hence reducing starch yield. However, Jenner et al. (1991) have disputed that leaf senescence is induced by the N demands of filling grains. Despite the continuing uncertainty over this hypothesis, it seems reasonable to suppose that remobilisation of stored N in preference to photosynthetic N from vegetative tissues would help delay leaf senescence (better yield) whilst meeting the needs for high grain protein (better quality). It would seem that storing N in high input situations is a desirable trait for both bread and feed wheat. However, there is little detailed information in the literature on where (which plant part) and how much N is present in individual plant organs particularly in relation to genetic variation in modern wheat varieties.

Many studies have reported on 'N-remobilisation during grain-filling' in wheat, but this has invariably been at a coarse level involving remobilisation from 'straw' (that is all the vegetative tissues pooled together) to grain. Examples include: Knowles and

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Watkin (1931), Spratt and Gasser (1970), Austin et al. (1977), Gregory et al. (1979), Simpson et al. (1983), Cox et al. (1986), Van Sanford and MacKown (1987), Barbottin et al. (2005), Gaju et al. (2011). Very few studies have provided a complete 'N audit' during grain filling of wheat; that is how overall crop uptake was partitioned to individual organs and subsequently remobilised to grain. Recent papers have given a more detailed breakdown of N dynamics in one or two varieties of wheat. For example, Bertheloot et al. (2008) monitored the spatio-temporal distribution of N post-anthesis in all organs of the main stems of two wheat varieties. Whilst Pask et al. (2012) measured N in (pooled) leaf laminae, sheaths and stems, and in ears of fertile shoots of a single wheat variety at anthesis and maturity. In addition, Pask attempted to partition the N in individual organs into functional pools – 'structural', 'photosynthetic' and 'reserve'.

The aim of the present study was to quantify genetic variation in the uptake, partitioning and remobilisation of N from vegetative organs to grain in a selection of wheat varieties, i.e. to provide a benchmark audit of wheat N relations. Twenty elite wheat varieties were grown at two extreme rates of N in a field experiment at Rothamsted, southern England, in the season 2004–05 and the plants subjected to a full N audit. The experiment was part of a larger series of trials conducted at Rothamsted in a 5-year period (2004–08) specifically designed to study the genetic and environmental variation in N-use efficiency in winter wheat (Barraclough et al., 2010).

2. Materials and methods

2.1. Site and weather

Rothamsted is located in southern England (latitude 52° N, longitude 1° W). The soil is a flinty, silt clay loam (25% clay) overlying clay with flints (50% clay) designated as 'Batcombe Series' in the UK Soil Classification, 'Aquic Paleudalf' in the USDA system and 'Chromic Luvisol' in the FAO system (Avery and Catt, 1995). In July, the mean maximum temperature at Rothamsted is 21 °C with 190 h of sunshine and a mean daily solar radiation of 15.66 MJ/m^2. Annual rainfall is typically 700 mm which is spread evenly over the year. In the period March–August 2005, total rainfall was 295 mm compared with the 30-year average of 314 mm. In the same period, mean daily solar radiation was 14.44 MJ/m^2.

2.2. Husbandry

The trial was conducted on Fosters field in the season 2004–05. Twenty winter wheat varieties were sown on 12 October 2004 following winter oats. Plot size was 3 m × 16 m. The wheat was precision-drilled in 12.5 cm rows at a seed rate of 350 m^{-2}. Available soil P, K and Mg were at 'Index 2' which is non-limiting to yield (MAFF, 2000). The site was top-dressed with 20 kg S/ha as potassium sulphate in March. Crops were given growth regulator and protected against weeds, pests and diseases as required.

2.3. Nitrogen fertiliser rates

Nitrogen fertiliser, as ammonium nitrate prills, was applied as a top-dressing at rates of 0 (N0) and 200 (N200) kg N/ha in a 2-way split in mid-March (50 kg N/ha at GS 24) and mid-April (150 kg N/ha at GS 31). Growth stage (GS) refers to Zadoks et al. (1974). Under UK conditions, N0 (plus 30 kg N/ha of N-min measured in the soil profile in February and any soil N mineralised during the season) would be considered deficient, and N200 sufficient for average yields (8–10 t/ha).

Table 1
Wheat varieties showing code, year of release in UK (approx.), NABIM quality group or country of origin (G – Germany).

No.	Variety	Code	Listed	Nabim
1	Avalon	AV	1979	1
2	Batis	BA	*	G
3	Cadenza	CA	1991	2
4	Claire	CL	1999	3
5	Hereward	HE	1991	1
6	Hurley	HU	2003	1
7	Istabraq	IS	2004	4
8	Lynx	LY	1993	2
9	Malacca	MA	1999	1
10	Monopol	MO	*	G
11	Maris W.	MW	1964	1
12	Paragon	PA	1999	1
13	Riband	RI	1989	3
14	Robigus	RO	2003	3
15	Savannah	SA	1998	4
16	Shamrock	SH	1999	1
17	Sokrates	SK	*	G
18	Solstice	SL	2002	1
19	Soissons	SS	1995	2
20	Xi19	XI	2002	1

* Not listed in UK.

2.4. Varieties

Twenty elite varieties of wheat (*Triticum aestivum* L.) were grown (Table 1). All varieties were of the winter habit except *cv*. Paragon which is a spring variety (but for this trial was sown in the autumn). The varieties represented a relatively narrow subset of elite genetic material with all but *cv*. Maris Widgeon carrying dwarfing genes. There were 3 varieties from Germany (Batis, Monopol and Sokrates). The remaining 15 varieties had short-straw and appeared on the UK Recommended List in the period 1979–2004 (HGCA, 2010). The UK varieties spanned the quality spectrum from 'bread' to 'feed' wheat as classified by the National Association of British and Irish Millers (NABIM, 2009). NABIM Group 1 comprises hard wheat with consistently good bread-making properties, Group 2 has bread-making potential in some seasons, Group 3 includes soft varieties suitable for making biscuits and cakes, and wheat in Group 4 is generally only suitable for animal feed.

2.5. Experimental design and statistical analysis

The 20 varieties at 2 N-rates were arranged in 3 fully randomised blocks (120 plots). Data were analysed by analysis of variance (ANOVA) using Genstat Release 13.1 (Genstat, 2010). Least significant differences (LSD) are reported at the 5% level of confidence (probably significant) ($^*P < 0.05$) together with the degrees of freedom (df).

2.6. Soil N-min

Six soil cores per block were taken to 90 cm depth in February 2005, before fertilizer was applied, to determine the mineral-N status of the site (NO_3-N and NH_4-N). The cores were taken with a 'Hydro Soil Sampler' fitted with a 3 cm diameter semi-cylindrical auger. Duplicate cores were taken at 3 random positions across each block. The cores were split into 3 depth sections, 0–30, 30–60 and 60–90 cm and the mineral-N extracted by shaking 40 g of fresh soil with 100 ml of 2 M KCl for 2 h. The slurry was allowed to settle for 30 minutes and then filtered (Whatman No.1). The solution was analysed for nitrate-N and ammonium-N with a 'Skalar San Plus' analyser. Concentrations in units of ppm in the extracted solution were converted to field units of kg N/ha by assuming a standard