Analysis of improvements in nitrogen use efficiency associated with 75 years of spring barley breeding

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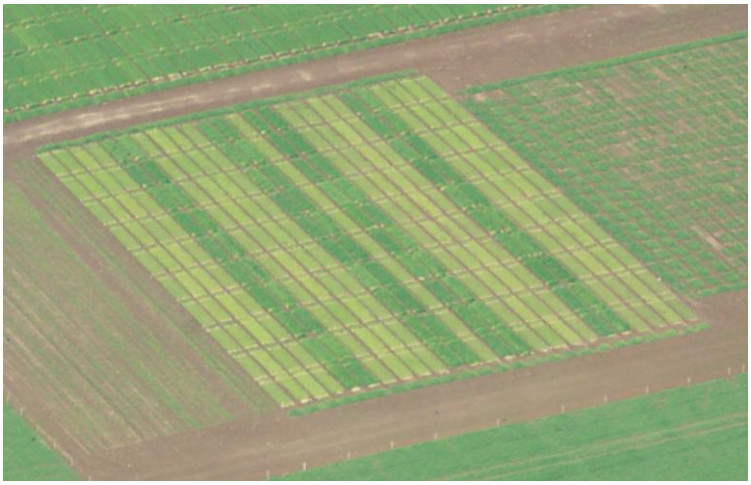

Poor access to N fertilizer is a major limitation to crop productivity in some developing countries, whilst in other more affluent countries increased productivity over recent decades has been associated with a substantial increase in N fertilizer use. However, high fertilizer N use is also environmentally damaging; the manufacture of inorganic N-fertilizer is an energy intensive process and N can be lost from the soil via leaching and gaseous emissions contributing to eutrophication and global warming. It is now widely recognised that nitrogen use efficiency (NUE) must be improved so that cereal yields can be increased to meet the growing global demand for grain, but with reduced inputs of fertilizer. These improvements can be sought in two complementary ways: firstly through changes to crop management and fertilizer practice and secondly through plant breeding and the development of more efficient varieties. The latter approach requires information on which phenotypic traits govern NUE, the scale of variation in these traits within the breeding population and the extent to which the environment influences the expression of the phenotype.

To this end a retrospective analysis of the effects of nearly 75 years of breeding for grain yield on the NUE of spring barley (*Hordeumvulgare* L.) was undertaken to identify physiological mechanisms governing NUE and targets for future improvement. Fifteen European varieties, selected to represent the breeding period from 1931 to 2005 and to be as genetically dissimilar as possible based on single nucleotide polymorphism markers, were grown at three site-year combinations in the NE of Scotland. Varieties were grown with zero or 110 kg N ha^{-1} supplied as ammonium nitrate. Averaged across site-years, breeding was shown to increase yield and NUE (grain yield N $supply^{-1}$) by 1 and 1.2% per year respectively in the presence of fertilizer. Modern varieties were able to produce more grains per m^2 in response to N-fertilizer and had a larger mean grain weight and lower grain N concentrationthan old varieties. In the absence of fertilizer, grain numbers were similar in old and modern varieties, but modern varieties still out-yielded old varieties because they maintained a larger mean grain weight.

NUE is the product of the N uptake efficiency (NupE; N offtake per unit N supply) and the N utilization efficiency ($NutE_g$, grain yield per unit N offtake). Significant variation was found between genotypes in both NupE and $NutE_g$. Differences in $NutE_g$ contributed 60% to the variation in NUE, whilst NupE contributed 40%. Across all varieties NupE was not related to $NutE_g$ suggesting that improvements in each may be selected independently. The improvement in $NutE_g$ was mostly the result of a greater allocation of dry matter to the grain (increasedharvest index) in modern varieties and importantly was stable across environments. The stability of $NutE_g$ makes it an attractive route to further improvements in NUE and there appears to be some scope for achieving this by continuing to increase post-anthesis dry matter production and partitioning to grain. However, as further reductions in grain N concentration may be unacceptable for some barley markets, increases in grain yield will need to be accompanied by improvements in N remobilisation and partitioning to the grain.

In contrast to $NutE_g$, effects of breeding on NupE were less stable across environments. NupE was positively correlated with post-anthesis, but not pre-anthesis, dry matter accumulation and N

uptake, which suggests that the greater NupE of some varieties might be the result of an increased N demand from a large grain sink. Improving N capture pre-anthesis to facilitate reductions in N-fertilizer applications may require investigation of root traits in a wider range of germplasm than that used in the current study, including landraces and wild relatives of barley. The current research has highlighted some of the mechanisms underlying improvements in NUE arising from breeding for grain yield in barley. This understanding will help target selection of traits specifically for improving NUE in the future. Genotypes that were found to contrast in NupEin the current study are now being used as tools to investigate the mechanisms regulating post-anthesis N uptake.

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