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ABSTRACT

All crops require nitrogen (N) for the production of a photosynthetically active canopy, whose functionality will strongly influence yield. Cereal crops also require N for storage proteins in the grain, an important quality attribute. Optimal efficiency is achieved by the controlled remobilization of canopy-N to the developing grain during crop maturation. Whilst N will always be required for crop production, targeting efficient capture and use will optimise consumption of this valuable macronutrient. Efficient management of N through agronomic practice and use of appropriate germplasm are essential for sustainability of agricultural production. Both the economic demands of agriculture and the need to avoid negative environmental impacts of N-pollutants, such as nitrate in water courses or release of Ncontaining greenhouse gases, are important drivers to seek the most efficient than yield alone will be required. Targets for genetic improvement involve maximising capture, partitioning and remobilization in the canopy and to the grain, and yield *per se.* Whilst there is existing genetic diversity amongst modern cultivars, substantial improvements may require exploitation of a wider germplasm pool, utilizing land races and ancestral germplasm.

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1. Introduction

There is an absolute requirement for N for plant growth, and crop yields and quality depend upon substantial N inputs. Chemical N fertilizers were first used in agriculture in the 19th century, and subsequently to a much greater extent after the development of the Haber–Bosch process at the beginning of the 20th century. At the present time, more than half of the chemically fixed N is used by agriculture, amounting to in excess of 80 Mt per year, worldwide.

Cereal crops are a major staple food worldwide, contributing more than 50% of total human calorie input directly. Crop production needs to continue to grow with increasing demand, and both improved yields and sustainability are major challenges facing current agriculture. Worldwide production systems vary greatly depending on climatic and soil fertility factors. In all agricultural systems there is a need for adequate nutrients, usually supplied as

Abbreviations: GPD, grain protein deviation; HI, harvest index; NHI, nitrogen harvest index; NUE, nitrogen use efficiency; NUpE, nitrogen utilization efficiency; SSA, sub-Saharan Africa; WGIN, Wheat Genetic Improvement Network.

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fertilizer in areas of higher production. N is a major macronutrient often limiting plant growth. The application of N fertilizers in agriculture has increased markedly since the middle of the 20th century due to the impact of the 'green revolution' which combined best agronomic practice with the use of germplasm better able to respond to applied N. Increasing N supply to a crop drives the production of a greater canopy biomass with the potential for higher photosynthesis and productivity. However, a penalty for a large biomass can be a susceptibility to lodging. The adoption of short and stiff strawed cultivars substantially overcomes this issue, which may be further alleviated with the use of chemical growth regulators. In addition, the high harvest indexes (ratio of grain to total biomass at harvest) associated with short cultivars, further contributes to resource use efficiency, with little residual N remaining in the straw after grain harvest.

Most measures of NUE (nitrogen use efficiency) relate production as a function of inputs, and given constant inputs, any yield increase will be reflected in greater NUE. However, comparisons of high versus low input systems are more difficult with such crude definitions, giving misleading indications of high efficiency at low or zero inputs.

Although greater N application has produced higher yields, this is not a linear relationship (see below) and there is an economic optimum application offsetting incremental yield increase against

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Review





the cost of additional N inputs, which needs to be determined for individual cultivars (Foulkes et al., 1998; King et al., 2003). Availability of N has impacts throughout crop development, affecting seedling establishment, tillering, canopy development as well as grain filling, all of which have the potential to influence final yield and together determine the N requirements of the crop. The optimization of crop production and NUE is a complex problem and will require a complex set of solutions to achieve improvement.

2. Trends in yield and NUE

In the second half of the 20th century cereal yields have increased, for example for wheat, worldwide from 1 to 3 t ha⁻¹ (Fischer and Edmeades, 2010; Hawkesford et al., 2013) and in the UK from less than $3 \text{ t} \text{ ha}^{-1}$ to around $8 \text{ t} \text{ ha}^{-1}$ (Fig. 1). This is exemplified by data on UK wheat yields (Fig. 1). Increases were greatest in the 1970s due to the introduction of short straw cultivars which enabled higher N inputs, facilitating larger canopies with reduced susceptibility to lodging. Since then, yield rises have been more modest or have even stagnated both in the UK and elsewhere (Brisson et al., 2010). In the UK, N fertilizer inputs increased up to the 1980s, supporting the increasing yields. Since then, legislation has limited N application and UK average N fertilizer rates have stabilised at under 200 kg N ha^{-1} (Fig. 1). The relatively modest recent yield increases $(1-2 \text{ t} \text{ ha}^{-1} \text{ over the past})$ 30 years) with stable N inputs equate to a higher NUE at the national level in the UK.

The impacts of adding more N are illustrated in Figs. 2 and 3. Data taken from the Broadbalk classical experiment at Rothamsted (Fig. 2) illustrate the positive benefit of increased yield with increasing N fertilizer addition up to around 192 kg ha⁻¹, after which there is little apparent increase in yield for the cultivars tested. These data also illustrate the negative impact of increased leaching at the higher N applications. When NUE is calculated as a function of grain yield per estimated N input, this decreases with the increasing N input (Hawkesford, 2011).

The positive impact of increasing yield together with the additional benefit of increasing N content of the crop with increasing N application is shown from an analysis of experimental data from the UK Wheat Genetic Improvement Network (WGIN) in trials at Rothamsted (Fig. 3). With N fertilizer application between 0 and 200 kg N ha⁻¹, both yield and N uptake increase substantially. At the highest N application rate (350 kg ha⁻¹), no further yield increase occurs although further N uptake is apparent. Much of the

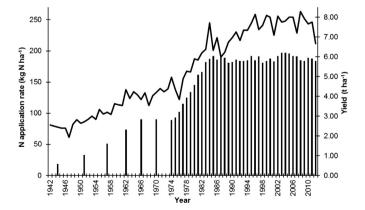


Fig. 1. Wheat yields (continuous line) since 1942 in Great Britain and available information on the pattern of N application rates for England and Wales (bar chart) to cereal crops over the same period. Data extracted from UK Department of Food and Rural Affairs, the Rothamsted archive and British Survey of Fertilizer Practice. Figure courtesy of Chris Dawson and Associates, UK.

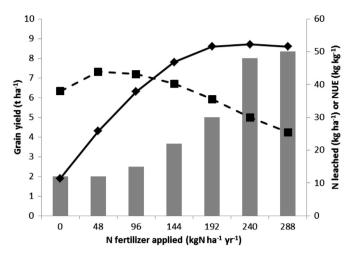


Fig. 2. Illustration of impact of N fertilizer application on winter wheat yield (solid line, diamonds), N-losses due to leaching (bar chart) and estimated grain NUE (dashed line, squares). Data taken from the Broadbalk long-term experiment at Rothamsted, from 1990 to 1998 (cv. Apollo 1990–1995 and cv. Hereward 1996–1998). Modified from Hawkesford (2011) and used with permission (Wiley and Sons, Ltd: Chichester).

additional N taken up is manifest in higher grain N content (data not shown). The scatter at each N input rate reflects the wide variation in cultivars used in the trials and the contrasting weather patterns in the 4 years of the trials presented. The inability of the crop to respond to the increased N above 200 kg ha⁻¹ in terms of increased yield reflects factors other than N-limited yield, most likely source productivity. This source limitation may be intrinsic photosynthetic efficiency or water limitation. The genetic potential of these cultivars should be well in excess of the mean achieved under these treatments (10–11 t ha⁻¹). The only modest increase in grain N, in spite of a huge increase in N application (350 compared to 200 kg N ha⁻¹), indicates either poor capture or a lack of sinks to utilize the available N.

3. Definitions and nitrogen cycles

Reducing the N requirements of cereals implies an increase in efficiency of use of applied N. Greater yields with less inputs would seem to be an ideal trait, however, there are severe constraints on such a simplistic goal and it is necessary to consider individually the final crop product and the component physiological traits which contribute to NUE. Increasing yield with no increase in inputs will by definition give greater use efficiency, but this may be at the expense of quality attributes. These issues are discussed below.

There are many definitions of NUE (Fageria et al., 2008; Good et al., 2004). For example, NUE may be defined as yield per unit of N available to the crop (Moll et al., 1982). Available N includes fertilizer inputs, atmospheric deposition and mineralization within the soil. N available from soil mineralization is dependent upon soil organic matter and the history of the crop land use. Additionally, rotations including leguminous crops will contribute to soil N from biological N fixation.

The overall trait of NUE may be divided into N uptake efficiency (NUpE) and N utilization efficiency (NUtE), with NUE being the product of the two (Moll et al., 1982). NUpE may be defined as the amount of N taken up by the crop as a fraction of the amount available to the crop from all sources. This trait is predominantly associated with root structure and functioning, although available sinks may limit the ability to efficiently take up available N. Ideal traits will include early root proliferation to scavenge N before fertilizer application, proliferation near to the surface to enable

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