Irish Journal of Agricultural and Food Research **45:** 85–101, 2006

Responses of grain yield, biomass and harvest index and their rates of genetic progress to nitrogen availability in ten winter wheat varieties

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Increased yields in winter wheat cultivars have been found to be largely attributable to improved partitioning of biomass to the grain, i.e., higher harvest index. However, there is a biological upper limit to harvest index and therefore breeders need to exploit increased biomass production as the mechanism by which yields are increased. Evidence for improved biomass was sought in experiments conducted over three years (1994 to 1996), at the Plant Testing Station, Crossnacreevy, near Belfast, with 10 varieties of winter wheat introduced over the period 1977 to 1991. Variation in grain yield was more strongly associated with variation in biomass (an increase of 0.78 t/ha in grain yield at 85% dry matter (DM) per 1 t/ha increase in biomass at 100% DM; R^2 = 0.71) than in harvest index (an increase of 0.1 t/ha at 85% DM per percentage point increase in harvest index; R^2 = 0.36). When age (= year of first harvest in UK National List trials) of the varieties was taken into account, yield (0.037 t ha^{-1} y^{-1}; R^2 = 0.42) and biomass (0.034 t ha^{-1} y^{-1}; R^2 = 0.31), but not harvest index (0.34%/year; R^2 = 0.001), increased as year increased. Genetic gain in yield was smaller without fertiliser N (0.021 t ha^{-1} y^{-1}; R^2 = 0.21) and at 40 kg ha N (0.025 t ha^{-1} y^{-1}; R^2 = 0.25) than at 215–250 kg/ha N (0.065 t ha^{-1} y^{-1}; R^2 = 0.39). Theoretically, if the maximum biomass (18.60 t/ha for Rialto), could have been combined with the maximum harvest index (55.3%) in Riband, yield would potentially have been increased by 2.5 t/ha compared with yields for either variety.

Keywords: biomass; harvest index; varieties; wheat; yield improvement

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Introduction

Yield of winter wheat crops in the British Isles continues to increase as breeders produce and market new varieties. In a direct comparison of varieties currently recommended in the UK, the variety Glasgow, introduced in 2005 and the highest yielding variety in the UK Recommended List for 2005 (Anon., 2005), had a five-year mean yield of 10.9 t/ha at 85% dry matter (DM) compared with 10.0 t/ha for Riband, the variety introduced in 1989 and the oldest variety. This equates to a yield increase (genetic gain) of 0.06 t/ha per year. Some recent indirect comparisons of varieties of different ages include that by Foulkes *et al.* (1998a) who reported that yield improved by 0.041 $t\,ha^{-1}y^{-1}$ in a set of 18 varieties introduced between 1969 and 1992. Ingram, MacLeod and McCall (1997) reported an annual improvement of 0.085 t/ha, also in an indirect comparison of Norman and Brigadier, the highest-yielding varieties on the 1982 National Institute of Agricultural Botany (NIAB) and 1997 Home-Grown Cereals Authority (HGCA) UK Recommended Lists, respectively. Sayre, Rajaram and Fischer (1997), working in Mexico with eight varieties of spring wheat introduced between 1962 and 1988, reported an increase in yield by 0.067 t/ha per year.

Various workers have discussed the mechanisms contributing to these increases in yield. Austin *et al*. (1980) reported a genetic gain in grain yield of 0.030 $t\,ha^{-1}y^{-1}$ in winter wheat varieties introduced between 1908 and 1978. However, the genetic gain was greater, 0.068 $t\,ha^{-1}y^{-1}$, in varieties introduced between 1953 and 1978 and grown in a soil with high fertility. They attributed a large proportion of the increased yield (compared to older varieties when lodging was prevented and disease and pest control applied) to increased allocation of biomass (total above-ground crop dry matter at harvest) to grain, i.e., higher harvest index. Recent varieties, particularly those with the *Rht2* dwarfing gene, had shorter, lighter straw and a greater proportion of biomass allocated to grain, either through having heavier and more grains per ear, or similar grain weight and grains per ear as older varieties but an increased number of ears/m^2 (Austin *et al.*, 1980). Little difference in total biomass was found between the varieties.

In a later paper, Austin, Ford and Morgan (1989) reported a similar genetic gain in grain yield, 0.038 $t\,ha^{-1}y^{-1}$, with varieties introduced between 1908 and 1985. This genetic gain was again found to be higher, 0.067 $t\,ha^{-1}y^{-1}$, when varieties introduced between 1953 and 1986 were examined. They found that in 1984, a high-yielding year, significant differences in total biomass were observed between age groups, with varieties introduced in the 1980s having a 14% higher mean biomass compared to varieties introduced between 1953 and 1972. Hence, they postulated that there is genetic variation in the capacity for biomass production in wheat, but that it is expressed mainly in favourable years when it can be of considerable benefit to yield. They suggested that, as it is unlikely that straw dry weight could be reduced much further without compromising the leaf canopy, it might be necessary for breeders to attempt to detect and exploit genetic differences in total biomass, while maintaining harvest index, for a continued genetic gain in yield.

Ortiz-Monasterio *et al.* (1997) detailed genetic gains of between 0.021 and 0.052 $t\,ha^{-1}y^{-1}$ at four nitrogen fertiliser application rates in eight semi-dwarf winter wheat varieties, released between 1962 and 1985, in experiments in Mexico. When two older taller varieties were included, significantly greater yield progress at the two higher nitrogen rates than at the two lower rates was attributed in part to higher incidences of lodging in the taller varieties. Foulkes, Sylvester-Bradley and Scott (1998b) postulated that a genetic gain of 0.096 $t\,ha^{-1}\,y^{-1}$, much higher than those of Austin *et al.* (1980, 1989), was associated with an increased requirement for fertiliser N in more modern winter wheat varieties accompanied by better acquisition of soil N by older varieties.

Donmez *et al.* (2001) found that yield was significantly correlated with both harvest index and biomass in experiments with 13 varieties of winter wheat ranging in year of release in the USA from 1873 to 1995, the four newest varieties showed significant genetic gain in biomass. Brancourt-Hulmel *et al.* (2003), in a study of 14 winter wheat varieties registered between 1946 and 1992 in France, reported genetic gains in yield of between 0.039 and 0.066 $t\,ha^{-1}\,y^{-1}$ at two fertiliser N rates and with and without fungicide applications. They also reported significant genetic gains in harvest index but not in biomass amongst these varieties. Shearman *et al.* (2005) attributed yield increase in eight winter wheat varieties introduced in the UK between 1972 and 1995 to increased harvest index in those varieties introduced before 1980 and increased biomass in varieties introduced after 1983.

In the 1990s, major research programmes were conducted in the UK, funded by the HGCA, in which winter wheat varieties were scrutinised for their capacity to respond to various agro-ecological scenarios, namely drought (Foulkes, Sylvester-Bradley and Scott, 2001, 2002), rotational position, sowing date and residual soil N. In a residual soil N programme the responses of 10 winter wheat varieties, varying in date of introduction between 1977 and 1991, to contrasting conditions of soil N and fertiliser N availability were examined at three locations, including Crossnacreevy, near Belfast, Northern Ireland. The results from Crossnacreevy are reported in this paper. The rates of genetic gain in yield, biomass and harvest index were estimated and the mechanisms by which yield improvement has occurred in the later years of the 20th century were examined.

Materials and Methods

Three experiments, each of two years' duration, were conducted between 1993 and 1996 at the Plant Testing Station, Crossnacreevy, near Belfast, Northern Ireland. The soil was a clay loam with an organic matter concentration of 106 g/kg and the previous cropping was grass in all three years of the experiment. The weather conditions at Crossnacreevy in each of the three seasons are presented in Table 1. The Plant Testing Station, Crossnacreevy,

Table 1. Summary of the climatic features of Crossnacreevy for the three seasons 1993–1994, 1994–1995 and 1995–1996

Climatic features	Harvest year		
	1994	1995	1996
Winter rainfall (total October–March in mm)	623	601	637
Spring/summer rainfall (total April–July in mm)	225	197	283
Mean summer temperature (°C) (mean June–August)	13.1	15.6	13.7
Incident radiation ($MJ\,m^{-2}\,d^{-1}$) (mean April–June)	13.4	15.2	14.2
Incident radiation ($MJ\,m^{-2}\,d^{-1}$) (mean July–August)	13.0	15.8	13.1

Northern Ireland contrasted with the other two locations, ADAS Boxworth, Cambridgeshire, UK, and Harper Adams Agricultural College, Shropshire, UK, involved in the project, in having cool wet summers and soil which was relatively high in organic matter. ADAS Boxworth had warm dry summers, moisture retentive soils and a high yield potential. Harper Adams had light soils, variable leaching and a low yield potential due to drought. Summer temperatures at Crossnacreevy were lower but the grain filling period was longer and harvest later (see Table 2), leading to greater production of biomass, more efficient partitioning and higher yield than at the other locations. The longer grain-filling period at Crossnacreevy may have compensated for lower levels of radiation received on a daily basis than at the other sites. Full details of meteorological measurements and the results from the experiments at ADAS Boxworth and Harper Adams were reported by White *et al.* (1998).

Each experiment consisted of a 'pre-treatment' season and an experimental season. In the pre-treatment season perennial ryegrass was grown on the trial area and supplied with fertiliser N at either 0 (R0), 200 (R1) or 800 (R2) kg/ha. In the autumn the ryegrass was removed from the R0 plots, while on the R1 and R2 plots it was ploughed in to provide a residual soil N supply for the next season. The overall objective was to create a range of residual soil N levels in a readily mineralisable form.

Following this, at the beginning of each experimental season, 10 varieties of winter wheat (Table 3), with a spread of 14 years in date of introduction, were sown in the residual nitrogen plots. Year of introduction was taken as the

Table 2. Management details for each experiment (production season)

Item	Harvest year		
	1994	1995	1996
Sowing date	22 October 1993	18 October 1994	3 October 1995
Soil N assessment date	21 January 1994	19 March 1995	26 February 1996
Residual soil N[†](kg/ha) for			
R0	22.6	13.3	41.1
R1	20.3	13.3	30.1
R2	20.4	29.9	69.3
Fertiliser N application date			
First application[#](F1 and F2)	31 March 1994	23 March 1995	5 March 1996
Second application (F2 only)	14 April 1994	5 May 1995	24 April 1996
Fertiliser N rate (kg/ha) at second application			
R0	235	250	205
R1	235	250	205
R2	220	220	175
Plant growth regulation treatments	Chlormequat 700 at 2.3 l/ha on 9 May 1994 Terpal at 2.0 l/ha + Agral on 11 June 1994	Chlormequat 700 at 1.5 l/ha on 11 April 1995 Terpal at 1.5 l/ha + Agral on 18 May 1995	Chlormequat 700 at 2.3 l/ha on 2 April 1996
Harvest date	26 September 1994	19 August 1995	14 September 1996

[†]Measured in soil sampled to a depth of 90 cm.
[#]N applied at 40 kg/ha to both F1 and F2.
R0, R1 and R2 represent three residual soil N treatments.
F1 and F2 represent low and high fertiliser N treatments.

Table 3. Details of the varieties included in the experiments at Crossnacreevy 1994–1996

Variety	End use	Year of introduction	Dwarfing genes present (*Rht*1, *Rht*2)/ not present (*rht*)	1B/1R chromosome translocation present/not present
Avalon	Bread	1977	*Rht* 2	non-1B/1R
Longbow	Biscuit	1979	*Rht* 2	non-1B/1R
Mercia	Bread	1983	*rht*	non-1B/1R
Apollo	Feed	1985	*Rht* 1	1B/1R
Riband	Biscuit and distilling	1985	*Rht* 2	non-1B/1R
Haven	Feed	1987	*Rht* 2	1B/1R
Hereward	Bread	1988	*Rht* 2	1B/1R
Hunter	Feed	1990	*Rht* 2	1B/1R
Cadenza	Bread	1990	*rht*	non-1B/1R
Rialto	Feed	1991	*Rht* 2	1B/1R

year of a variety's first harvest in UK National List trials, a more consistent stage in variety introduction in relation to their breeding history than year of first inclusion on the England & Wales Recommended List but less well-known or available as information. In this set of varieties year of first inclusion on the England & Wales Recommended List, a measure of their value to agriculture, was either three or four years later than year of first harvest in UK National List trials. The varieties included bread and feed types and covered a range in N uptake (based on an analysis of data provided by Levington Agriculture (Levington Park, Ipswich, Suffolk) from a variety/fertiliser N trial series 1982–1992) and canopy N requirement (based on an experiment on length of growing season conducted at Cockle Park, 1993, as part of the same HGCA-funded project in which the experiments reported here were included). The varieties also varied in their inclusion of the dwarfing genes, *Rht1* and *Rht2*, and the wheat-rye translocation, 1B/1R, which has been reported to increase biomass production (Villareal *et al.,* 1994; Villareal *et al.,* 1995 and Carver and Rayburn, 1994).

All the varieties remained on the England & Wales Recommended List for a minimum of four years (Cadenza and Hunter), while two varieties, Hereward and Riband, were still included 14 and 16 years, respectively, after their first recommendation (Anon., 2005).

During the growing season a nil fertiliser treatment (F0) and two rates of fertiliser N (F1, F2) were applied to different plots of each of the residual N treatments. The F1 treatment consisted of N at 40 kg/ha applied in early spring. The F2 treatment was calculated as sufficient fertiliser N to make the total N available in spring, from the soil plus fertiliser, equal to or as close to 300 kg/ha as possible, taking into account the settings for rates on the fertiliser spreader. The soil N availability was based on an early spring soil analysis (Table 2) and the F2 treatment consisted of an early spring N application of 40 kg/ha (as for F1) and the remainder in a further application in late spring.

The treatments were replicated in two blocks in a split-plot design with the residual soil N and fertiliser N as main plots and varieties as sub-plots. Thus, there were 180 plots (3 residual N levels × 3 fertiliser N rates × 10 varieties × 2 blocks).

Sufficient P and K fertiliser and lime were applied for high yields. The experiments were managed to limit weeds, pests and diseases to very low levels. Details of the nitrogen and plant growth regulator applications, sowing and harvest dates in all experiments are presented in Table 2.

Prior to harvest, quadrat samples (0.5 m^2) of all above-ground material were taken from each plot and total biomass (at 100% DM) and harvest index were determined. Yield (t/ha at 85% DM) was determined by combine harvesting of whole plots. Biomass also could have been ascertained by calculation using harvest index determined on the quadrats and yield determined by combine, but the independence of biomass from yield was maintained by using the data from the quadrats.

The effects of fertiliser N, soil N, variety and their interactions on yield, biomass and harvest index were analysed by ANOVA using Genstat 5. Year and replication were regarded as random effects with other effects considered fixed. In order to assess whether varietal differences in the three harvest characteristics were age related, i.e., if variation in values for yield, biomass and harvest index were linked to genetic improvements in varieties, linear and quadratic functions of the variety means of each characteristic were fitted to variety age (year of first harvest in UK National List trials). The variance was partitioned into the amounts which could be explained by the main effects and their interactions and by the linear and quadratic functions and the deviations from the quadratic polynomial for all factors and their interactions. Regressions for individual treatments were calculated using Microsoft Excel allowing coefficients of determination (R^2) for each treatment to be calculated.

An interaction was expected between the residual soil N and fertiliser N treatments. The F0 treatment had no additional N applied to the residual soil N while the F1 treatment had 40 kg/ha of fertiliser N applied, regardless of soil N level. Hence, the total N available in the F0 and F1 treatments differed between experiments, depending on the amount of N available from the different residual soil N treatments. The F2 treatment, on the other hand, involved applying varying rates of fertiliser N, taking into account the amount of residual soil N available, so that the total N available in all F2 treatments was 300 kg/ha. It was expected, therefore, that where residual soil N treatments differed in the amount of N available, there would be an inherent residual soil N × fertiliser N interaction for any characteristic which showed a response to nitrogen.

Results

Yield

Fertiliser N, soil N and variety significantly affected yield, and the responses of the varieties varied significantly with fertiliser N rate (Table 4). Yields were highest, 9.79 to 10.30 t/ha, in the three F2 treatments, and lowest, 3.68 t/ha, in the R0F0 treatment (Table 4).

Fertiliser N had a more marked effect on yield ($P < 0.001$) than did soil N ($P < 0.01$), as indicated by F-ratios of 374.6 and 8.8, respectively. However, the effect of fertiliser N differed with the three residual soil N treatments ($P < 0.001$). This was due to mean yields for the three residual soil N levels being very similar at the high fertiliser treatment (F2) (a range of 0.51 t/ha about a mean of 10.03 t/ha), but differing when no fertiliser (F0), or a low amount of fertiliser (F1), was applied, ranging, for F0, from

Table 4. The effects† of soil-N, fertiliser N and variety on grain yield (t/ha at 85% dry matter), averaged over three years

Soil N	Fertiliser N	Variety										Mean
		Apollo	Avalon	Cadenza	Haven	Hereward	Hunter	Longbow	Mercia	Rialto	Riband	
R0	F0	3.64	3.33	3.69	3.71	3.88	3.60	3.53	3.67	4.07	3.74	3.68
	F1	5.49	4.89	5.21	4.81	5.06	4.91	4.79	5.01	5.44	4.91	5.05
	F2	10.50	9.45	10.45	10.81	9.76	10.45	10.28	9.70	10.77	10.90	10.30
	Mean	6.54	5.89	6.45	6.44	6.23	6.32	6.20	6.13	6.76	6.51	6.34
R1	F0	4.42	3.94	4.35	4.55	4.25	4.27	4.52	4.83	4.60	4.83	4.46
	F1	5.07	5.00	5.15	5.53	5.01	5.40	5.49	5.21	5.59	5.29	5.27
	F2	10.24	8.47	10.14	10.29	9.48	9.95	9.76	9.51	10.36	9.69	9.79
	Mean	6.58	5.80	6.55	6.79	6.25	6.54	6.59	6.51	6.85	6.60	6.51
R2	F0	5.14	5.21	5.39	5.99	5.41	5.79	5.48	5.97	6.20	5.79	5.64
	F1	6.30	5.40	5.38	5.63	5.67	6.04	5.83	5.93	6.52	6.00	5.86
	F2	10.48	9.61	10.21	10.67	9.59	9.84	9.62	9.47	10.55	10.82	10.09
	Mean	7.31	6.74	6.99	7.43	6.89	7.22	6.98	7.12	7.76	7.54	7.20
Mean	F0	4.40	4.16	4.48	4.75	4.52	4.55	4.51	4.82	4.96	4.79	4.59
	F1	5.62	5.10	5.24	5.32	5.24	5.45	5.37	5.38	5.85	5.40	5.39
	F2	10.41	9.18	10.27	10.59	9.61	10.08	9.89	9.56	10.56	10.47	10.06
	Mean	6.81	6.14	6.66	6.89	6.46	6.69	6.59	6.59	7.12	6.88	

†Summary of F-tests and s.e.d. for fixed effects and interactions.

Effect	Significance	s.e.d.[1]
Soil N (R)	**	0.216
Fertiliser N (F)	***	0.216
R × F	*	0.374
Variety (V)	***	0.117
R × V		0.289
F × V	***	0.289
R × F × V		0.500

[1]df = 13 for main plot factors and 135 for sub-plot factors.

3.68 t/ha at R0 to 5.64 t/ha at R2 and for F1 from 5.05 t/ha at R0 to 5.86 t/ha at R2. Thus, when yield was low and little or no fertiliser N was applied, residual soil N had a relatively greater effect than at higher yields and higher fertiliser N applications.

Variety had a significant ($P < 0.001$) effect on yield which varied between 6.14 t/ha for Avalon, the oldest variety in the trials, and 7.12 t/ha for Rialto, the most recently introduced variety in the trials, an increase of 1.0 t/ha over the 14-year period of introduction (Table 4). The responses of the varieties to fertiliser N varied significantly ($P < 0.001$). Mercia yielded well at F0 but poorly at F1 and F2 relative to other varieties. Apollo and Cadenza yielded well at F2, and Apollo at F1, but poorly at F0 relative to other varieties.

Biomass

Like yield, fertiliser N, soil N and variety significantly affected biomass, the responses of the varieties varying significantly with fertiliser N rate ($P < 0.001$) (Table 5). Fertiliser N had a more marked effect than soil N (F ratios 250 and 12.7, respectively). Biomass in the F2 treatment was more than double that at F0, increasing from 8.75 to 17.83 t/ha (Table 5). Increase in soil N resulted in a smaller increase in biomass, averaged across all F treatments, of 2.06 t/ha (Table 5).

Biomass was significantly affected by variety ($P < 0.05$) and varied from 11.9 t/ha for Avalon to 13.0 t/ha for Rialto, an increase of 1.1 t/ha over the 14-year period of introduction (Table 5). Fertiliser N, but not soil N, significantly affected the differences among varieties with respect to biomass ($P < 0.05$) (Table 5). Mercia and Hunter produced greater biomass at F0 but were poorer at F1 and F2 relative to other varieties. Apollo, and to a lesser extent Longbow, produced greater biomass at F1 and F2 but were poorer at F0 relative to other varieties.

Harvest index

Fertiliser N and variety, but not soil N, significantly affected harvest index, with no interactions amongst the factors (Table 6). Year had a much greater effect on harvest index than on yield or biomass as indicated by the much greater variance ratio for harvest index for year, 34.8, than for other factors, 11.0 for fertiliser N ($P < 0.01$) and 0.70 (non-significant) for soil N, compared with yield and biomass (see above). Harvest index was low at F1 (49.0%), and higher at F0 (51.9%), and F2 (52.8%). Harvest index varied by less than one percentage point with soil N.

Harvest indices of the varieties, averaged across all treatments, varied ($P < 0.001$) between 49.6% for Avalon and Hereward and 53.9% for Riband, a range of 4.3% (Table 6). Rialto, with highest yield and biomass, had an intermediate harvest index (51.2%). There was no interaction between variety and either fertiliser N or soil N.

Discussion

Effect of fertiliser N and soil N

The amount of N available to crops throughout the whole life cycle is the net product of several soil processes. Nitrogen supplied by fertiliser applications is not all taken up by crops because of leaching and immobilisation. Mineralisation makes nitrogen available to crops from crop residues and older organic matter. These processes are dynamic and so the availability of nitrogen is continually changing and, in addition, is highly spatially variable. Mineral nitrogen levels in the soil in spring were low in these experiments at Crossnacreevy and were considerably lower than in those at Boxworth and

Table 5. The effects† of soil and fertiliser N and variety on total biomass (t/ha at 100% dry matter) averaged over three years

Soil N	Fertiliser N	Variety										Mean
		Apollo	Avalon	Cadenza	Haven	Hereward	Hunter	Longbow	Mercia	Rialto	Riband	
R0	F0	6.79	7.17	6.99	7.91	7.38	6.97	6.09	7.56	7.20	6.87	7.09
	F1	10.66	10.06	10.96	10.46	9.97	9.83	10.16	9.89	10.18	8.71	10.08
	F2	17.92	16.75	17.33	18.31	17.06	16.13	18.50	16.83	18.41	18.04	17.53
	Mean	11.79	11.33	11.76	12.23	11.47	10.98	11.58	11.43	11.93	11.21	11.57
R1	F0	7.73	7.01	7.95	8.33	8.55	8.34	8.10	8.60	8.61	9.27	8.25
	F1	10.73	10.34	9.37	9.79	9.99	10.66	10.65	10.93	11.75	11.51	10.57
	F2	18.38	15.61	17.69	17.26	17.85	17.40	17.27	17.41	18.12	15.79	17.28
	Mean	12.28	10.99	11.67	11.79	12.13	12.13	12.01	12.31	12.83	12.19	12.03
R2	F0	9.66	10.70	10.57	11.23	11.07	12.17	10.51	11.88	11.45	9.92	10.91
	F1	11.73	11.01	10.20	11.08	10.38	12.01	11.24	11.66	11.81	11.79	11.29
	F2	19.37	18.56	18.63	19.78	18.41	18.29	18.46	17.60	19.28	18.44	18.68
	Mean	13.58	13.42	13.13	14.03	13.29	14.16	13.40	13.71	14.18	13.38	13.63
Mean	F0	8.06	8.29	8.50	9.15	9.00	9.16	8.23	9.35	9.08	8.69	8.75
	F1	11.04	10.47	10.18	10.44	10.11	10.83	10.68	10.83	11.25	10.67	10.65
	F2	18.56	16.98	17.88	18.45	17.78	17.27	18.08	17.28	18.60	17.43	17.83
	Mean	12.55	11.91	12.19	12.68	12.30	12.42	12.33	12.48	12.98	12.26	

†Summary of F-tests and s.e.d. for fixed effects and interactions.

Effect	Significance	s.e.d.[1]
Soil N (R)	***	0.428
Fertiliser N (F)	***	0.428
R × F		0.742
Variety (V)	*	0.266
R × V		0.612
F × V	*	0.612
R × F × V		1.061

[1]df = 13 for main plot factors and 135 for sub-plot factors.

Table 6. The effects† of soil and fertiliser N and variety on harvest index (%) averaged over three years

Soil N	Fertiliser N	Variety										Mean
		Apollo	Avalon	Cadenza	Haven	Hereward	Hunter	Longbow	Mercia	Rialto	Riband	
R0	F0	54.3	49.5	52.9	50.3	49.6	51.2	55.0	53.3	52.9	55.6	52.4
	F1	47.2	45.9	45.7	48.7	46.9	46.7	50.8	49.1	48.3	53.3	48.3
	F2	53.9	52.6	54.8	56.2	52.7	55.1	54.4	54.6	54.4	57.5	54.6
	Mean	51.8	49.3	51.1	51.8	49.7	51.0	53.4	52.3	51.8	55.5	51.8
R1	F0	53.4	51.8	52.0	51.9	50.6	51.9	53.9	52.8	50.9	54.8	52.4
	F1	48.8	46.0	48.3	52.0	47.9	49.1	50.6	49.6	49.2	52.7	49.4
	F2	50.4	49.1	50.9	52.8	49.6	50.7	51.5	50.7	50.0	53.5	50.9
	Mean	50.9	49.0	50.4	52.2	49.4	50.6	52.0	51.0	50.0	53.7	50.9
R2	F0	52.2	47.3	51.0	50.7	49.1	49.0	51.9	52.1	50.1	53.8	50.7
	F1	50.8	46.0	49.5	49.3	47.8	46.2	51.3	50.5	50.5	51.0	49.3
	F2	51.6	50.6	53.4	54.3	50.4	52.7	54.1	52.5	53.5	54.9	52.8
	Mean	51.6	48.0	51.3	51.4	49.1	49.3	52.4	51.7	51.4	53.2	50.9
Mean	F0	53.3	49.5	51.9	51.0	49.8	50.7	53.6	52.7	51.3	54.7	51.9
	F1	48.9	46.0	47.8	50.0	47.5	47.3	50.9	49.7	49.3	52.3	49.0
	F2	52.0	50.8	53.0	54.4	50.9	52.8	53.3	52.6	52.6	55.3	52.8
	Mean	51.4	48.7	50.9	51.8	49.4	50.3	52.6	51.7	51.1	54.1	

†Summary of F-tests and s.e.d. for fixed effects and interactions.

Effect	Significance	s.e.d.[1]
Soil N (R)		0.84
Fertiliser N (F)	**	0.84
R × F		1.45
Variety (V)	***	0.61
R × V		1.30
F × V		1.30
R × F × V		2.26

[1]df = 13 for main plot factors and 135 for sub-plot factors.

Harper Adams in spring (White *et al.*, 1997). High rainfall during the winter months at Crossnacreevy is likely to have led to leaching of mineral nitrogen from the soil and denitrification in the wet soils may also have reduced the mineral nitrogen available to crops in the spring. Nevertheless, yields increased both as fertiliser N application increased and as the supply of nitrogen to the previous crop increased, despite very low soil N in the spring.

With the limited number of fertiliser N rates in this experiment, the purpose was not to examine nitrogen responses in detail. Rather, comparison of wheat growth and performance in the absence of fertiliser (F0) and when nitrogen was not limiting (F2) has provided the opportunity to examine the influence of genetic and environmental factors on the response to nitrogen. The small increase in yield in response to a fertiliser N application of 40 kg/ha varied with soil N level, the increment decreasing as yield at F0 increased from R0 to R2 (Table 4). The response of biomass to a fertiliser N application of 40 kg/ha was much greater, 2 t/ha on average, than that of yield (0.8 t/ha). This is reflected in the harvest index which was much higher, 51.8%, at F0 than at F1, 49.2%. The fertiliser N application of 40 kg/ha in spring may have encouraged leaf growth and tiller production which could not be sustained by low availability of soil N later in the growing season resulting in poorer partitioning of biomass to the grain at F1 than at F0.

In the F2 treatments, differing amounts of fertiliser N were applied depending on the soil mineral nitrogen present in the spring to achieve a fixed total supply of N from both soil and fertiliser. Yield, biomass and harvest index would therefore have been expected to be similar for F2 at the three soil N levels. Yields in the F2 treatments were similar, the range being 0.51 t/ha (Table 4). These similar yields were associated with higher biomass at R2 and lower harvest index at R1 than at the other soil N levels (Tables 5 and 6).

Across all the residual soil N and fertiliser N treatments the large responses of yield, 3.68 to 10.30 t/ha, and biomass, 7.09 to 18.68 t/ha, relative to the small responses of harvest index, 48.3 to 54.6%, to variation in availability of nitrogen were as expected. However, when soil N and fertiliser N treatments are considered individually, the range of values for yield and biomass were much smaller and similar to the variation in harvest index. Thus, at R0F0 yield varied between 3.3 and 4.1 t/ha, biomass between 6.1 and 7.9 t/ha and harvest index between 49.5 and 55.6%. At R2F2 yield varied between 9.5 and 10.8 t/ha, biomass between 17.6 and 19.8 t/ha and harvest index between 50.4 and 54.9%. The marked effect of N on overall yield and biomass but not harvest index reflects its influence on yield formation processes prior to anthesis when capacity to photosynthesise is developed in parallel with capacity to receive photosynthate. After anthesis, these are roughly in balance so that harvest index, a measure of the efficiency of the balance between supply of and demand for photosynthate, is relatively constant irrespective of variation in the initial availability of N.

Variety characteristics

Yield, biomass and harvest index showed substantial variation amongst this group of varieties, yield varying by 1.0 t/ha at 85% DM, biomass by 1.2 t/ha at 100% DM and harvest index by 4.3 percentage points. The higher yielding varieties were found to have both greater biomass and higher harvest indices when correlations were calculated between the characteristics without taking into account age of the varieties. Yield increased by 0.1 t/ha for every 1% increase in harvest index (R^2 = 0.36), an increase of 0.56 t/ha at 85% DM across the range of harvest indices in this set of varieties (Figure 1a). Yield increased by 0.78 t/ha for every 1 t/ha increase in biomass at 100% DM (R^2 = 0.71), an increase of 0.84 t/ha across the range of biomass in this set of varieties (Figure 1b).

The positive association between yield and biomass could be of major significance in encouraging breeders in their quest for increased yield in wheat varieties. Little variation in biomass amongst varieties was found by Austin *et al.* (1980) although in a later study (Austin *et al*., 1989) a difference of 14% between variety age groups was observed. The increase of 1.1 t/ha in the present studies and its relatively greater magnitude and stronger correlation with yield (Figure 1b) than with harvest index (Figure 1a) provides robust evidence that breeders have succeeded in improving yield by improving the total production of biomass.

The varieties showed significantly different responses to fertiliser N in both yield and biomass but not in harvest index. Two varieties, Mercia and Apollo, showed consistent behaviour in both yield and biomass and contributed to the significant variety × fertiliser N interactions. Mercia produced higher yields and biomass at F0 than at F1 or F2 relative to other varieties and Apollo gene higher yields and biomass at F1 and F2 than at F0 relative to other varieties. These two varieties are similar in age. Apollo is unique in this set of varieties, being the only one to have the *Rht*1 gene, but Mercia has the same features as Cadenza, a younger variety, which coincidentally behaved similarly to Apollo in terms of its yield response to fertiliser N. The uniqueness of Mercia in responding better at low fertiliser N rate and Apollo in responding better at higher N rates is of value to breeders who seek such features in parents for their breeding programmes. Looking further at yield components (ear and grain number and grain size) and at yield formation processes (shoot production and survival, grain production and survival and the production and utilisation of carbohydrate reserves in the stem) may explain their uniqueness. Knowledge that variation exists amongst wheat varieties justifies further evaluation under specific inputs or management regimes to identify adapted varieties. For example, the results obtained in this project suggest that Mercia is well adapted to low fertiliser N availability and so might be expected to do better in organic systems.

There was a complete absence of significant variety × soil N interactions which may be associated with both the low mineral soil N levels and the small differences between the three residual N treatments in soil mineral N level (Table 2) and in yield (Table 4) and biomass (Table 5). Therefore, it is not possible to conclude that there might not have been variety × soil N interactions if the soil mineral N levels had been higher and/or the differences between the treatments greater. If soil N × variety interactions had been identified they may also not have been the same as those obtained in response to fertiliser N because they might have occurred during earlier phases of the life cycle.

Relationship of characteristics to variety age

The results in this programme were also examined in relation to the age of the varieties by conducting regressions of yield, biomass and harvest index against varietal age. Varietal differences in yield were found to be related to the date of introduction of the variety, increasing significantly by 0.037 $t ha^{-1} y^{-1}$ (R^2 = 0.42). The significant deviations ($P < 0.001$) (Table 7) from

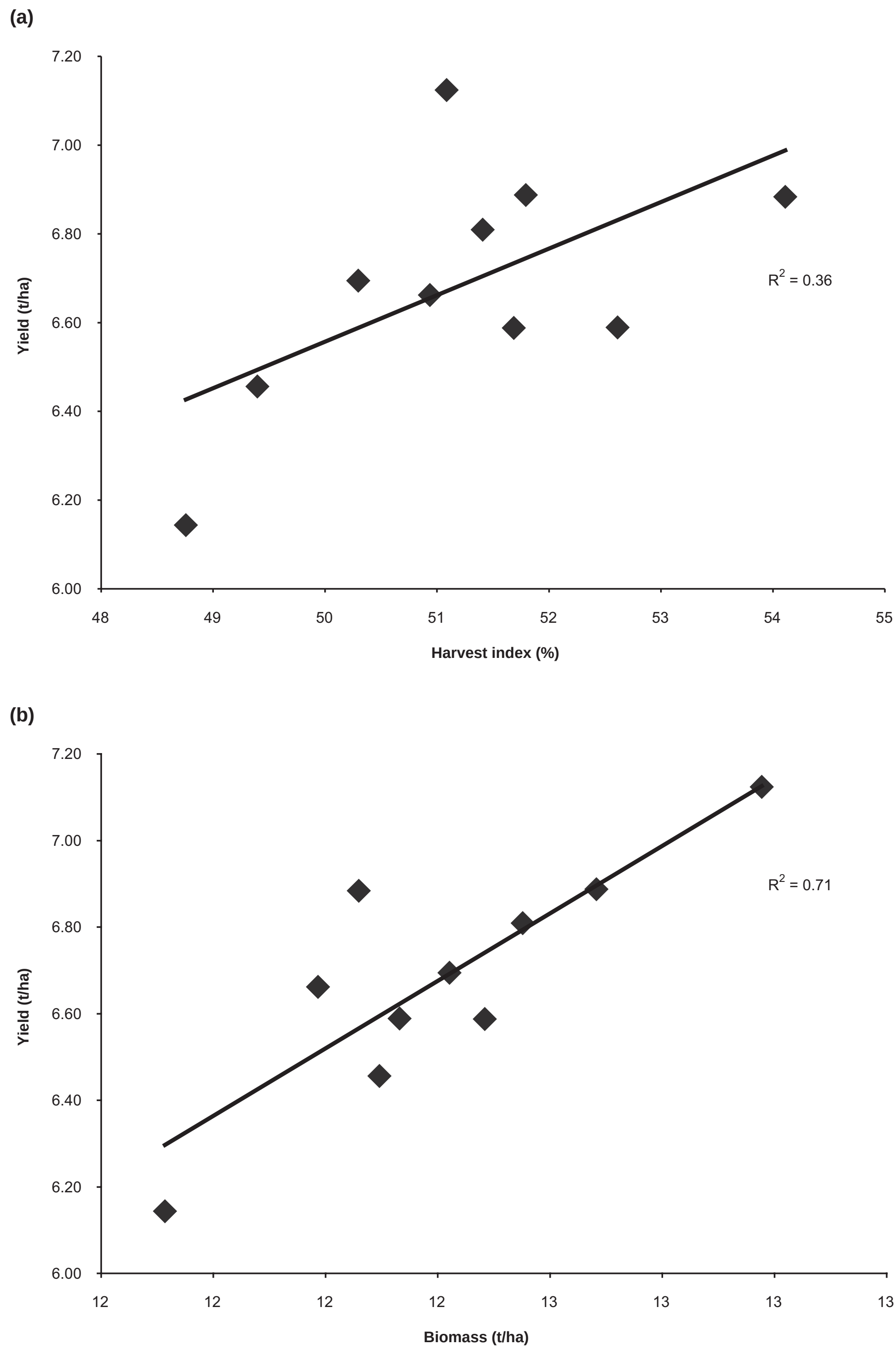

Figure 1: Average values for grain yield (at 85% dry matter) for 10 wheat varieties plotted against the corresponding averages for (a) harvest index and (b) biomass yield (at 100% dry matter).

this trend were attributable to Longbow, an older variety first harvested in National List trials in 1979, which was higher yielding, and Hereward, introduced in 1988, which was lower yielding compared with the linear relationship. This age-related yield response was affected by the level of fertiliser N application ($P < 0.01$) but not soil N. Rates of increase in yield were smaller at F0 (0.025 $t\,ha^{-1}y^{-1}$) and F1 (0.021 $t\,ha^{-1}y^{-1}$), where yields were lower, while at F2 the rate of increase was greatest (0.065 $t\,ha^{-1}y^{-1}$). The significant deviations ($P < 0.01$) (Table 7) from the age-related linear trends for the three fertiliser N rates appeared to be attributable to Mercia and Apollo which have already been identified from the ANOVA.

Varietal increases in biomass were also related to how recently the varieties were introduced ($P < 0.05$) (Table 7). Biomass increased significantly by 0.034 $t\,ha^{-1}y^{-1}$ ($R^2 = 0.31$). Soil N did not significantly affect the age-related change in biomass of the varieties. Differences in rate of increase amongst the three fertiliser N rates (F0: 0.049; F1: 0.005; F2: 0.048 $t\,ha^{-1}y^{-1}$) were not significant and did not correspond to those for yield at the three fertiliser N rates (Table 8). As for yield, the significant deviations ($P < 0.01$) (Table 7) from the age-related linear trends for the three fertiliser N rates for biomass appeared to be attributable to Mercia and Apollo.

There was no significant linear age-related trend for varietal differences in harvest index, a decrease of 0.34%/year (Table 7). However, the quadratic function fitted to harvest indices of the varieties was significant ($P < 0.001$; $R^2 = 0.33$) (Figure 2). This trend was strongly influenced by Rialto and Cadenza, the youngest varieties in this programme, which had low harvest indices (both 51%), and Longbow, one of the oldest varieties, which had a high harvest index (53%) (Table 6). Fertiliser N did not significantly affect this trend, the regression coefficients for the linear functions which corresponded to those for yield and biomass presented above being 0.056%/year for F2, –0.017%/year for F1 and –0.049%/year for F0 (Table 8). Soil N did not have a significant age-related effect on harvest index of the varieties.

The significant effect of fertiliser N on the age-related responses of yield but not biomass or harvest index is confusing. Summarising the regression coefficients presented above shows that fertiliser N had differing effects on the three variables, albeit not detected as significant against the overall variability (Table 8).

While for each fertiliser N rate the regression coefficients are internally consistent, the lack of consistency across fertiliser rate is potentially problematical. Variety performance is very sensitive to environment and, therefore, significant numbers of trials at different locations and

Table 7. Significance tests[†] for regression analysis of the effects of varietal age on yield, biomass and harvest index and interactions with fertiliser N and soil N

Source of variation	Regression term	Yield	Biomass	Harvest index
Varietal (age)	Linear	***	*	
	Quadratic	*		***
	Deviations	***		***
Fertiliser N × Age	Linear	**		
	Quadratic			
	Deviations	**	**	

[†]The interactions between effects, varietal age and soil N were not significant. Likewise, the three-way interactions between age and fertiliser N × soil N were not significant.

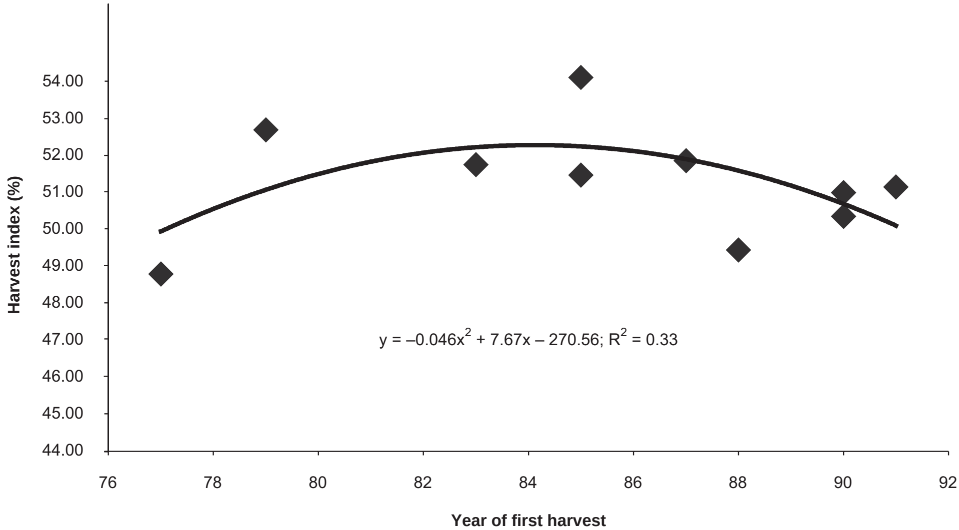

Figure 2: Quadratic relationship between harvest index, y, and varietal age, x, (= year of first harvest in UK National List trials).

in different years are required to separate out the variety effect from the environmental influence on the crop. Fertiliser N could therefore be regarded as a surrogate for environment since it did not have a consistent effect but did contribute to the expression of the variety age-related responses of yield, biomass and harvest index.

The genetic gains in yield of 0.025, 0.021 and 0.065 $t\,ha^{-1}y^{-1}$ at F0, F1 and F2, respectively are similar to those reported by Austin *et al.* (1980, 1989), Ortiz-Monasterio *et al.* (1997) and Sayre *et al.* (1997) but they are much smaller than that, 0.096 $t\,ha^{-1}y^{-1}$, reported by Foulkes *et al.* (1998b). The smaller genetic gains in yield at F0 and F1 than at F2 may have been associated with better acquisition of soil N by older varieties as was postulated by Foulkes *et al.* (1998b), soil N having a relatively greater effect than fertiliser N on yield at these low fertiliser N rates. Ortiz-Monasterio *et al.* (1997) found that greater yield progress at two higher N rates than at two lower rates was attributed in part to higher incidences of lodging in the older taller varieties. In the studies reported here, lodging rarely occurred and, therefore, did not accentuate variety differences, all but two of the varieties, Cadenza and Mercia, having a *Rht* dwarfing gene. In a study of yield of winter wheat grown without N or with 170 kg/ha N in France, Le Gouis *et al*. (2000) found that most of the interaction between varieties and N rate was accounted for by three of the 20 varieties

Table 8. Regression coefficients (R^2) for the relationships between yield, biomass and harvest index of the varieties and their age

Fertiliser N	Yield ($t\,ha^{-1}y^{-1}$)	Biomass ($t\,ha^{-1}y^{-1}$)	Harvest index (%/year)
F0	0.025 (0.25)	0.049 (0.26)	–0.049 (0.019)
F1	0.021 (0.22)	0.005 (0.004)	–0.017 (0.002)
F2	0.065 (0.39)	0.048 (0.15)	0.056 (0.036)

involved. Two varieties introduced in the 1980s gave similar yields at the high N rate but one was low-yielding and the other high-yielding in the absence of fertiliser. Brancourt-Hulmel *et al.* (2003), in a study of 14 winter wheat varieties, concluded that older varieties performed better with low inputs and more modern varieties with higher inputs. However, they identified two modern varieties, Alliage and Renan, which yielded well with low inputs.

Harvest indices of the most modern varieties in the studies conducted by Austin *et al.* (1980, 1989), Sayre *et al.* (1997) and Shearman *et al.* (2005) were in the order of 50%, similar to those reported here. Coincidentally the maximum harvest index reported in a review of a wide range of crops by Sinclair (1998) was also 50%. Austin *et al.* (1980) suggested that there was a limit of 60% to the level of harvest index that breeders may be able to achieve. In the studies reported here harvest index was greater than 50% in eight of the ten varieties. The maximum harvest index was that of Riband at F2, 55.3%, which approaches the suggested biological limit. However, there would still appear to be scope for producing increases in yield through further improvements in partitioning to the grain. If the biomass production of Rialto, 18.60 t/ha at 100% dry matter at F2, was partitioned at 55.3%, a grain yield of 13.96 t/ha at 85% dry matter would result. This is approximately 2.5 t/ha higher than the maximum yields (11.33 t/ha for Riband and 11.51 t/ha for Rialto) calculated from biomass and harvest index quadrat assessments and much greater than the margin of 0.9 t/ha by which Glasgow, the highest yielding variety on the current HGCA UK Recommended List, outyielded Riband.

The results reported here suggest that genetic improvement in yield was more strongly associated with a genetic gain in biomass than in harvest index. Although Austin *et al.* (1980) did not find that increased yield in modern varieties was attributable to increased biomass, later work (Austin *et al.*, 1989) did show some improvement in biomass in high-yielding situations. Shearman *et al.* (2005) also attributed yield improvements in varieties introduced in the UK between 1983 and 1995 to increased biomass rather than harvest index. Donmez *et al.* (2001) showed that biomass, as well as harvest index, had been improved through breeding. Other work provides evidence that harvest index but not biomass can be credited with increased yield of newer varieties. Sayre *et al.* (1997) reported that increased grain yield was highly significantly correlated with harvest index and grain numbers per unit area but not with total biomass production. Brancourt-Hulmel *et al.* (2003) also found that varietal age was associated with increases in harvest index but not in biomass. It is not surprising that harvest index is associated with yield increases, but what is encouraging from the results reported here and from those of some other studies is that increases in yield attributable to increase in biomass are being found more frequently than in earlier work.

The number of varieties used in this programme was relatively small and although not exhaustive compared to the large numbers of varieties entering National List trials every year, they were quite representative of the varieties which attain recommendation within the United Kingdom. However, it would be valuable to confirm these results with a larger set of varieties, including more recent introductions. Unfortunately, collecting and processing quadrat samples for biomass measurements is time-consuming and not routinely carried out in variety trials. The results presented here, however, do appear to indicate that genetic differences in biomass potential have begun to be exploited in the breeding of successful wheat varieties.

Acknowledgements

The authors are grateful to colleagues at the Plant Testing Station for all their help with practical aspects of trial management and collection and processing of samples. Advice and guidance from Dr. Sally Watson, Biometrics Branch, Agri-Food and Biosciences Institute is appreciated.

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Received 22 June 2004