The Diversity of Nitrogen Use Efficiency for Wheat Varieties and the Potential for Crop Improvement

By Malcolm J. Hawkesford

Nitrogen use efficiency (NUE) is a complex process and must be de-convoluted into tractable and measurable sub-traits, which may be targeted for specific improvement that can be included in new wheat varieties. Current research conducted at Rothamsted Research aims to define the key traits contributing to yield and NUE, and to quantify existing diversity. Evolving from these studies are genetic and molecular analyses aimed at identifying specific markers for breeding and the underlying genes involved.

Global food security requires yield improvements or an expansion of land area used for agriculture. In addition optimum resource use efficiency (RUE) is a prerequisite for sustainability. A major driver for yield, especially in intensive agricultural systems, is N fertilizer. Canopy growth requires N, and it is canopy photosynthesis that ultimately drives yield. The canopy also acts as a reservoir of N and other minerals, which are recycled into grain tissues with potentially high efficiency. Inappropriate use of N fertilizers, particularly excessive or ill-timed application can lead to poor uptake, wasted valuable resource, and potential environmental damage. Well-informed agronomic management has a crucial role in optimum fertilizer use to exploit the full potential of existing germplasm. Additional greater efficiency will require improved germplasm, with more effective capture and biomass conversion.

Definition of Nutrient Use Efficiency

There are many interpretations of nutrient and specifically N use efficiency. Fertilizer use efficiency reflects the recovery of applied fertilizer by the crop, however from the crop perspective, N (or other nutrient) use efficiency is a measure of biomass produced as a function of the N (or other nutrient) available to that crop. Key traits are illustrated in **Figure 1**. NUE in wheat is the grain yield divided by available N (fertilizer N + soil mineralized N); NUE is the product of two definable and independent major sub-traits, N uptake efficiency (NUpE) and N utilization efficiency (NUtE). NUpE is the total N taken up by the crop as a fraction of the total N available; as such it is a measure of the ability of the crop to capture available N and is principally determined by root-associated traits such as root depth proliferation and activity (e.g. transporter efficiency). Total N-uptake may be affected by sink size, in the form of above ground biomass, but also in turn, directly determines the size of this biomass. NUtE reflects the functionality of the aboveground biomass, and for wheat is defined as the grain yield as a function of the total amount of N taken up (grain + straw). Canopy architecture, function and longevity determine the production of carbohydrate for grain filling and hence yield. A complication is the need for N by the grain during grain filling, a requirement fulfilled mainly by remobilization from the senescing (and hence decreasingly functionally active) canopy. Hence the harvest index (HI) and N harvest index (NHI) are important considerations for efficient crop production.

Yield and Nitrogen

NUE and yield are being investigated in the Wheat Genetic Improvement (WGIN) trials (http://www.wgin.org.uk/). The aim is to dissect and assess variability in NUE, NUpE, and NUtE amongst modern wheat germplasm. Multiple elite commercial cultivars (primarily dwarf or short-straw varieties) are being grown, including many released in the UK over the past 25-year period, a selection of continental European varieties, and older, tall varieties. Varieties span the quality spectrum from bread to feed types. Fertilizer inputs are ammonium nitrate at five rates in the range 0 to 350 kg N/ha. A preliminary report of the first 4 years of this 10-year project has been published (Barraclough et al. 2010). Grain yield ranged from 2.1 to 11.8 t/ha (85% DM), grain %N from 1.1 to 2.8% (in DM), total N uptake from 31 to 264 kg N/ha, and grain NUtE from 27 to 77 kg DM/kg N. There were significant varietal differences in total N uptake and grain NUtE both between dwarf and non-dwarf varieties and within dwarf varieties. The best dwarf varieties took up 31 to 38 kg/ha more N than the worst, and grain NUtE was 24 to 42% better, depending on N rate. Up to 77% of the variation in grain NUtE was accounted for by

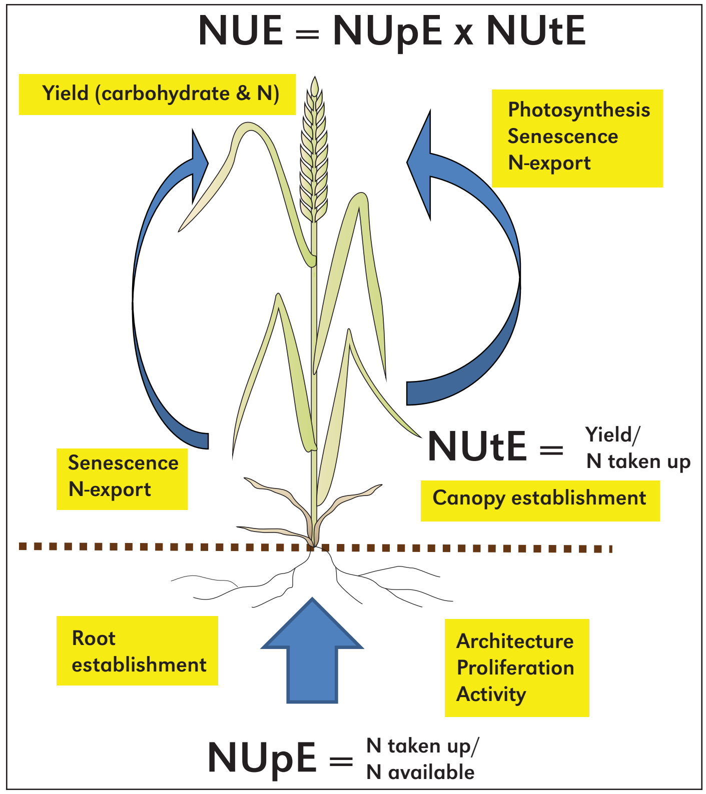

Figure 1. Diagrammatic representation of the key terms used to describe wheat nutrient use efficiency, focussing on N. Underlying physiological processes are indicated.

Common abbreviations and symbols: N = nitrogen; DM = dry matter.

yield. All interactions between the varieties, year, and N rate were highly significant.

For both yield and grain NUtE, there was an inverse relationship with grain %N; high yield is achieved by high carbohydrate content and a dilution of N (protein) and other minerals; high-quality wheat (high grain %N) can be expected to have a low grain NUtE because of the low yields of these varieties (less carbohydrate) and often the need to use even more N fertilizer to boost grain protein. Improving grain NUtE for fixed total NUp and NHI can only be achieved at the expense of grain %N. To improve grain NUtE and maintain grain %N requires a simultaneous increase in NHI and grain starch yield, which may be difficult to achieve in practice.

The summary performance for four key traits is presented in **Figure 2**. The quartile performance of 39 varieties for each of the traits is indicated. The bread-making varieties (nabim Group 1) have generally low yields but high grain %N; nabim Group 3 and 4 (biscuit and feed wheat) have the converse; uptake and utilization efficiencies reflect these performances. Clearly a goal would be to have upper ranking performances for all traits for an ideal bread wheat, however for high starch end-use wheats, high N-uptake may be a negative trait. For a subset, a detailed analysis of protein composition and the influence on dough functionality and bread-making quality has been investigated for multiple sites and years (data not shown). Grain total protein content and composition of protein have fundamental influences on quality parameters of wheat flour. Genetic variation exists in all of these traits and component traits and improvement strategies need to clearly define the targeted components and identify specific genetic variation in each, as well as environmental interactions.

Variety	nabim group	Years	Yield	%N	Uptake	Utilization
Avalon	1	5	Inter-Q	Inter-Q	Upper-Q	Inter-Q
Flanders	1	1	Lower-Q	Upper-Q	Inter-Q	Lower-Q
Hereward	1	5	Inter-Q	Inter-Q	Upper-Q	Inter-Q
Hurley	1	5	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Malacca	1	5	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Mercia	1	4	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Maris Widgeon	1	5	Lower-Q	Upper-Q	Lower-Q	Lower-Q
Shamrock	1	4	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Solstice	1	5	Inter-Q	Inter-Q	Inter-Q	Upper-Q
Spark	1	1	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Xi 19	1	5	Upper-Q	Lower-Q	Inter-Q	Upper-Q
Cadenza	2	5	Inter-Q	Inter-Q	Upper-Q	Inter-Q
Cordiale	2	3	Upper-Q	Inter-Q	Upper-Q	Inter-Q
Einstein	2	1	Inter-Q	Lower-Q	Lower-Q	Inter-Q
Lynx	2	5	Upper-Q	Inter-Q	Upper-Q	Inter-Q
Rialto	2	1	Inter-Q	Upper-Q	Inter-Q	Lower-Q
Scorpion	2	1	Upper-Q	Lower-Q	Inter-Q	Upper-Q
Soissons	2	5	Inter-Q	Upper-Q	Inter-Q	Lower-Q
Beaver	3	4	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Claire	3	4	Upper-Q	Inter-Q	Upper-Q	Upper-Q
Riband	3	5	Inter-Q	Lower-Q	Inter-Q	Upper-Q
Robigus	3	4	Upper-Q	Lower-Q	Upper-Q	Upper-Q
Istabraq	4	4	Upper-Q	Lower-Q	Inter-Q	Upper-Q
Napier	4	3	Upper-Q	Inter-Q	Upper-Q	Inter-Q
Savannah	4	4	Upper-Q	Lower-Q	Inter-Q	Upper-Q
Paragon (spring)	1	5	Inter-Q	Upper-Q	Inter-Q	Inter-Q
Chablis (spring)	2	1	Lower-Q	Lower-Q	Lower-Q	Upper-Q
Arche	F	1	Lower-Q	Inter-Q	Lower-Q	Inter-Q
Batis	G	5	Inter-Q	Inter-Q	Upper-Q	Inter-Q
Caphorn	F	1	Lower-Q	Upper-Q	Lower-Q	Lower-Q
Cappelle Desprez	F	1	Lower-Q	Upper-Q	Lower-Q	Lower-Q
Enorm	G	1	Inter-Q	Inter-Q	Upper-Q	Inter-Q
Isengrain	F	1	Lower-Q	Upper-Q	Lower-Q	Lower-Q
Monopol	G	5	Lower-Q	Upper-Q	Inter-Q	Lower-Q
Opus	G	1	Upper-Q	Lower-Q	Lower-Q	Upper-Q
PBis	G	1	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Petrus	G	1	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Sokrates	G	5	Inter-Q	Inter-Q	Inter-Q	Inter-Q
Zyta	P	1	Lower-Q	Upper-Q	Lower-Q	Lower-Q

Upper-Q | Inter-Q | Inter-Q | Lower-Q

Figure 2. Indicative performance of 39 wheat varieties for four key traits (grain yield, grain % N, total N uptake and NUtE). Varieties are grouped according to the national association of British and Irish millers (nabim) classification system, except for those originating from France (F), Germany (G), and Poland (P). Ranking in quartiles is indicated. Used with permission from Barraclough et al. 2010.

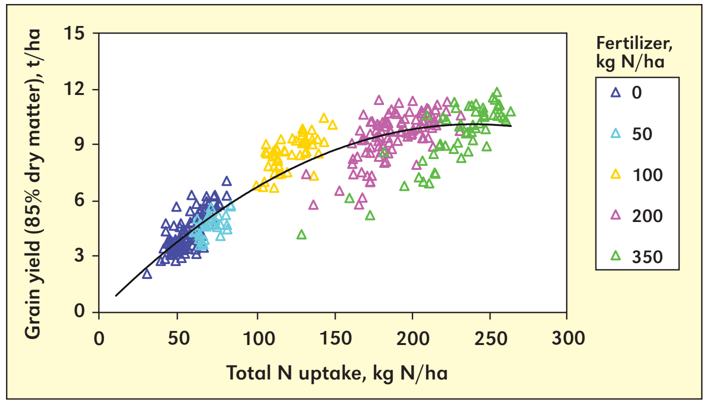

Figure 3. Effect of N fertilizer inputs on grain yield and total N uptake in 39 wheat varieties grown at Rothamsted from 2004 to 2007. A trend line shows the non-linear relationship. Adapted and used with permission from Barraclough et al. 2010.

Importantly, multiple trials facilitate evaluation of trait stability, a desired attribute with huge economic implications. Site and year-to-year seasonal variation had a major influence on trait expression, which was both a useful and valuable experimental parameter as well as a hindrance in terms of the need for replication. Over the 8 years to date, yield stability at 200 kg N/ha varied greatly, with Cadenza being the most stable variety (range: 8.3 to 10.2 t/ha) and Soissons the least (range: 5.8 to 15.5 t/ha). The year-to-year variability was mostly due to rainfall patterns and consequent influences on the duration of the grain filling period.

Limits to Yield

The relationships between N uptake and the conversion into grain yield for the WGIN dataset (2004 to 2007) are shown in **Figure 3**. Increased N application generally resulted in both increased yield and total N uptake, particularly below 200 kg N/ha; between 200 and 350 kg N/ha there was no trend for increased yield, however the total amount of N taken up increased and this was reflected in higher grain %N; generally NHI was little affected by N input (Barraclough et al. 2010). The fitted trend line shows this plateau of yield increase. This leads to a decreased NUE (for grain) but higher protein content and quality. However it is evident that factors other than N uptake are limiting yield. Whilst increasing fertilizer applications above 200 kg N/ha have little impact on yield, the benefits in

Aerial view of the N use efficiency experiments at Rothamsted.
Photograph contributed by M. Hawkesford.

terms of grain protein (increased N) positively influence flour quality and dough properties (Godfrey et al. 2010). This quality improvement comes at the cost of a decreased overall NUE at the high N inputs, and additionally, and significantly, there is greater N runoff from the crop. In the UK, wheat yields have continued to rise over the past 20 years at around 0.1 t per year due to husbandry and genetic improvements, whilst N fertilizer use has remained static at 190 kg/ha, largely as a result of legislative control (limiting N inputs in Nitrogen Vulnerable Zones in the UK); this data indicates that this would be at the cost of grain N and furthermore that raising N inputs would not impact directly on yield with current germplasm.

Prospects

The key target traits for improved NUE are focused on improved capture and consist of enhancing root depth and proliferation and possibly root functioning. Increasing yield is focused on canopy longevity with early flowering or late maturation offering benefits but with high risk of crop failure. Screening has focused on the analysis of a relatively restricted set of germplasm and mapping populations where there is limited diversity. Evolving strategies such as the Wheat Strategic Improvement Programme (WISP) (http://www.wheatisp.org/), and others, are examining older and more diverse germplasm or are generating novel germplasm by the production of synthetic hexaploids or through chromosome segment introgression using wheat relatives. Linking screening programmes to transcriptome analyses and high-density genotyping has the potential to identify the specific genes and alleles involved which will speed plant breeding, including genes for high yield and efficient nutrient scavenging.

Summary

Is striving for efficient fertilizer use at odds with the need for increased crop production and food security? The two objectives are bound together: an important and essential component of crop production is efficient use of N fertilizer. In spite of the costs, both economic and environmental, worldwide efficiency has been estimated at only 30% of that applied to that recovered as harvested grain. As such NUE is a key target for crop improvement, both in terms of agronomy management and germplasm selection. BC

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Notes on Describing Nutrient Use Efficiency

There are many ways to assess nutrient use efficiency depending on the purpose to which the data will be put. In this article, nitrogen use efficiency is assessed using two measures. The Table below summarizes the terms used in this article compared to other commonly used nutrient efficiency terms.

Term	Calculation
Nutrient Uptake Efficiency	NUpE = (kg nutrient taken up)/(kg nutrient available) = U/(F+S)
Nutrient Utilization Efficiency (Internal Utilization Efficiency)	NUtE = (kg grain produced)/(kg nutrient taken up) = Y/U
Apparent Recovery Efficiency	RE = (kg increase in uptake)/(kg fertilizer applied) = $(U - U_0)/F$ (whole plant) = $(Ug-U_0g)/F$ (grain only)
Physiological Efficiency	PE = (kg yield increase)/(kg fertilizer nutrient uptake) = $(Y-Y_0)/(U-U_0)$
Agronomic Efficiency	AE = (kg yield increase)/(kg nutrient applied) = $(Y-Y_0)/F$ = RE x PE
Partial Nutrient Balance (Nutrient Removal Ratio)	PNB = (kg nutrient removed)/(kg applied) = Ug/F
Partial Factor Productivity	PFP = (kg yield)/(kg nutrient applied) = Y/F = (Y_0/F)

Y = crop yield with applied nutrient; Y_0 = crop yield with no applied nutrient; F = fertilizer applied; S = nutrient in the soil; U = plant nutrient uptake of above ground biomass at maturity; U_0 = plant uptake with zero fertilizer; Ug = grain nutrient content with applied nutrient; U_0g = grain nutrient content with no applied nutrient.