

Nitrogen Uptake, Utilisation and Use Efficiency of Different Wheat Species

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Abstract

Breeding wheat (*Triticum aestivum* L.) for high nitrogen use efficiency while maintaining adequate yield, is widely accepted as one of the approaches to maximise farmers' revenue and minimise pollution risk. However, due to random hybridization events during evaluation and selective breeding for high yield, genetic diversity of existing bread wheat is narrowed down. The present study was conducted to investigate the nitrogen use efficiency and its components of ancient wheat species, a potential source to expand the genetic diversity of bread wheat. Three field experiments were carried out in 2012, 2013 and 2014 at Sutton Bonnington Campus, University of Nottingham, UK. Ten genotypes belonging to einkorn, emmer, spelt and modern bread wheat were used as genetic materials of the experiments and three nitrogen levels were compared. Nitrogen uptake efficiency, nitrogen utilisation efficiency and nitrogen use efficiency were calculated at harvest. Nitrogen use efficiency among genotypes varied significantly and bread wheat recorded the highest value followed by spelt, emmer and einkorn. However, in general, nitrogen uptake efficiency was high in emmer and spelt compared to bread wheat. Nitrogen utilisation efficiency of bread wheat was always higher than ancient wheat genotypes resulting in high nitrogen use efficiency. Nitrogen supply has a negative relationship with nitrogen uptake efficiency. According to the results, it can be concluded that ancient wheat genotypes uptake more nitrogen hence high nitrogen uptake efficiency when compared to modern bread wheat. However, the ability to utilise nitrogen in the plants to develop grains is high in modern bread wheat.

Keywords: Ancient wheat species, Genotypes, Nitrogen uptake efficiency, Nitrogen utilisation efficiency, Nitrogen use efficiency

Introduction

Dependence of food production on nitrogen (N) fertiliser increases significantly with the influence of global population growth. Without N fertiliser in agriculture, it is not possible to fulfil the current demand of food energy and protein. Wheat (*Triticum aestivum* L.) is the major arable crop with a total annual production of about 15 Mt in the UK. Wheat requires large inputs of fertiliser N to achieve high yield under intensive cultivation. However, all applied fertiliser is not taken up by the crop and large amounts are lost to the environment. Breeding crops for high N use efficiency (NUE; grain dry matter yield per unit availability of N from soil and/or fertiliser) while maintaining acceptable yield, is widely accepted as one of the approaches to maximise farmers' revenue and minimise pollution risk by reducing N fertiliser application.

Responses of NUE to different levels of N supply are well documented for bread wheat. Additional supply of N fertiliser always decreases NUE [Chamorro *et al.*, 2002, Gaju *et al.*, 2011]. The level of N in the soil plays an important role in the expression of NUpE and NUtE [Ortiz-Monasterio, 1997]. Low NUE is associated with high N loss and cost of production. Genetic variation in NUE and the interaction between varieties and N regimes were reported in major cereal crops like wheat [Ortiz-Monasterio, 1997], maize [Moll, 1982] and rice [Borrell *et al.*, 1998]. However, genotype and/or environment contribute significantly to the expression of either NUpE or NUtE under different soil N regimes [Coqueue & Gallais, 2006]. Gaju *et al.* (2011) reported significant genetic variation for NUE, NUpE and NUtE in bread wheat.

Dhugga & Waines (1989) found that the NUpE to be the dominant component of NUE at low and

high N levels for field grown spring bread wheat and durum wheat [Ehdaie *et al.*, 2001]. NUpE showed a strong relationship with NUE under low N while NUtE was more important under high N for 10 wheat varieties grown in Mexico [Ortiz-Monasterio, 1997]. Gaju *et al.* (2011) found a stronger relationship between NUE and NUtE than the relationship between NUE and NUpE in winter wheat under high N and low N conditions. The lack of relationship between NUpE and NUtE in barley suggests that improvement of each component can be done independently [Bingham *et al.*, 2012]. Further, NUtE has a strong relationship with harvest index while increased NUpE of some barley varieties may be associated with a large grain sink. Contribution of components of NUE varied in different varieties having similar levels of NUE. It is suggesting that potential traits related to each component could be used to improve NUE in wheat. Fischer (1981), more than 30 years ago in his review of water and N use efficiency, concluded that there is a possibility to improve NUpE in wheat though NUtE automatically increased with improved yield.

Development of new varieties/cultivars with high NUE through traditional plant breeding and modern biotechnology could be used to improve NUE. However, one of the many challenges faced by wheat breeders is the narrowed genetic diversity of existing bread wheat cultivars due to the selective breeding for high yield. Desirable traits could be identified using existing varieties and ancient wheat germplasm. For example, ancient wheat species of einkorn, emmer, and spelt could be used to strengthen the variation of traits related to NUE in wheat breeding. Appropriate crosses between selected varieties or species may be implemented to introduce new traits to a segregation population. Further, QTL studies can be performed to identify useful lines having high NUE within the segregation population [Hirel, 2007]. Therefore, the present study was conducted to investigate the nitrogen use efficiency and its components of ancient wheat species, a potential source to expand the genetic diversity of modern bread wheat.

Methods

Nitrogen uptake efficiency (NUpE), N utilisation efficiency (NUtE) and consequently N use efficiency (NUE) were calculated for four wheat

species under recommended nitrogen fertiliser in 2011-2012 (2012 hereafter) and three nitrogen regimes in two field experiments in 2012-2013 (2013 hereafter) and 2013-2014 (2014 hereafter). They included cultivated einkorn (*Triticum monococcum* L., a diploid), cultivated emmer (*T. dicoccum*, a tetraploid) and spelt (*T. spelta* L., a hexaploid), together with modern bread wheat (*T. aestivum*, a hexaploid). Ten genotypes were used; three einkorn (1, 2 and 3), two emmer (1 and 2), three cultivars of spelt (SB, Oberkulmer and Tauro) and two cultivars of modern bread wheat (Xi 19 and JB Diego). Due to the poor establishment and growth performances emmer 1 and einkorn 3 were removed from the 2013 experiment and all einkorn genotypes were excluded from the experiment in 2014. Randomised complete block design was used in 2012 experiment while split plot design was used in both experiments in 2013 and 2014 where N treatment was randomised on main plot and genotypes on the sub-plot with three replicates. Three N regimes equal to zero N (no fertiliser N applied; NN), 100 kgN ha⁻¹ (Low N; LN) and 200 kgN ha⁻¹ (High N; HN) were used in 2013 while 100 kgN ha⁻¹ and 150 kgN ha⁻¹ was applied to LN and HN plots, respectively in 2014, based on the results of soil mineral N analysis of the respective year. Recommended N fertiliser level for wheat in the UK (220 kgN ha⁻¹) was applied for the 2012 experiment. NH₄NO₃ was applied as N fertiliser and plant growth regulators were applied three times from stem elongation to flag leaf emergence at 1.4 ha⁻¹ (Chlormequat chloride), 0.2 ha⁻¹ (Trinexapac-ethyl) and 0.5 ha⁻¹ (Mepiquat chloride and 2-chloroethylphosphonic acid). All experiments were conducted at University of Nottingham Farm in Sutton Bonington, UK (52° 50' N, 1° 15' W).

Pre-harvest sampling and N analysis

The pre-harvest sampling was done at maturity when all plants were fully senesced using a quadrant. A quadrat of 0.72 m² (1.2 m × 0.6 m) was used in 2013 field experiments due to the uneven establishment of the genotypes while 0.25 m² (0.5 m × 0.5 m) was used in 2012 and 2014 field experiments. Plants were uprooted and placed directly into pre-labelled paper sacks in the field to avoid grain losses during transport. Grain yield and above-ground biomass were taken at harvest while NUpE (equation 1), NUtE (equation 2) and NUE (equation 3) were calculated based on

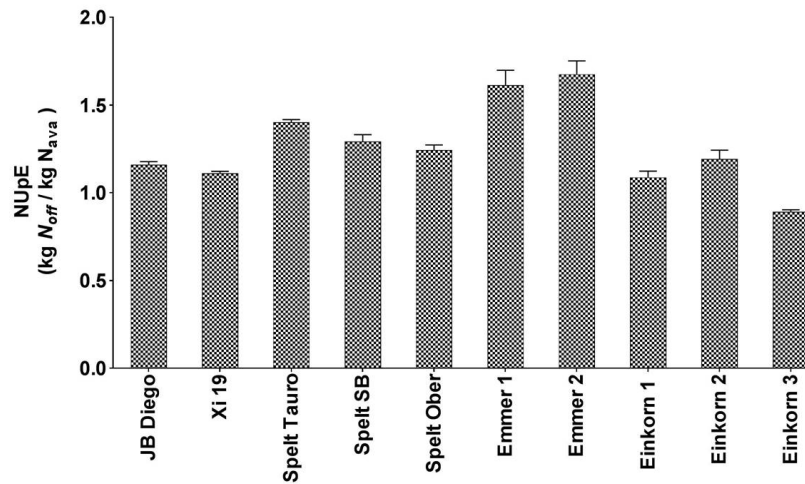


Figure 1: NUpE of ten genotypes at maturity in 2012 experiment. Error bars represent SE of the mean of genotype ($df = 27$)

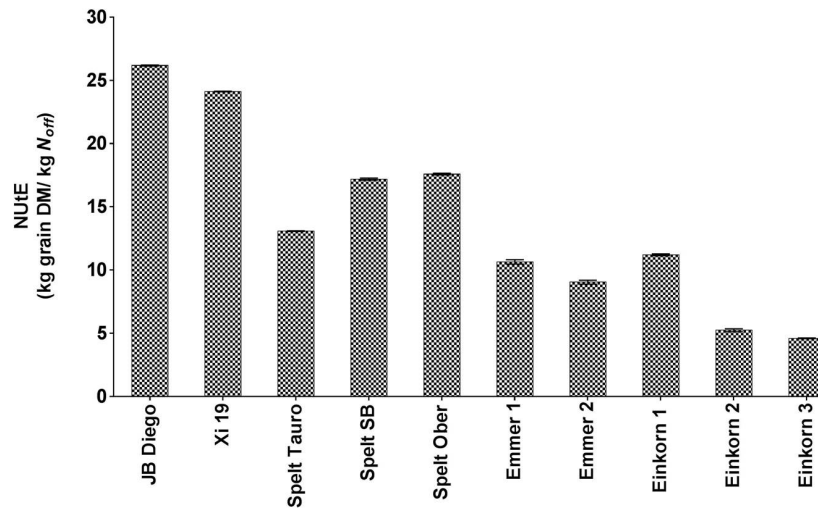


Figure 2: NUtE of ten genotypes at maturity in 2012 experiment. Error bars represent SE of the mean of genotype ($df = 27$)

nitrogen content of the plant dry matter [Bingham *et al.*, 2012]. N_{off} does not include root N in the calculation. In the laboratory, fresh weight of the quadrat sample was recorded before being oven dried to obtain dry weight at 80°C for 48 hours. The dried ears were hand threshed carefully and separated grains from the chaff. Grain samples were re-dried to achieve dry weight of the seeds.

N_{ava} = nitrogen supply as fertiliser and soil mineral nitrogen availability of the soil

$$NUtE = \frac{Grain\ yield\ (kg\ ha^{-1})}{N_{off}(kgN\ ha^{-1})} \quad (2)$$

Therefore,

$$NUpE = \frac{N_{off}\ (kgN\ ha^{-1})}{N_{ava}\ (kgN\ ha^{-1})} \quad (1)$$

where N_{off} = total shoot nitrogen content,

$$NUtE = \frac{N_{off}\ (kgN\ ha^{-1})}{N_{ava}\ (kgN\ ha^{-1})} \times \frac{Grain\ yield\ (kg\ ha^{-1})}{N_{off}(kgN\ ha^{-1})}$$

Table 1: NUpE of the genotypes at maturity in 2013 and 2014 experiments for three N levels

GT	NUpE (kg N _{off} / kg N _{ava})					
	2013			2014		
	NN	LN	HN	NN	LN	HN
JB Diego	1.99	1.28	0.91	1.74	1.28	1.34
Xi 19	2	1.23	0.94	1.82	1.15	1.06
Spelt Tauro	2.55	1.28	1.01	2.03	1.3	1.45
Spelt SB	2.26	1.4	0.98	2.11	1.39	1.31
Spelt Oberkulmer	2.31	1.57	0.95	1.9	1.22	1.35
Emmer 1	-	-	-	1.9	1.23	1.37
Emmer 2	2.31	1.37	1.11	1.88	1.29	1.56
Einkorn 1	1.85	1.13	0.68	-	-	-
Einkorn 2	1.73	1.04	0.81	-	-	-
SED ; GT (df)	0.116 (42)***			0.082 (36)*		
N (df)	0.170(4)**			0.025 (4)***		
GT × N (df)	0.254 (17.2) ^{NS}			0.135(38.3) ^{NS}		

NN; zero fertiliser applied, LN; 100 kg N ha⁻¹ and HN; 200 kg N ha⁻¹ in 2013 and LN; 100 kg N ha⁻¹ HN; 150 kg N ha⁻¹ in 2014

***significant at P<0.001, **significant at P<0.01, *significant at P<0.05, NS - Not significant

Table 2: NUtE of the genotypes at maturity in 2013 and 2014 experiments for three N levels

GT	NUtE (kg grain DM/ kg N _{off})					
	2013			2014		
	NN	LN	HN	NN	LN	HN
JB Diego	49.87	39.63	32.32	49.18	40.56	31.97
Xi 19	45.63	36.28	32.23	39.98	36.24	30.06
Spelt Tauro	29.83	25.95	23.92	33.45	26.33	20.81
Spelt SB	31.27	27.48	25.12	36.68	28.69	22.33
Spelt Oberkulmer	27.83	26.03	23.53	33.12	28.1	21.46
Emmer 1	-	-	-	34.71	26.7	16.13
Emmer 2	35.79	25.78	22.7	36.54	25.81	15.17
Einkorn 1	26.6	19.35	22.06	-	-	-
Einkorn 2	30.74	22.55	23.66	-	-	-
SED ; GT (df)	0.779 (42)***			0.497 (36)***		
N (df)	0.422(4)***			0.628(4)***		
GT × N (df)	1.331 (45.9)***			1.015(38.3)***		

NN; zero fertiliser applied, LN; 100 kg N ha⁻¹ and HN; 200 kg N ha⁻¹ in 2013 and LN; 100 kg N ha⁻¹ HN; 150 kg N ha⁻¹ in 2014

***significant at P<0.001

or

$$NUE = NUpE \times NUtE \quad (3)$$

Plant materials were ground to achieve a particle size of <200 m. Then, 45 to 50 mg

of samples were weighed and encapsulated in tin capsules. The encapsulated samples were then analysed for N% according to the Dumas method using a Fisons NA-2000 elemental analyser (Fisons, Ipswich, UK) calibrated against Methyl-

N standard (N content = 9.28%). N content in straw, grain and chaff was analysed at maturity and presented as a percentage.

Statistical Analysis

Analysis of variance relevant to the experimental design was performed to test the phenotypic differences and N fertiliser effect on NUpE, NUtE and NUE. Data were analysed using GenStat 15th edition.

Results and Discussion

Nitrogen uptake efficiency

Nitrogen uptake efficiency (NUpE) of emmer 2 was higher than all other genotypes (Figure 1) ($P < 0.01$). The lowest NUpE was observed in einkorn 3. Nine out of ten genotypes had NUpE greater than one which was due to residual N in the soil and N supply through mineralisation during the season. For NUpE, the effect of error accounted for a larger percentage (66%) of the variation than genotype (34%) in 2012. As a species, emmer had the highest NUpE followed by spelt, bread wheat and einkorn. Moreover, NUpE of emmer was 18, 29 and 36% higher than spelt, bread wheat and einkorn, respectively. NUpE of the genotypes varied significantly ($P < 0.001$) and decreased with N supply ($P < 0.01$) in 2013. Spelt Tauro and emmer 2 had the highest NUpE at NN and HN, respectively while einkorn 2 and einkorn 1 recorded the lowest NUpE at NN and HN, respectively. However, NUpE of bread wheat, spelt and emmer genotypes were not significantly different at HN but significant at NN in 2013 (Table 1). In 2014, genotypes ($P < 0.05$) and N treatment ($P < 0.001$) had a significant effect on plant NUpE. At NN and HN, spelt SB and emmer 2 recorded the highest NUpE, respectively (Table 1). At HN, NUpE of emmer 2 and spelt Tauro was significantly higher than all other genotypes but at NN, significant differences between genotypes of emmer, spelt and bread wheat were not found.

Effect of the species and N treatment ($P < 0.01$) were significant for NUpE in 2013 where the highest NUpE was observed in spelt followed by emmer, bread wheat and einkorn at NN. However, emmer had a greater NUpE than spelt at HN. In 2014, NUpE was more strongly affected by N treatment ($P < 0.001$) than species ($P < 0.05$). The 2013 and 2014 experiments showed a similar contribution of genotype, N and $GT \times N$ on total

variance of NUpE. Total variance of NUpE varied mainly due to N treatment than genotypic effect for both years (Figure 4A).

N utilisation efficiency

NUtE was significantly affected by genotype ($P < 0.001$) where bread wheat cvs had the highest NUtE (26.18 for cv. JB Diego and 24.12 for cv. Xi 19) while einkorn 2 (5.24) and einkorn 3 (4.61) had low values (Figure 2) in 2012. The contribution from genotype for the total variance of NUtE was 90%. Therefore, it could be suggested that the genotypic effect is more prominent for NUtE than the environment. As a species, bread wheat had the highest NUtE followed by spelt, emmer and einkorn.

In 2013 and 2014 experiments, genotype, N treatment and $GT \times N$ interaction significantly affected NUtE where bread wheat cv. JB Diego had the highest NUtE at any level of N and decreased with N supply. Einkorn 1 recorded the lowest NUtE for all N regimes in 2013 and spelt Oberkulmer at NN and emmer 2 at HN in 2014. NUtE of bread wheat was 40, 38 and 25% higher than einkorn, spelt and emmer at NN and 29, 25 and 30% at HN in 2013 experiment (Table 2). Interestingly, the genotypic contribution for total variance was high for NUtE reporting 63% and 40% in 2013 and 2014, respectively where variance due to N was also high (26% and 55% in 2013 and 2014, respectively) (Figure 4B).

Nitrogen use efficiency

The highest NUE was recorded in bread wheat cv. JB Diego (29.95) while the lowest value was observed for einkorn 3 (4.14) ($P < 0.001$). Nevertheless, NUE of spelt SB and spelt Oberkulmer was not significantly different from bread wheat cv. JB Diego and cv. Xi 19 (Figure 3). The effect of genotype accounted for 66% of the total variance. As a species, as expected, NUE of bread wheat was higher than three ancient wheat species where NUE of bread wheat was 22, 33 and 71% greater than spelt, emmer and einkorn, respectively. NUE was not significantly different between spelt and emmer in 2012. As expected, bread wheat (JB Diego and Xi 19) recorded the highest NUE at all N treatments while einkorn genotypes had lowest NUE (Table 3) in 2013. However, N supply significantly decreased NUE of all the genotypes. In general, NUE at NN was 67% higher than HN. When averaged across species, bread wheat

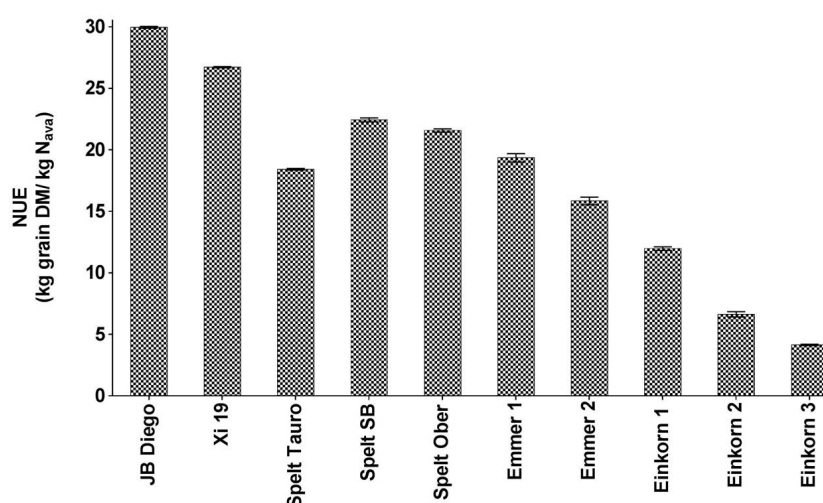


Figure 3: NUE of ten genotypes at maturity in 2012 experiment. Error bars represent SE of the mean of genotype ($df = 27$)

Table 3: NUE of the genotypes at maturity in 2013 and 2014 experiments for three N levels

GT	NUE (kg grain DM/ kg N _{ava})					
	2013			2014		
	NN	LN	HN	NN	LN	HN
JB Diego	96.61	50.31	29.25	85.26	51.59	42.94
Xi 19	89.06	44.64	30.28	72.91	41.7	31.89
Spelt Tauro	76.11	33.25	24.36	67.83	34.11	30.15
Spelt SB	70.23	38.56	24.68	77.1	40.02	29.25
Spelt Oberkulmer	65.05	40.75	22.35	62.9	34.37	28.85
Emmer 1	-	-	-	65.84	32.92	22.15
Emmer 2	83.05	35.29	24.99	68.88	33.42	23.68
Einkorn 1	49.05	21.87	15.12	-	-	-
Einkorn 2	53.06	23.84	19.19	-	-	-
SED ; GT (df)	3.572 (42)***			2.653 (36)***		
N (df)	5.487 (4)**			1.213 (4)***		
GT × N (df)	7.975 (16)*			4.424 (39.7) ^{NS}		

NN; zero fertiliser applied, LN; 100 kg N ha⁻¹ and HN; 200 kg N ha⁻¹ in 2013 and LN; 100 kg N ha⁻¹ HN; 150 kg N ha⁻¹ in 2014

***significant at $P < 0.001$, **significant at $P < 0.01$, *significant at $P < 0.05$, NS - Not significant

had the highest NUE followed by emmer, spelt and einkorn although spelt and emmer was not significantly different from each other. NUE in 2014 was significantly different between genotype ($P < 0.001$) and N levels ($P < 0.001$) while no GT × N interaction was found. The same trend of NUE among different N regimes was found as in 2013

where bread wheat cv. JB Diego had the most NUE at all N treatments (Table 3). Nevertheless, NUE of the genotypes was 58% higher in NN than in HN treatment. Overall, NUE of the genotypes in the 2014 experiment was less than that of the 2013 experiment. This may be due to more N supply through soil mineralisation in 2014 than

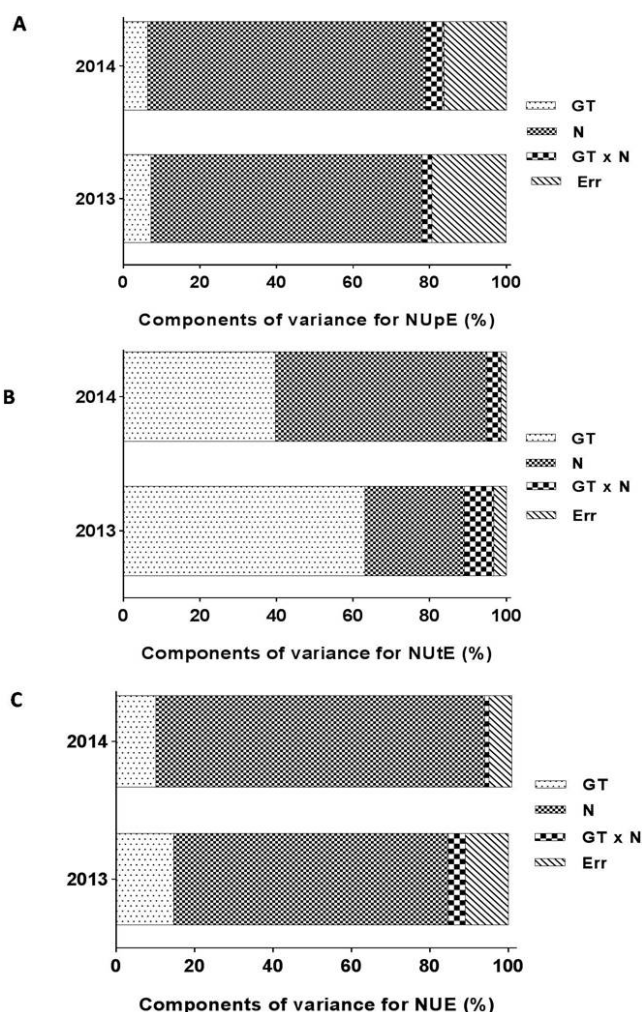


Figure 4: Contribution of components of variance on total variance of (A) NUpE (B) NUtE and (C) NUE at maturity in 2013 and 2014 experiment. (GT; genotype, N; N supply, GT × N; genotype by N level interaction and Err; error)

in 2013. The contribution of the variance due to N treatment of total variance was high in 2014 (Figure 4C).

NUE of the genotypes was regressed against NUpE and NUtE. According to the results of the 2012 field experiment, NUpE and NUtE explained 25.5% and 72.2% of the variation in NUE, respectively ($P < 0.001$). Therefore, NUtE was more important to determine NUE than NUpE in the 2012 field experiment (Figure 5A and B). However, this was different in 2013 and 2014 field experiments. In 2013, NUpE explained 60% of the variation in NUE at HN and 50% at NN (Figure 6A and B) while NUtE explained 47% and 40% of

the variation in NUE at HN and NN respectively (Figure 6C and D) ($P < 0.001$). It seems that when NUpE increased by 1, NUE increased 24.97 and 25.95 at HN and NN respectively. Remarkably, in the 2014 experiment, there was no significant relationship between NUE and NUpE both at NN and HN conditions but NUtE explained 70% of the variation in NUE at HN and 54% at NN (Figure 7A and B).

In the present study, NUE among genotypes varied significantly with highest NUE for bread wheat followed by spelt, emmer and einkorn. However, in general, NUpE were high in emmer and spelt when compared to bread wheat. NUtE of bread wheat was always higher than ancient wheat genotypes resulting in high NUE. NUE of bread wheat genotypes in field experiments varied from 20-43 kg grain DM kg⁻¹N while spelt was 20-30 kg grain DM kg⁻¹N, emmer 18-25 (kg grain DM kg⁻¹N and einkorn 8-19 kg grain DM kg⁻¹N. Gaju *et al.* (2011) reported a significant variation of NUE (18-38 kg grain DM kg⁻¹N) among 16 UK and French wheat genotypes under optimum N availability in the field. In the present study, NUE among genotypes varied significantly with the highest NUE for bread wheat followed by spelt, emmer and einkorn. However, it is difficult to compare NUE data between experiments since people use different methods to calculate N availability for the plant.

With regards to the positive and strong relationship with plant height and nitrogen uptake of ancient wheat genotype in our study, it can be suggested that tall plants need more N to develop structural materials of the stem hence uptake N efficiently (but einkorn had lower nitrogen uptake throughout the study). Generally, in cereals, maximum plant N accumulation occurs at anthesis and subsequently decreases through maturity [Martre, 2003]. At anthesis about 35% of the total N in the wheat canopy is in the leaf lamina and rest of the N is partitioned between leaf sheath, true stem and ear. Among them 30% of canopy N can be found in true stems [Critchley, 2001]. Stem N can be located as structural, transport, storage and metabolic functions [Pask, 2009]. However, majority of stem N is allocated between structural and reserve pools which, during grain filling, remobilise to fulfil grain N demand. Pask (2009) working with four UK feed winter wheat cultivars, indicated that 60% of the N in the stem belongs to

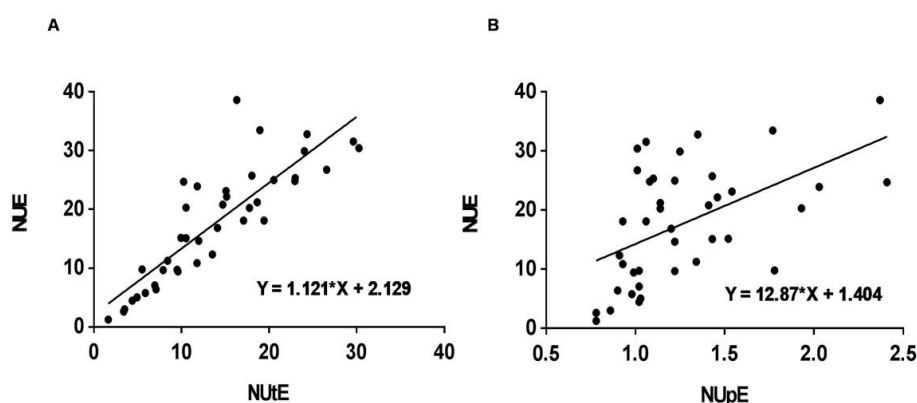


Figure 5: Linear regression between (A) NUE and NUtE ($R^2 = 0.25$, $P < 0.001$) (B) NUE and NUpe ($R^2 = 0.72$, $P < 0.001$) in 2012 field experiment

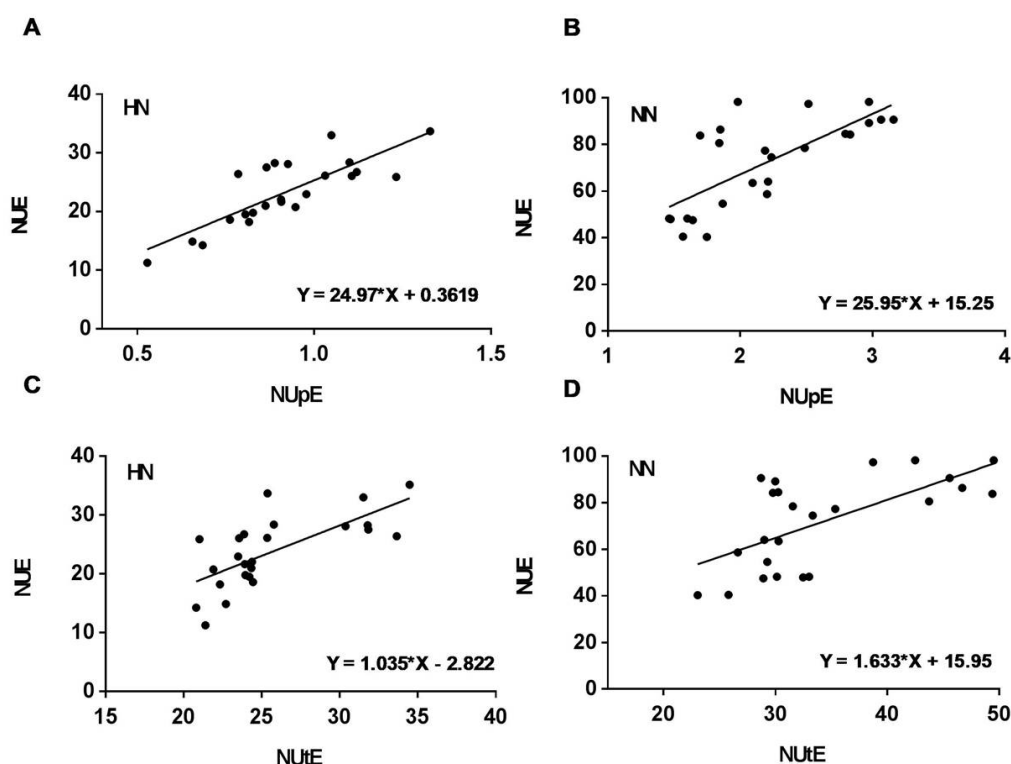


Figure 6: Linear regression between NUE and NUpe at (A) HN ($R^2 = 0.6$, $P < 0.001$) (B) NN ($R^2 = 0.5$, $P < 0.001$) and NUtE at (C) HN ($R^2 = 0.47$, $P < 0.001$) (D) NN ($R^2 = 0.4$, $P < 0.001$) in 2013 field experiment

reserve N pool under optimum conditions. Foulkes *et al.* (2009) suggested that a high capacity to absorb N in the true stem together with storage capacity subsequently enhances nitrogen uptake hence high NUpe. True stem N absorption has therefore been identified as a favourable trait to improve NUpe, especially, under high soil N mineralisation. In the present study, N_{off} increased with additional N supply though NUpe decreased

massively. Higher NUpe of the genotypes at NN was observed in 2013 than in 2014.

Post-anthesis assimilates directly transferred to grains and remobilisation of stored assimilates in vegetative parts of the plant takes place in grain crops [Gebbing & Schnyder, 1999]. When abiotic stress is severe during the grain filling period, pre-anthesis stored reserves play a major role for

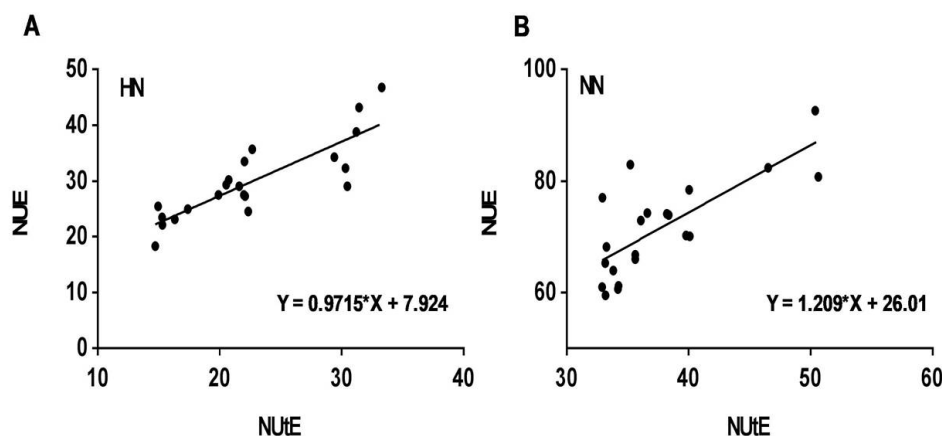


Figure 7: Linear regression between NUE and NUtE at (A) HN ($R^2 = 0.7$, $P < 0.001$) (B) NN ($R^2 = 0.54$, $P < 0.001$) in 2014 field experiment

grain filling [Tahir & Nakata, 2005]. On the other hand, the importance of pre-anthesis assimilate translocation was also reported under biotic stress [Katsantanis, 2008]. Under optimum conditions, stored carbohydrates in stems contribute 10-12% of the final grain yield in wheat while it increased up to 40% under drought [Bidinger *et al.*, 1977] may be due to high biomass remobilisation efficiency hence N remobilisation efficiency. The present results indicated a strong relationship between NUtE and grain yield of the genotypes. Improved harvest index and introduction of semi-dwarf genes are associated with high NUtE of bread wheat than ancient wheat genotypes.

NUE in relation to its components

According to the results of the 2012 experiment, genetic variation in NUE was more associated with NUtE than NUpE. This may be due to the high nitrogen uptake of all genotypes despite their grain yield. In contrast, experimenting on 25 varieties of wheat in USA illustrated significant variation for NUE with NUpE accounting for 54% of the variation [Van Sanford & Macknow, 1986]. However, in the 2013 field experiment a stronger relationship was found between NUE and NUpE than NUtE under HN and NN conditions.

Similarly, Le-Gouis, (2000) experimenting on 20 winter wheat cultivars in France found that NUpE accounted for more of the genetic variation in NUE at LN than HN. Interestingly, in the 2014 field experiment, there was no significant

relationship between NUE and NUpE either at HN or NN. This may be due to the less variation of NUpE among genotypes in the 2014 experiment. However, NUtE explained more variation in NUE at HN than NN. Gaju *et al.* (2011) reported that the genetic variation in NUE was more closely associated with NUtE than NUpE under both HN and LN conditions. In barley, NUtE explained 60% of the variation in NUE while NUpE explained only 40% [Bingham *et al.*, 2012]. However, effective management strategies of N can have a large potential to increase NUE by improving NUpE [Foulkes *et al.*, 2009].

Conclusion

According to the results, it can be concluded that ancient wheat genotypes have the ability to uptake more nitrogen hence high NUpE when compared to modern bread wheat. However, NUtE is high in modern bread wheat due to its ability to remobilise storage nitrogen in the plant to develop more grains than ancient types of wheat species. As a result of that, NUE is high in modern bread wheat. Identification of favourable traits associated with high NUpE of ancient wheat species could be useful to improve NUpE of modern bread wheat.

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References

- Bidinger, F., Musgrave, R. B. & Fischer, R. A. (1977) Contribution of Stored Pre-anthesis Assimilate to Grain Yield in Wheat and Barley. *Nature*. V.270, pp. 431-433. DOI: 10.1038/270431a0
- Bingham, I.J., Karley, A.J., White, P.J., Thomas, W.T.B. & Russell, J.R. (2012) Analysis of Improvements in Nitrogen Use Efficiency Associated with 75 years of Spring Barley Breeding. *European Journal of Agronomy*. V. 42, pp. 49-58. DOI: 10.1016/j.eja.2011.10.003
- Borrell, A.K., Garside, A.L., Fukai, S. & Reid, D.J. (1998) Season, Nitrogen Rate, and Plant Type Affect Nitrogen Uptake and Nitrogen Use Efficiency in Rice. *Australian Journal of Agriculture Research*, V. 49, pp. 829-843. DOI: 10.1071/a97057
- Chamorro, A.M., Tamagno, L.N., Bezus, R. & Sarandon, S.J. (2002) Nitrogen Accumulation, Partition, and Nitrogen Use Efficiency in Canola under Different Nitrogen Availabilities. *Communications in Soil Science and Plant Analysis*. V. 33, pp. 493-504. DOI: 10.1081/css-120002759
- Coqueue, M. & Gallais, A. (2006) Genomic Regions Involved in Response to Grain Yield Selection at High and Low Nitrogen Fertilization in Maize. *Theoretical and Applied Genetics*. V. 112, pp. 1205-1220. DOI: 10.1007/s00122-006-0222-5
- Critchley, C.S. (2001) A Physiological Explanation for the Canopy Nitrogen Requirement of Winter Wheat. Ph.D. Thesis. University of Nottingham, UK.
- Dhugga, K.S. & Waines, J.G. (1989) Analysis of Nitrogen Accumulation and Use in Bread and Durum Wheat. *Crop Science*. V. 29, pp. 1232-1239. DOI: 10.2135/cropsci1989.0011183x002900050029x
- Ehdaie, B., Shakiba, M.R. & Waines, J.G. (2001) Sowing Date and Nitrogen Input Influence Nitrogen-Use Efficiency in Spring Bread Wheat and Durum Wheat Genotypes. *Journal of plant Nutrition*. V. 24, pp. 899-919. DOI: 10.1081/pln-100103781
- Fischer, R.A. (1981) Optimizing the Use of Water and Nitrogen through Breeding of Crops. *Plant and Soil*. V. 58, pp. 249-278. DOI: 10.1007/978-94-015-0861-2_10
- Foulkes, M.J., Hawkesford, M.J., Barraclough, P.B., Holdsworth, M.J., Kerr, S., Kightley, S. & Shewry, P.R. (2009) Identifying Traits to Improve the Nitrogen Economy of Wheat: Recent Advances and Future Prospects. *Field Crops Research*, V.114, pp. 329-342. DOI: 10.1016/j.fcr.2009.09.005
- Gaju, O., Allard, V., Martre, P., Snape, J.W., Heumez, E., Le Gouis, J., Moreau, D., Bogard, M., Griffiths, S., Orford, S., Hubbard, S. & Foulkes, M.J. (2011) Identification of Traits to Improve the Nitrogen Use Efficiency of Wheat Genotypes. *Field Crops Research*. V. 152, pp. 123-139. DOI: 10.1016/j.fcr.2011.05.010
- Gebbing, T. & Schnyder, H. (1999) Pre-anthesis Reserve Utilization for Protein and Carbohydrate Synthesis in Grains of Wheat. *Plant Physiology*. V.121, pp. 871-878. DOI: 10.1104/pp.121.3.871
- Hirel, B., Le Gouis, J., Ney, B. & Gallais, A. (2007) The Challenge of Improving Nitrogen Use Efficiency in Crop Plants: Towards a More Central Role for Genetic Variability and Quantitative Genetics within Integrated Approaches. *Journal of Experimental Botany*. V. 58, pp. 2369-2387. DOI: 10.1093/jxb/erm097
- Katsantanis, D., Ntanos, D.A., Koutroubas S.D. & Lupotto, E. (2008) Effect of Blast Disease on Nitrogen Accumulation and Remobilization to Rice Grain. *Journal of Plant Pathology*. V.90, pp. 263-272. DOI: 10.4454/jpp.v90i2.661
- Le-Gouis, J., Beghin, D., Heumez, E. & Pluchard, P. (2000) Genetic Differences for Nitrogen Uptake and Nitrogen Utilisation Efficiencies in Winter Wheat. *European Journal of Agronomy*. V. 12, pp. 163-173. DOI: 10.1016/s1161-0301(00)00045-9
- Martre, P., Porter, J.R., Jamieson, P.D. & Triboi, E. (2003) Modelling Grain Nitrogen Accumulation and Protein Composition to Understand the Sink/source Regulations of Nitrogen Remobilization for Wheat. *Plant Physiology*. V. 133, pp. 1959-1967. DOI: 10.1104/pp.103.030585

- Moll, R.H., Kamprath, E.J. & Jackson, W.A. (1982) Analysis and Interpretation of Factors which Contribute to Efficiency of Nitrogen Utilization. *Agronomy Journal*. V. 74, pp. 562-564. DOI: 10.2134/agronj1982.00021962007400030037x
- 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 Science*. V. 37, pp. 898-904. DOI: 10.2135/crop-sci1997.0011183x003700030033x
- Pask, A.J.D. (2009) Optimising Nitrogen Storage in Wheat Canopies for Genetic Reduction in Fertiliser Nitrogen Inputs. PhD thesis, University of Nottingham, UK.
- Tahir, I.S.A. & Nakata, N. (2005) Remobilisation of Nitrogen and Carbohydrate from Stems of Bread Wheat in Response to Heat Stress during Grain Filling. *Journal of Agronomy and Crop Science*. V. 191, pp. 106-115. DOI: 10.1111/j.1439-037x.2004.00127.x
- Van Sanford, D.A. & Macknow, C.T. (1986) Variation in Nitrogen Use Efficiency among Soft Red Winter Wheat Genotypes. *Theoretical and Applied Genetics*. V. 72, pp. 158-163. DOI: 10.1007/bf00266987