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Reanalyses of the historical series of UK variety trials to quantify the contributions of genetic and environmental factors to trends and variability in yield over time

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Abstract Historical datasets have much to offer. We analyse data from winter wheat, spring and winter barley, oil seed rape, sugar beet and forage maize from the UK National List and Recommended List trials over the period 1948–2007. We find that since 1982, for the cereal crops and oil seed rape, at least 88% of the improvement in yield is attributable to genetic improvement, with little evidence that changes in agronomy have improved yields. In contrast, in the same time period, plant breeding and changes in agronomy have contributed almost equally to increased yields of forage maize and sugar beet. For the cereals prior to 1982, contributions from plant breeding were 42, 60 and 86% for winter barley, winter wheat and spring barley, respectively. These results demonstrate the overwhelming importance of plant breeding in increasing crop productivity in the UK. Winter wheat data are analysed in more detail to exemplify the use of historical data series to study and detect disease resistance breakdown, sensitivity of varieties to climatic factors, and also to test methods of genomic selection. We show that breakdown of disease resistance can cause biased estimates of variety and year effects, but that comparison of results between fungicide treated and untreated trials over years may be a means to screen for durable resistance. We find the greatest sensitivities of the winter wheat germplasm to seasonal differences in rainfall and temperature are to summer rainfall and winter temperature. Finally, for genomic selection, correlations between observed and predicted yield ranged from 0.17 to 0.83. The high correlation resulted from markers predicting kinship amongst lines rather than tagging multiple QTL. We believe the full value of these data will come from exploiting links with other experiments and experimental populations. However, not to exploit such valuable historical datasets is wasteful.

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Introduction

Many public and private organisations have archives of substantial quantities of high quality phenotype data on multiple varieties tested in multiple environments. These datasets are generally highly unbalanced: most varieties are outclassed after a few years, so in series of trials extending over decades there is much missing data. Nevertheless, the extent of data available makes these collections very useful in several areas of crop genetics. For example, they have been used to provide phenotypes for association mapping studies (Kraakman et al. 2004; Crossa et al. 2007; Malosetti et al. 2007), where collection of de novo data on a sufficient scale to provide adequate statistical power would otherwise be prohibitively costly (Mackay and Powell 2007). Equally, in studies of genotype–environment interaction (GEI), although the data are so incomplete that methods such as AMMI (Gauch and Zobel 1996) may no longer be appropriate, the large numbers of varieties and environments sampled can be mined for information about the influence of biotic and abiotic factors on variety performance (Pidgeon et al. 2006). In contrast, in experimental

studies, which are of necessity conducted over limited numbers of years, locations and varieties, the range of environmental effects sampled can be limited and important effects may be missed. Finally, these collections can be used to partition changes in performance over time into those attributable to genetic gain and those due to changes in other factors (Silvey 1978, 1981, 1986), the latter usually attributed to changes in agronomy, but potentially also originating from changes in climate.

Systems for the independent assessment of plant breeders' new varieties of crops have been in place in the UK since 1919 (Wellington and Silvey 1997). Typically, a new variety is tested for a minimum of 2 years before national listing, with an additional 1–3 years of testing required before a variety is eligible for the recommended list for that crop (Wellington and Silvey 1997; Silvey 1999; HGCA Recommended Lists 2009). Successful varieties generally remain in trial until outclassed. In this study, we reanalyse data from 1948 to 2007 for winter wheat, winter barley, spring barley, sugar beet (from 1975 to 2007), winter oil seed rape (from 1979 to 2007) and forage maize (from 1977 to 2007) to quantify the contribution of environment and genotype to the changes over time in national average yields observed in these crops. For the cereals, these gains are typical of those seen in much of the developed world over this period (Brancourt-Hulmel et al. 2003; Calderini and Slafer 1998; Feil 1992; Fischer and Edmeades 2010). These analyses update previous work for the UK by Silvey (1978, 1981, 1986) for the period 1947–1983. We interpret trends in environmental effects as predominantly attributable to changes in agronomic practice, though other causes such as climate change cannot be ruled out, and trends in genotypic effects as attributable to the effects of plant breeding and selection. In the post-war decades, many agronomic improvements were introduced in the UK: mechanisation, improved soil preparation, fertiliser, pesticides and herbicides. For this period, Silvey found roughly 50% of the gain was attributable to selection. We are not aware of published estimates of the relative contribution of genetic and environmental effects to changes in national yield in the more recent decades. In addition, for winter wheat, we have analysed the data more thoroughly to assess the importance of major climatic variables on variety stability and the consequences of disease resistance breakdown on yield. Finally, we illustrate that these datasets, with the addition of suitable genetic marker data, may have uses as training and test sets for methods of genomic selection. Together, the analyses illustrate the value of historical datasets for genetic study and some of the potential problems in their exploitation.

Materials and methods

Phenotype data

Table 1 summarises the structure of the data analysed for each crop. We have analysed yield for all crops. For winter oil seed rape and sugar beet, the major components of crop quality, oil content and sugar content, respectively, are clearly defined and measured and for these two crops these have also been analysed. Data were available electronically from 1948 to 2007 for cereal crops. For sugar beet, electronic data were available from 1975, so we have restricted our analysis to that period. Oil seed rape data are available from 1979 and forage maize from 1977.

Prior to analysis, data were validated to remove duplicate records and to check and remove recording errors. The data analysed were means of varieties from each trial site in each year. Although replicate plot data were available for later years, these were not incorporated into the analyses. Throughout the period under study, trials of all crops have always been randomised, typically with three or four replicates, initially as randomised complete blocks but later as alpha designs (Patterson and Williams 1976; Patterson et al. 1978) following their development in the late 1970s. Although there will be variability in the precision of estimates of variety means within each trial, this

Table 1 Summary of data structure for crops included in the analyses

Crop	No. of observations	No. of varieties[a]	Start year	No. of site–year combinations	Varieties per year	Mean variety lifetime	Percentage of missing data[b]
Winter wheat	52,909	308	1948	3,590	5.1	5.8	95
Spring barley	42,035	299	1948	3,017	5.0	5.8	95
Winter barley	36,562	215	1948	2,155	3.6	6.0	92
Forage maize	14,419	456	1977	461	14.7	5.2	93
Sugar beet	17,105	321	1975	476	9.7	4.6	89
Winter rape	15,920	169	1979	915	5.8	5.0	90

[a] Only varieties present in trial for at least 3 years were included in the analyses

[b] The percentage of the varieties × site–years table with no entry

has not been studied here. Given the large number of sites and years over which each variety is tested, failure to take this into account is highly unlikely to be a source of error or bias in the analyses. Trials were located throughout the relevant growing area of England, Scotland and Wales, though the greatest density of trials, for all crops, was in East Anglia. For cereals, until 1981, trials were managed by "best local practice". With some exceptions, this meant that they would receive the same fungicide, fertiliser and other inputs as applied to the surrounding crop. From 1982, the cereal trials were split into a treated series of trials and an untreated series. Treated trials routinely receive a full fungicide regime, even if levels of disease are very low. Untreated trials receive no fungicide. This system was also introduced for oil seed rape in 1987. Sugar beet and forage maize do not have this distinction, except for a very small number of rhizomania resistance trials grown on infected soil, which were excluded from these analyses. Untreated trials are frequently, but not always, located on the same site as a treated trial. Varieties in trial for only 1 or 2 years contribute little information to the estimation of trends over years; so, for all crops, we restricted the dataset to varieties that were in trial for at least 3 years in the period studied. In practice, this restricts the dataset to varieties which were placed on the UK National List (requiring 2 years of testing) and were then entered into the Recommended List process in the third year. It also reduced the size of the dataset to more manageable numbers. To avoid selection bias in the estimation of variety effects all data employed in selection decisions should be included in the analysis (Piepho and Möhring 2006). However, this is unlikely to be a problem in our analyses. Selection on yield in the first 2 years of testing is by comparison of new candidates against established control varieties rather than by direct selection amongst the candidates themselves. Full data on these controls are inevitably included within the dataset.

Marker data

For wheat, DArT marker data (Akbari et al. 2006) were available on a subset of 159 winter wheat varieties from a previously published analysis (White et al. 2008) combined with additional data from ongoing work in association analysis (White *pers. comm.*). Here, we restricted the analysis to 217 mapped markers.

Historical meteorological records, N use records and national yields

National annual yields for wheat from 1885 and barley from 1948 are available for downloading from the economics and statistics section of the Defra Web site (http://www.defra.gov.uk/evidence/statistics/foodfarm/index. htm).

Weather records were taken from the Meteorological Office Hadley Centre Observation Data (http://www. metoffice.gov.uk/climate/uk/2001/). England and Wales monthly totals were used to estimate total seasonal precipitation. Central England average monthly temperatures were used as average seasonal temperatures. Seasons were defined as 3-month periods, starting with winter as December, January and February.

Statistical analysis

Changes in performance over time

To study changes over time, the following model was fitted to the incomplete varieties × sites matrix using REML as implemented in GenStat10 (Payne et al. 2007).

$$y_{ijk} = \mu + v_i + y_j + vy_{ij} + s_{jk} + e_{ijk}$$

y_{ijk} is the historical yield of variety i in year j at site k; μ is the overall trial series mean; v_i is the effect of the ith variety; y_j is the effect of the jth year; vy_{ij} is the interaction of variety i in year j; s_{jk} is the effect of site k within year j; e_{ijk} is the residual, attributable to the combined effects of within-trial error and variety × site within-year interaction.

Because of anticipated large, potentially non-linear trends over time for both variety and year effects, neither of these factors could simply be fitted as random terms. For example, if variety effects increase over time, the estimated variance component for varieties will also increase as time progresses and the distribution of variety effects becomes increasingly non-normal. In addition, simple simulations suggest that the correlation of both variety effects and year effects with time might result in biased estimates when these factors are treated as random: variability in one factor can be allocated to the other, whereas this does not happen when factors are fixed (results not shown). Here, therefore, we have adopted a robust two-stage process of analysis in which varieties and years were first treated as fixed factors, with varieties × years and sites within years treated as random. Residual error is then a combination of varieties × sites within years and the within-site error. Trends have then been examined in a second stage of analysis by regression of the estimated year and variety means on calendar year or year of variety entry into trials, respectively. A better approach could be to fit a mixed model, in which the year and genotype main effects are each modelled directly by regression terms with random residuals (H–P Piepho, *pers. comm.*), but this has not been tested. No attempt in these analyses was made to study variation across regions or variation between locations over years.

Data were analysed twice: with either the treated trial series excluded or the untreated trials excluded.

Comparison of treated and untreated trial results for wheat

For winter wheat, to evaluate the effect of disease resistance breakdown, we worked on 747 treated and untreated trial pairs where both members of the pair were grown at the same location. For each pair, the differences between the treated and untreated variety means were calculated as a measure of the loss in yield at that site as a result of disease. Working on differences, the common environment effects (including the year effect) cancel. These differences were then analysed by REML using the following model:

$$y_{ijk}^d = \mu^d + v_i^d + a_j + va_{ij} + s_{jk}^d + e_{ijk}^d$$

y_{ijk}^d is the difference in historical yield of variety i between treated and untreated trials at site k after j previous years in the trial; μ^d is the mean difference; v_i^d is the effect of variety i on difference in yield between treated and untreated trials; a_j is the effect of variety age, j, on difference in yield between treated and untreated trials; va_{ij} is the interaction for difference in yield of variety i and variety age j; s_{jk}^d is the mean effect of site k on difference in yield within year j; e_{ijk}^d is the residual, attributable to the combined effects of within-trial error and variety × site within-year interaction.

Here 'a' is a fixed effect with levels representing the number of years the varieties have previously been in trial. This age-of-variety effect estimates the reduction in yield in the untreated trial series as a result of disease resistance breakdown.

Genotype–environment interactions (GEI)

The extreme incomplete nature of the sites × varieties data matrix makes approaches such as AMMI (Gauch and Zobel 1996) to GEI analysis difficult. Our prime interest is in climatic variables. To examine the sensitivity of winter wheat varieties and to illustrate the information available within the historical data, we correlated individual variety × year terms (vy_{ij}) from the analysis above, for treated trials only, with each of eight climatic measures for that year: average seasonal rainfall in England and Wales and average seasonal temperature. The source and derivation of the climatic variables is outlined under "*Historical meteorological records*" above. This gave 1,320 correlation coefficients (8 climatic variables × 165 varieties), based on between 21 and 3 observations (depending on the number of years a variety was in trial).

Statistical significance was calculated for each correlation. Then for each environmental variable, the numbers of varieties with significance exceeding a false discovery rate (FDR) threshold, or Q-value (Storey 2002) < 0.5 was tabulated to assess the degree to which the germplasm tested in the UK over this period was sensitive to these climatic drivers. Q-values were computed by the package Qvalue (Storey and Tibshirani 2003), implemented in R (R Development Core Team 2005).

Genomic selection

A total of 217 mapped DArT markers (Akbari et al. 2006) were available on a subset of 159 of the winter wheat lines. The estimated variety mean yields ($\mu + v_i$) for these lines were partitioned into test and training sets of 79 and 80 varieties, respectively, in two ways: firstly, so that the test and training sets had equal representation of old and new varieties and, secondly, such that the test set contained the newer varieties and the training set the older. Missing marker data were imputed from allele frequency estimates. Marker regression coefficients were estimated in the training set by ridge regression (Whittaker et al. 2000; Piepho 2009) of the mean yields on all markers, with penalty set equal to the number of markers. These regression coefficients were then used to predict yield in the test set, and observed and predicted yields were compared.

Linking trials data to national yields

For wheat and barley, trends in yield observed in the treated trial series were linked to national yields for the period 1982–2007, based on procedures similar to those outlined by Silvey (1978). For years where data were available, national yields for spring and winter barley were estimated from the total barley crop yield published by Defra (2009), adjusted by the area of spring and winter crop sown and by the relative yield of spring and winter barley observed in that year's trials. For years where data on spring and winter crop area were not available, yields of spring and winter barley were estimated by linear interpolation. For winter wheat, national yield of the wheat crop was used directly, since very little spring wheat is sown in the UK. Yields fluctuate markedly over years, so a 3 *df* spline was fitted to the national yields to highlight trends over time.

Statutory records of the areas of certified seed grown in the previous year were assumed to be representative of the proportion of the national crop grown for each variety in the current year. Since the late 1990s there has been a significant increase in the use of farm-saved seed in the UK, which might invalidate this procedure. However, using data supplied by the British Society of Plant Breeders, the correlation between farmer-saved seed royalties in 1 year and certified seed areas in the previous year was

estimated at 1. We are therefore justified in continuing to use certified seed areas as a measure of variety composition.

An estimate of national yield from the trials data is then:

$$z_j = \mu + \sum_i w_{ij} v_i + y_j$$

where z_j is the estimated national yield for the jth year; y_j is the year effect for year j estimated from the treated trials series; v_i is the variety effect for variety i estimated from the treated trials series; w_{ij} is the weight for variety i in year j, taken as the proportion of certified seed of variety i grown in year $j − 1$; μ is the trials mean.

Estimated national yield in trials was always greater than observed national yield. The estimated contribution of variety improvement to national yield for each year was therefore scaled by the ratio of observed to estimated national yield for that year. In addition, variety contributions for each year were adjusted to a reference year (here 1982) by subtracting the $\sum_i w_{ij} v$ for the reference year from all $\sum_i w_{ij} v$. The estimated contribution of variety improvement to national yield in any year is then:

$$c_j = (\mu + \sum_i w_{ij} v_i − \sum_i w_{i\text{ref}} v_i)$$
$$\times (\text{observed national yield in year } j)/z_j$$

where subscript ref refers to the reference year.

Results

Relative contribution of genotype and environment to trial yields

Figure 1 shows yield increases over time for all crops from 1948 to 2007. For those crops in which parallel series of treated and untreated trial series are introduced, results are shown from the treated trials analysis only. To facilitate comparison across crops, yields (t/ha) are plotted to the same scale on both axes for all crops (though with different origins). In all plots, estimated variety means are plotted as points, and estimated year means by an unbroken line. For all crops variety effects are seen to increase on average, nearly linearly over time, though at different rates. Year effects are more variable. For winter wheat and barley, year effects rise steadily until 1981, when a jump in performance corresponds to the change in the trial system to separate fungicide treated and untreated series. From 1982, there is little trend in year effects over time. For spring barley, there is little change in year effect over the whole 60-year period, aside from a slight increase following the change in trial system.

Data are less extensive for winter oil seed rape. Variety effects increase steadily, though year effects show little trend over time and the effect of the change to treated trials in 1987 is less marked.

Data are also more limited for forage maize and sugar beet, but both crops show strong increasing trends in yield for both year and variety effects, though with much greater variation in year and variety effects for maize.

Sugar content of sugar beet and oil content of oil seed rape were also analysed and results are shown in Fig. 2. Variety effects for these quality traits have increased over time, though with considerable variation amongst varieties within years. The year effects for these traits are also particularly variable, notably for sugar beet, where the drought year of 1976 corresponded with very high virus yellow infections with a major effect on both yield and quality.

Table 2 summarises these graphs as linear regression coefficients for each trait and crop. In addition to regression coefficients over the whole time period, coefficients are presented separately for the period 1982–2007 for all crops and for 1948–1981 for wheat and barley. Splitting the data in this manner allows a comparison across all crops for a common recent time period and a comparison with previous analyses by Silvey (1978, 1981), whilst for the cereal crops, fortuitously circumventing problems associated with the change in testing system after 1981.

For all crops, over the whole period of testing, it is clear that genetics (varietal) have been responsible for major improvements over the time periods analysed. Trends in year effects are more complex. These will be predominantly a result of changes in agronomy (including the change in trials system) but are confounded with other possible environmental trends, from climate change for example. The contribution of genetic effects to any linear increase in yield can be estimated as (varieties regression/ varieties regression + years regression). For the winter cereals, it is noticeable that genetic effects and environmental effects are of roughly equal importance up to 1981, but after this period 88% of the linear gain in yield, averaged over the two crops, is attributable to genetic improvement. For spring barley from 1948 to 1981 and from 1982 to 2007 there is virtually no trend in yield as a result of change in agronomy or from other causes, though there is an increase over the whole period as a result of the change in trial systems. Consequently, the contribution of genetic change to the linear increase in yield is 71% over the whole period, but 86% from 1948 to 1981 and 110% from 1982 to 2007.

Forage maize shows the most dramatic increase in yield of all crops analysed, with genetic and environmental sources of equal importance.
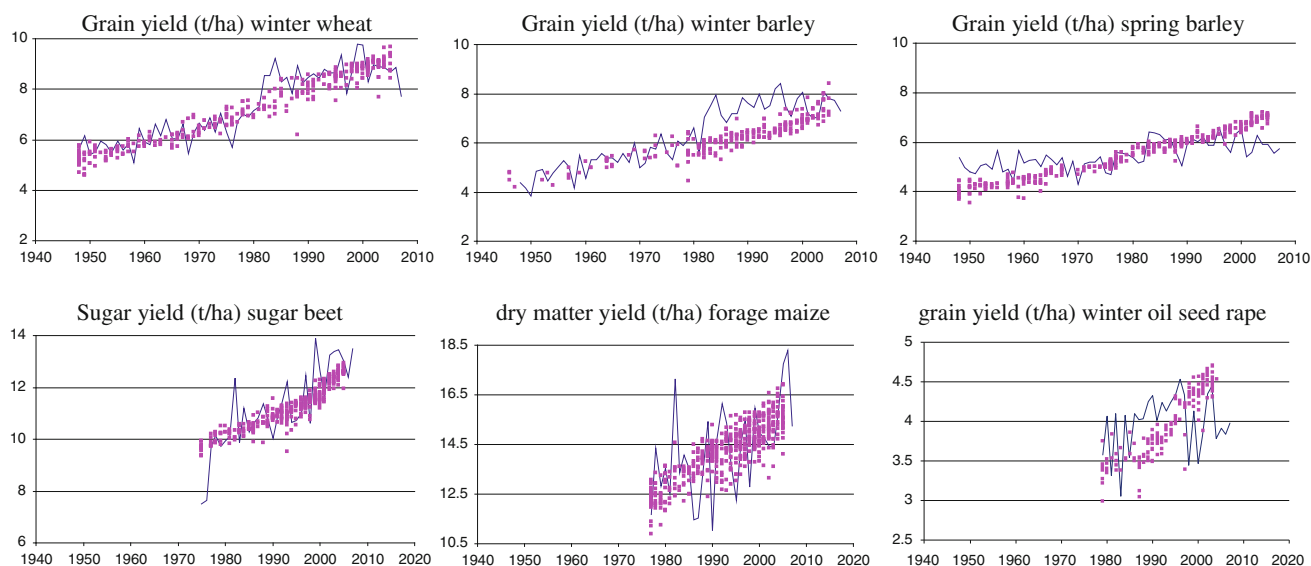
Fig. 1 Trends in variety and year effect for yield (t/ha) from 1948 to 2007. Ordinate and abscissa are on the same scale for all crops except oil seed rape. Variety and year means were estimated as described in "Materials and methods" section. Variety effects (*squares*) are plotted against the year in which the variety first entered the trial. Year means are plotted as a *line*
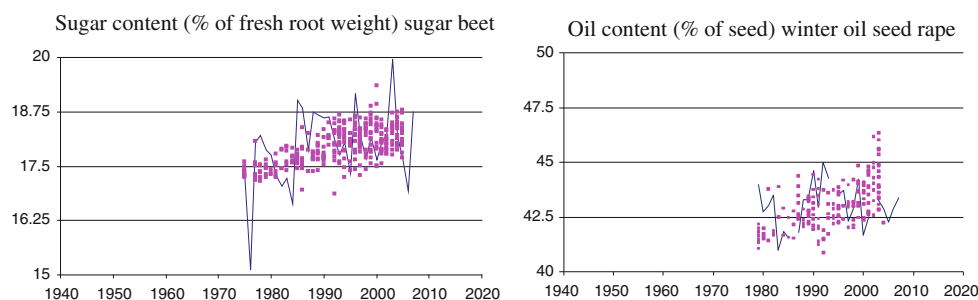

Fig. 2 Trends in variety and year effect for sugar content in sugar beet and oil content in winter oil seed rape yield (t/ha) from 1948 to 2007. Abscissa is on the same scale as Fig. 1. Variety and year means were estimated as described in "Materials and methods" section. Variety effects (*squares*) are plotted against the year in which the variety first entered the trial. Year means are plotted as a *line*

Table 2 Rates of change in variety and year effects over time

Crop	Trait	Period analysed	Linear trend over varieties			Linear trend over years		
			All years	1948–1981	1982–2007	All years	1948–1981	1982–2007
Winter wheat	Grain yield	1948–2007	0.071	0.061	0.074	0.069	0.041	0.010 ns
Spring barley	Grain yield	1948–2007	0.053	0.043	0.060	0.021	0.007 ns	−0.006 ns
Winter barley	Grain yield	1948–2007	0.051	0.038	0.071	0.066	0.052	0.010 ns
Forage maize	Dry matter yield	1977–2007	0.117	na	0.109	0.104	na	0.108
Sugar beet	Sugar yield	1975–2007	0.092	na	0.105	0.134	na	0.112
Winter rape	Seed yield	1979–2007	0.052	na	0.059	0.010 ns	na	0.004 ns
Sugar beet	Sugar content (%)	1975–2007	0.031	na	0.027	0.031	na	0.014 ns
Winter rape	Oil content (%)	1979–2007	0.091	na	0.092	0.007 ns	na	0.019 ns

ns regression coefficients are not significant

All yields are in tonnes/ha

The regressions for sugar beet yield are strongly influenced by the disastrous years of 1975 and 1976 in which yields were severely depressed by drought. This results in an inflation of the regression for year effects over the whole period, compared to 1982–2007. Nevertheless, even for the latter period, there is a strong increase of 0.112 t/ha/year

from environmental improvement. This is greater than the rate of genetic improvement for the same period (0.105 t/ha/year), which is itself close to 0.109 t/ha/year for genetic change in forage maize. Sugar content in beet also shows both genetic and environmental improvements over time, though with substantial variation from year to year and amongst varieties entering trial in the same year.

Genetic gain in oil seed rape yield is comparable to that for the other combinable crops, though lower than for maize and beet. The environmental trend in yield is low and non-significant at 0.010. Genetic improvement has raised average oil content from about 42 to 44% over the study period.

Breakdown of disease resistance

Figure 3 plots estimated environmental (year) means against year from both the analysis of data excluding untreated trials and the analysis excluding treated trials, following the introductions of the two testing systems in 1982 (cereals) and 1987 (oil seed rape). For winter wheat, winter barley and spring barley, year effects from the two analyses follow each other quite closely until the introduction of the treated and untreated trial series: as they should since the data covering this period are common to both analyses. However, after this introduction of the two trial series, the year effects diverge over time, with the effects in the untreated trial series declining strongly. Yield and oil content in oil seed rape show a similar pattern: even though year effects in the treated trial series

decline, those in the untreated trial series decline more strongly.

Although year effects diverge between the two sets of analyses, variety effects correlate strongly. However, analysing data only from years in which both trial series were present shows that in every case, the rate of increase in variety performance is lower in the treated trial series than the untreated series. Figure 4 plots variety effects from the two series for winter wheat. Table 3 summarises regression coefficients for all the crops with treated and untreated trial series. All rates of change of environment in untreated trials are lower than in treated trials and all are negative. All rates of change in variety effect in untreated trials are larger than in treated trials. We argue below that this pattern is consistent with loss of disease resistance by a proportion of the varieties during their period in trial.

To quantify the loss of resistance for winter wheat, we analysed the difference in variety yield between 747 treated and untreated trial pairs, which were co-located. Figure 5 plots the estimated age-of-variety means against variety age. From an initial difference of 1.7 t/ha between the two trial series, there is a strong linear increase of 0.08 t/ha/year. This is indicative of a decline in average variety performance in the untreated trial series with variety age.

Regression coefficients were also calculated for each variety difference separately by regression of the GEI terms for each variety difference × age-of-variety term against variety age. Figure 6 gives a histogram of these regression coefficients. A list of variety names and these regression coefficients, together with their estimated yield
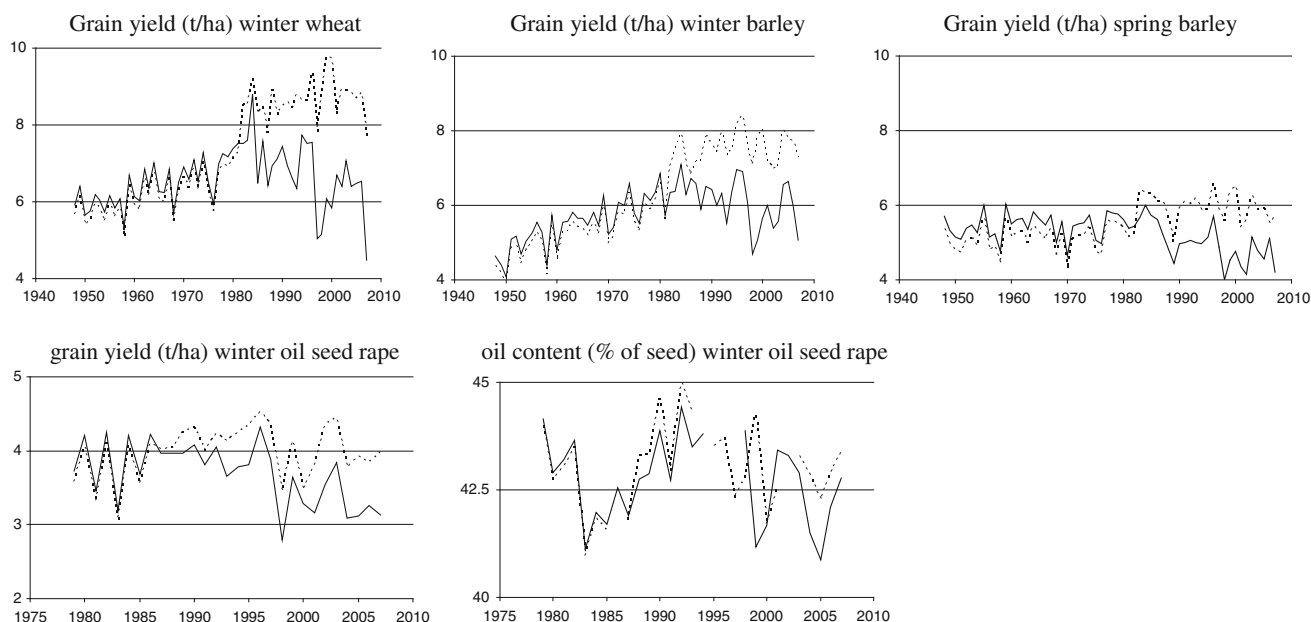

Fig. 3 Trends in year effect for yield (t/ha) from 1948 to 2007: untreated trials only from 1982 (1987 oil seed rape). Year means were estimated as described in "Materials and methods" section. *Dotted line* analysis with treated trials only. *Solid line* analysis with untreated trials only
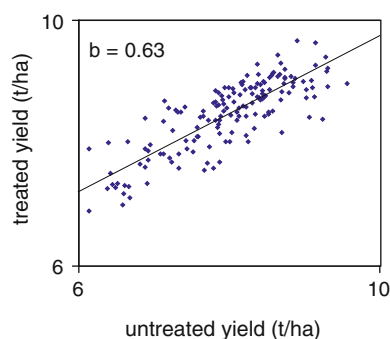
Fig. 4 Relationship between variety means for winter wheat estimated independently from the treated trial series and the untreated trial series 1982–2007

in treated trials, is given in Table 1 of the supplementary information.

Genotype × environment interaction (GEI)

For winter wheat, variety × year interaction terms for treated trials (1982–2007) were correlated with each of eight climatic variables and tested for statistical significance. The numbers of varieties, out of 165 with at least 3 years' data in the treated trials series and with an FDR < 0.5 are tabulated in Table 4 for each climatic variable. In total, 64 such interactions were detected, involving 49 varieties. Five varieties had FDR < 0.5 for two variables and five had FDR < 0.5 for three variables.

Genomic selection

Figure 7a plots observed yields and predicted yields from independent test and training sets containing equal representation of old and new varieties. Figure 7b is the equivalent plot for a training set consisting of varieties first tested from 1948 to 1989 and the test set from 1989 to 2007. With equal representation of old and new varieties, correlations between predicted and observed yields are high (0.83). However, the correlation is much lower if the yield of new varieties is predicted from the old (0.17).

Comparison with national yields

Figure 8 plots national yield together with the estimated contribution from variety improvement (adjusted to a base of 1982 national yields) for wheat, spring barley and winter barley. For all three crops, national yields fluctuate, but have increased over the 25-year period. However, there is an indication that in the latter half of this period, the rate of increase has reduced, or even declined, in the case of winter wheat. In agreement with results from the trials analysis alone, improvements in yields over the period 1982–2007 appear to be predominantly, if not wholly, attributable to variety improvements in all three crops.

Discussion

Relative contribution of genetic and environmental change in trials

Figures 1 and 2 demonstrate that the increases in yield and quality attributable to plant breeding have been remarkably linear over the period 1948–2007 for all crops and traits studied. It is noticeable that there are no apparent step changes in performance, which might be expected to result from the introduction of new traits such as reduced height genes in wheat or monogermity in sugar beet. There are several reasons for the lack of such marked changes. Firstly, changes that were dramatic at the time were first introduced by only one or two varieties and were therefore lost in the spread of variety performance about the mean in any specific year. Secondly, when viewed over the 60-year period, large changes can be lost in the relentless (so far) incremental increase in variety performance. Finally, such changes do not necessarily have an immediate dramatic effect on yield per se, but permit changes in agronomy which are themselves responsible for yield or productivity improvements. For example, the initial effects of monogermity on sugar yield in beet were adverse as a result of linkage drag around the monogermity locus, which was introgressed from a very poorly adapted USA line (Bosemark 1993).

Table 3 Rates of change in variety and year effects in treated and untreated trial series, 1982–2007 (1987–2007 for oil seed rape)

| Crop	Trait	Linear trend over varieties		Linear trend over years	
		treated	untreated	treated	untreated
Winter wheat	Grain yield	0.074	0.104	0.010 ns	−0.071
Spring barley	Grain yield	0.060	0.075	−0.006 ns	−0.044
Winter barley	Grain yield	0.071	0.078	0.010 ns	−0.037
Winter rape	Seed yield	0.067	0.077	−0.014 ns	−0.047
Winter rape	Oil content (%)	0.094	0.100	−0.036 ns	−0.056 ns

ns regression coefficients are not significant
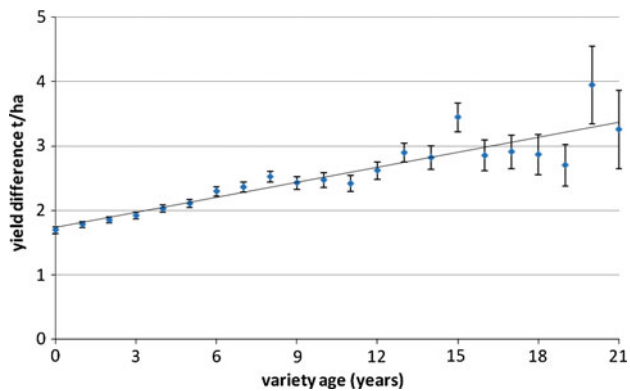
Fig. 5 The effect of variety age on the difference between treated and untreated means for 747 matched trial pairs of winter wheat. *Yield difference* difference in yield between treated and untreated trials. *Variety age* number of previous years a variety was present in the trial series. *Vertical bars* are standard errors

Table 4 Numbers of winter wheat varieties, out of 165 total with false discovery rate <0.5 for eight climatic variables

	Autumn	Winter	Spring	Summer
Rainfall	0	0	1	26
Temperature	0	27	8	2

Although the genetic gain in performance in all crops is linear, there are large differences between crops. Table 2 compares these for the period 1982–2007. Sugar beet and forage maize show the greatest increases. However, it is dangerous to read too much into these differences: the crop types are very different.

As expected, environmental effects for yield vary greatly from year to year for all crops, and also for quality in oil seed rape and sugar beet. The most dramatic variation is seen in sugar content in beet in 1976, when a summer drought and accompanying virus yellow infection reduced average sugar content from around 17.5 to 15%. In spite of the considerable year-to-year variation, for sugar beet and forage maize there is a general trend for an improving environment. Much of this must reflect improvements in agronomy. Forage maize has only recently been grown extensively in the UK and opportunities to improve yields through tuning its agronomy for UK conditions have been great. All sugar beet is grown under contract for a single customer, British Sugar plc, which provides high quality

agronomic advice to all growers through their field staff. However, some of the change attributable to the environment will still be genetic in origin. For example, in beet, there has been a steady improvement in the bolting resistance of many varieties. This has allowed earlier drilling of the crop (and the variety trials). The longer growing season results in improved yields. This improvement in environment (earlier sowing) was only possible because of the efforts of breeders in increasing bolting resistance.

The environmental trends for the other crops are more complex and are partly confounded with the change in the trialling system to include treated and untreated trial series. This can clearly be seen in Fig. 1 for winter wheat: the jump in year effect from 1981 to 1982 corresponds to the introduction of treated trials in 1982. Similar jumps are seen for barley and oil seed rape (from 1986 to 1987). For winter wheat and winter barley, this split also corresponds, coincidentally, to a change in rates of environmental improvement. From 1948 to 1981, these crops show strong linear increases in yield as a result of environmental change. These results correspond to those reported by Silvey (1986) who reported 45 and 32% of the increase in yield for wheat and barley, respectively, to result from genetic improvement for the period 1947–1983. The equivalent figures here, from the trials data, for the period 1948–1981 are 60% for winter wheat, 45% for winter barley and 86% for spring barley. These are calculated from Table 2 as (varieties regression)/(varieties + years regressions). The disparity for barley is a consequence of the change to increasing use of winter barley rather than spring barley in the national

Fig. 6 Histogram of regression coefficients of difference in yield of 175 winter wheat varieties in 747 matched treated and untreated trials
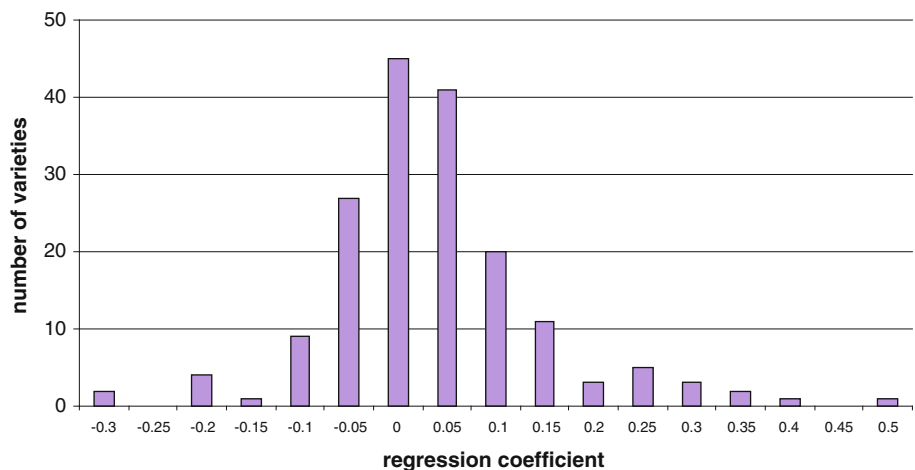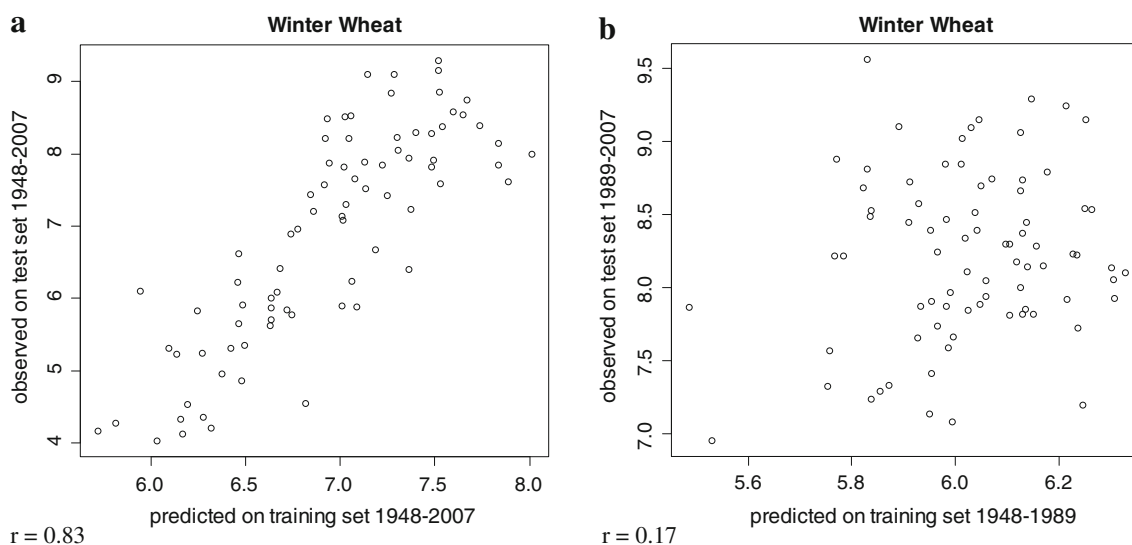
Fig. 7 Comparison of observed yield on a test set of 79 winter wheat varieties with yield predicted from regression of a separate set of 80 winter wheat varieties on 217 DArT markers. **a** Test and training sets sampled in the range 1948–2007. **b** Test set 1989–2007, training set 1948–1989
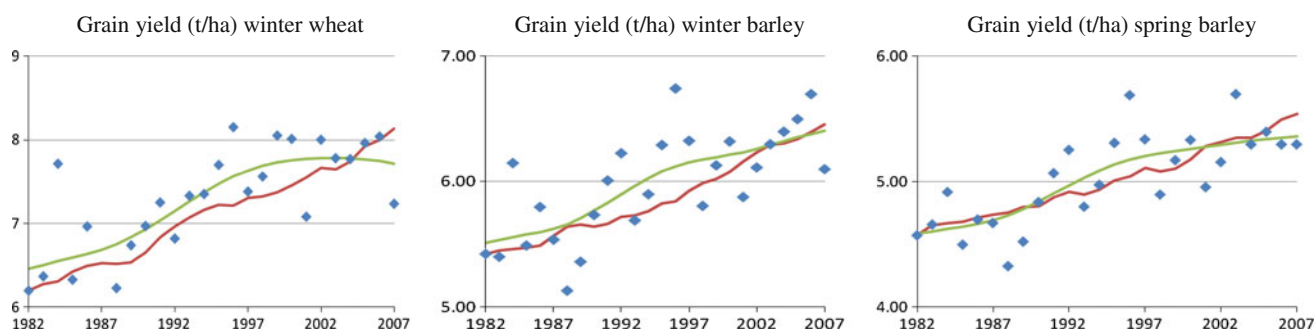

Fig. 8 Estimated contribution of variety improvement to national yield increases (t/ha) 1982–2007. *Blue diamonds* national yield, *green line* spline (3df) fitted to national yield, *red line* contribution of variety effect to national yield

crop over this period. Silvey did not treat the two types as separate crops and the higher yield of the winter types contributes to an increasing environmental trend over the years. For wheat, the figures agree acceptably well, given differences in time period and analysis methods. From 1982 to 2007, wheat and barley trials yields show only a very weak trend due to environmental change. Given that the fungicide treated trials are managed to maximise yield, this implies that there were no agronomic improvements available to increase productivity in these trials over this period. This seems reasonable: although changes in the agronomy of these crops have undoubtedly taken place in the last 20 years, those gross changes which increased yields were largely in place by 1981. More recent changes have concentrated on maximising gross margins or minimising environmental impact, rather than total yield, and may even reduce yield (see "Conclusion" below).

In spring barley, there appears to have been little environmental change in performance over the whole 60-year

period (ignoring the jump in 1982 attributable to the change in trial regime). The reason for this is unclear. However, the agronomy of spring barley is focussed predominantly on quality rather than yield, and maximising yield and crop quality are antagonistic. Barley for brewing and malting requires a low grain nitrogen content, so application rates of N are much lower (of the order of 100 kg/ha in contrast to 150 kg/ha for winter barley and 200 kg/ha for winter wheat).

Oilseed rape has long been recognised as the UK crop in which attempts to improve yield appear to have had least effect (Berry and Spink 2006). This is confirmed by the analyses presented here. This shows that although variety yield and oil content are apparently increasing over time, there is no significant environmental trend from 1982 onwards. The reasons for this are unknown. Nitrogen input for oil seed rape has fallen from 275 kg/ha in 1983 to 200 kg in 2007. This is close to the current optimum economic rate (Peter Berry *pers. comm.*). If nitrogen was

applied to maximise yields, the expected gain in yield would be about 0.1–0.2 t/ha (Peter Berry *pers. comm.*). Equally, increased prevalence of a disease to which there is little or no disease resistance in current varieties would reduce trends. A possible candidate is *Olpidium brassicae,* a soil-borne fungus pathogen associated with reduced rotation of oil seed rape (Stobart 2009), though the potential effect of this pathogen on yield is yet to be quantified.

Breakdown of disease resistance

In a series of variety trials with selection for improved performance, a consequence of a decline in individual variety performance over time can be that year effects are biased down with time, and variety effects are biased upwards. This is illustrated in Fig. 9. We believe that the apparent trend downward in year effect that is seen in Fig. 3 for the untreated trials is a reflection of this breakdown. This would also account for the lower than unity regression coefficient of 0.6 of treated on untreated yield seen in Fig. 4, in spite of the very high correlation between the two trial series. To model this in a single trial series is difficult: age-of-variety effects and year effects cannot adequately be fitted simultaneously, as variety × year and variety × years-in-trial interaction terms are completely confounded. However, with two independent trial series, fungicide treated and untreated, the effect can be tested directly by comparing change in performance over time in the two series. For winter wheat, using paired treated and untreated trials to give the most robust dataset, this provided a remarkable linear relationship between age-of-variety and year difference seen in Fig. 5. The simplest explanation is that variety performance, averaged over all varieties, declines at a linear rate over years. In reality,
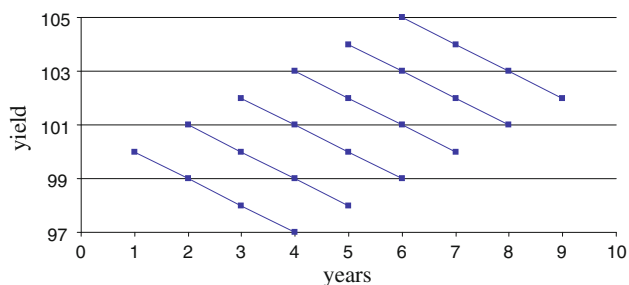

Fig. 9 Model to demonstrate that breakdown of disease resistance can result in biased estimation of variety and year effects. Variety effects increase by one unit per annum, then decline linearly as a result of loss of disease resistance. There is no change in year effect. The *estimated* difference in year effect for successive years is the difference in performance of varieties tested in both years, which is −1. Differences in variety performance are estimated from differences between varieties within years, −2. Variety effects are therefore biased upwards and year effects are biased downwards

individual varieties will succumb to disease at different and often non-linear rates. Nevertheless, over the whole dataset, the net relationship is linear. To pursue this further, we regressed the age × variety interaction term on age for each variety separately and show the distribution of regression coefficients in Fig. 6. Those varieties with large coefficients indicate varieties in which the reduction in yield in the untreated trials is most dramatic. It is of note that out of 176 varieties, of the top 20 varieties, 9 were immediately recognisable to a wheat breeder as losing resistance to yellow rust or brown rust during their lifetime (P. Howell *pers. comm.*). These included the well-documented cases of Slepjner, Brigadier and, more recently, Oakley. The full list of regression coefficients is given in Supplementary Table 1. Some regression coefficients are negative, implying that the difference between the two trial series gets smaller with time. However, these regression coefficients are based on very few data points for most varieties and many are undoubtedly the result of sampling variation. Moreover, no varieties with large negative coefficients were recognised as having suffered breakdown of disease resistance. It is interesting to speculate that these analyses may provide a means of selecting subsets of varieties enriched for durable disease resistance, though these would require validation in subsequent experiments.

Oil seed rape shows the least difference between year effects amongst the treated and untreated trials. However, the year effect in treated trials also shows a decline with time. As discussed earlier, it is possible that this decline is an indication of build up of disease for which there is little or no resistance.

The potential bias in estimated variety and year effects from untreated variety performance may also have a direct effect on the published Recommended List. Within the 5-year window of data that is used to create these, some varieties are present in trial only 3 years. Older varieties, in which disease resistance broke down during the 5-year window, may bias the performance of these newer varieties. The effect may be slight, and greater emphasis on variety selection for yield is usually placed on the treated trial series, but this warrants further study by the testing authorities.

GEI

The highly unbalanced datasets studied here, when coupled with the systematic pattern of extensive missing data, are not ideal for studies of genotype × environment interaction using such approaches as AMMI. However, the vast extent of the data, ∼53,000 variety–site combinations for winter wheat, compensate for this. As a first approach, we have regressed variety × year interaction terms on seasonal national climatic variables, but have then used FDR

rather than simple significance tests to seek those climatic variables to which varieties appear to be most sensitive. FDR gives to the experimenter a means, after the experiment is complete, of balancing the risk of false discoveries against the risk of false positives. Here, we have adopted a threshold of 0.5 to ensure detection of sufficient variety–climate combinations to discriminate between the different climate variables. That this has picked up summer rainfall as of greatest importance is not particularly surprising, though the importance of winter temperature was less expected. To date, we have only studied seasonal measures of the average UK climate. The variety showing the most extreme sensitivity to any climatic variable was Cadenza, to summer rainfall. Cadenza is a spring wheat; it has no vernalisation requirement, but it has been grown commercially as both a winter and spring wheat. Eight years in trial shows a linear increase in yield with increasing rainfall (data not shown). We anticipate that extending these analyses to include (co)variation amongst sites within years-in-variety performance and local climate could be more powerful and provide a simple method to screen historical variety collections for lines showing resistance or sensitivity to various components of abiotic and biotic stress. This approach has been implemented successfully in studying drought resistance amongst sugar beet varieties (Pidgeon et al. 2006). Although the data matrix is highly and non-randomly imbalanced, testing individual variety responses to specific environmental variables, coupled with suitable FDR thresholds, provides a promising and simple method of screening for variety sensitivity to multiple environmental varieties in highly unbalanced datasets. Such an approach can also be extended to assess the consequences of predicted climate change on existing and historical germplasm by studying variety responsiveness at selected sites and years for which combinations of climatic variables, possibly unusual at the time, are predicted to be more common in the future, an "analogue years" approach in the terminology of climate change research; used for example, to study possible changes in damaging weed communities in maize (McDonald et al. 2009).

Genomic selection

It is clear from Fig. 7a that modest numbers of markers can provide very accurate estimates of yield in winter wheat ($r = 0.83$). However, this is only the case when varieties in the test and training sets both span the 60-year period, 1948–2007. When the training set comprises older varieties and the test set is new varieties, the correlation drops to 0.17 (Fig. 7b). This correlation then rises to 0.44 if prediction is confined to varieties which entered the trials system within 10 years of the training set threshold. The pattern of correlation is most simply explained if markers predict yield indirectly by estimating kinship between varieties in the test and training sets rather than by directly tagging large numbers of trait loci of very small effect. Consistent with this explanation, it is clear from Fig. 1 that the year of entry into trial of a variety is a very good predictor of yield. Markers cluster wheat varieties by year of release (White et al. 2008; Horvath et al. 2009). It is therefore inevitable that markers predict yield in any set of varieties covering a sufficiently long time period for improvements in yield to have occurred: the difference in age between varieties is another surrogate measure of kinship.

Divergence between the test and training sets can also be compared through differences in allele frequency. For the partition of data used for Fig. 7a, the correlation in allele frequency between test and training sets is 0.97 with a mean absolute difference in frequency of 0.05 (maximum 0.18). Clearly. there is little difference between the two sets. For the partition of data used for Fig. 7b, with the training set comprising the older varieties, the correlation in allele frequencies drops to 0.78, with a mean absolute difference in allele frequency of 0.14 (maximum 0.53). In this dataset, therefore, the ability to predict yield can also be viewed as dependent on the magnitude of differences in allele frequency between test and training sets. Methods of selection of markers for inclusion in training sets or schemes to weight the analysis by allele frequency (Goddard 2009) might also be tested empirically on historical datasets such as this.

The tendency for markers to predict breeding value through kinship rather than by tagging trait loci has been discussed (Zhong et al. 2009; Jannink et al. 2010). Prediction of yield via kinship is routinely used in animal breeding (Falconer and Mackay 1996; Henderson 1984) and has been advocated in plants (Piepho et al. 2007). In the context of genomic selection, however, its use is limited. With additive gene action, kinship-based predictions work by assuming blending inheritance: in the absence of progeny phenotype data, the expected breeding value of a progeny line is the weighed mean breeding value of the two parents, with weights equal to the proportion of the genome contributed by each parent (estimated from the marker data, but with an expected value of one half). In this example, no line can be predicted to exceed the best parent. However, the promise of genomic selection is to predict phenotypes with performances which exceed the best lines currently available. Whilst datasets such as those described here can therefore be used to evaluate and test methods, care must be taken not to draw overly confident conclusions of the merits of genomic selection from the ease with which high correlations between observed and predicted yield can be generated. To test methods more fully, it is necessary to control for kinship (Lee et al. 2008).

Relationship between performance in variety trials
and national yields

Average yields in variety trials are routinely higher than
those achieved for the national crop. Trials are generally
located with better farmers, on better soils and are likely to
be managed better than the average crop. The trials are
generally located in the middle of fields and will not
therefore suffer from the reduced yields found at field
margins as a result of increased soil compaction and
competition with hedgerow and tree species for water
and other resources. Nevertheless, average trial yields and
national yields generally correlate well. To project the
results of the analyses described above onto national yields,
we followed procedures modified from Silvey (1978, 1981)
in which variety uptake by growers was estimated from
seed certification records, and relative variety performance
from trials was used to estimate the effect of variety on the
national crop. Figure 8 demonstrates that for these three
crops, genetic improvement appears to account for effec-
tively all of the increase in national yields seen over this
period. This even greater proportion of improvement
accounted for by breeding in the national crop (∼100%)
compared to the trial series alone (∼90%) may have sev-
eral causes. We feel the most likely is that whilst the trials
environment may still be improving, or at least not dete-
riorating, the on-farm environment may be declining as a
result of economic pressures to reduce inputs. For example,
Fig. 10 shows total overall nitrogen application rates for
England and Wales from 1969 to 2007 (British Survey of
Fertilizer Practice). Nitrogen application peaked in 1984
and has subsequently declined. Crop-specific data from
1983 (British Survey of Fertilizer Practice 2007) indicate
that N application rates in winter wheat and barley have
been relatively constant in these crops since 1984, whilst
that for oil seed rape has declined.

The use of the treated trial series from 1982, rather than
the untreated series, requires justification. Both trial series
are imperfect representations of farming practice, but we
believe the treated trial series is closer to it. This is sup-
ported by correlations between trial yields and the national
crop for the two series, ignoring differences in variety
uptake. For winter wheat, these are 0.561 and 0.878 for
untreated yields and treated yields, respectively. Here, trial
yields were taken as the estimated year effect plus a linear
increase as a result of variety improvement calculated from
the regression coefficients in Table 2. Also, as discussed
earlier, the estimates of variety and year effects in the
untreated trials are biased by the breakdown of disease
resistance, so variety effects estimated from treated trials
are more appropriate: use of untreated trials data would bias
the estimated contribution of variety upwards and of year
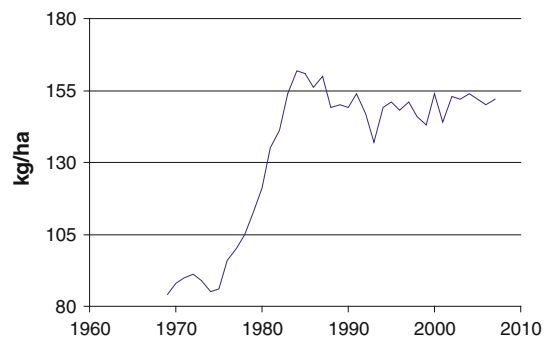downwards. It is possible that a slight upward bias remains

Fig. 10 N use for tillage crops: England and Wales 1967–2007

when estimating variety performance from the treated trials
series if disease control is inadequate. Nevertheless, we feel
that the analyses presented here provide reasonable esti-
mates of the contribution of variety performance to national
yield increases in the three cereals studied for the UK. From
trials data alone, these are 88, 111, and 88% for winter
wheat, spring barley and winter barley, respectively (esti-
mated from the regression coefficients listed in Table 3).
However, a comparison of the fitted curves in the projection
onto national yields given in Fig. 8 indicates that national
yields could well be in decline for all three crops in the
absence of any variety improvement.

We must emphasise that we are not stating that chemical
inputs have had no effect on yields over the period
1982–2007. Rather, changes in agronomy and chemical input
in these crops have had no detectable effect on increasing
yields in this latter period. If agronomy and/or chemical
treatment revert to previous practice, yields will decline.

Conclusion

In the UK, the retrospective analysis of the NL/RL trials
series was first used by Silvey (1978, 1981, 1986) to
quantify the relative contribution of plant breeding and
agronomy to the increase in yields in the post-war period.
We have updated these analyses and confirmed that the
importance of plant breeding has not diminished: in the
case of the major UK cereal crops, it is now the principle
reason why yields continue to increase. For some crops it is
quite likely that, in the absence of any plant breeding,
yields would decline.

We have extended, but not exhausted, the areas of study
to which these historical datasets can be put. Although on
their own they do not provide unambiguous tests of
hypotheses, they can be used to generate hypotheses for
testing elsewhere in areas of relevance to climate change,
disease resistance and selection theory. The advent of
cheap molecular markers will make these datasets even
more valuable for uses in association mapping (Malosetti

et al. 2007; Kraakman et al. 2004; Crossa et al. 2007) and in genomic selection. We believe the full value of these datasets will come from exploiting links with other experiments and experimental populations. However, not to use these historical sources is wasteful.

References

Akbari M, Wenzl P, Caig V, Carling J, Xia L, Yang S, Uszynski G, Mohler V, Lehmensiek A, Kuchel H, Hayden MJ, Howes N, Sharp P, Vaughan P, Rathmell B, Huttner E, Kilian A (2006) Diversity arrays technology (DArT) for high-throughput profiling of the hexaploid wheat genome. Theor Appl Genet 113:1409–1420

Berry PM, Spink JH (2006) A physiological analysis of oilseed rape yields: past and future. J Agric Sci 144:381–392

Bosemark NO (1993) Chapter 3. Genetics and breeding. In: Cooke DA, Scott RK (eds) The sugar beet crop. Chapman & Hall, London

Brancourt-Hulmel M, Doussinault G, Lecomte C, Bérard P, Le Buanec B, Trottet M (2003) Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. Crop Sci 43:37–45

British Survey of Fertilizer Practice (2007) Fertilizer use on farm crops for crop year. http://www.defra.gov.uk/evidence/statistics/foodfarm/enviro/fertiliserpractice/index.htm

Calderini DF, Slafer GA (1998) Changes in yield and yield stability in wheat during the 20th century. Field Crops Res 57:335–347

Crossa J, Burgueño J, Dreisigacker S, Vargas M, Herrera-Foessel SA, Lillemo M, Singh RP, Trethowan R, Warburton M, Franco J, Reynolds M, Crouch JH, Ortiz R (2007) Association analysis of historical bread wheat germplasm using additive genetic covariance of relatives and population structure. Genetics 177:1889–1913

Defra (2009) United Kingdom cereal yields, 1885 onwards. http://www.defra.gov.uk/evidence/statistics/foodfarm/index.htm

Falconer DS, Mackay TFC (1996) Introduction to Quantitative genetics, 4th edn. Longmans Green, Harlow

Feil B (1992) Breeding progress in small grain cereals—a comparison of old and modern cultivars. Plant Breed 108:1–11

Fischer RA, Edmeades GO (2010) Breeding and cereal yield progress. Crop Sci 50:S85–S98

Gauch HG, Zobel RW (1996) Chapter 4. AMMI analysis of yield trials. In: Kang MS, Gauch HG (eds) Genotype by environment interaction. CRC Press, New York

Goddard M (2009) Genomic selection: prediction of accuracy and maximisation of long term response. Genetica 136:245–257

Henderson CR (1984) Applications of linear models in animal breeding. University of Guelph, Guelph

HGCA Recommended Lists (2009). http://www.hgca.com

Horvath A, Didier A, Koenig J, Exbrayat F, Charmet G, Balfourier F (2009) Analysis of diversity and linkage disequilibrium along chromosome 3B of bread wheat (*Triticum aestivum* L.). Theor Appl Genet 119:1523–1537

Jannink J-L, Lorenz AJ, Iwata H (2010) Genomic selection in plant breeding: from theory to practice. Brief Funct Genomic Proteomic 9:166–177

Kraakman ATW, Niks RE, Van den Berg PMMM, Stam P, Van Eeuwijk FA (2004) Linkage disequilibrium mapping of yield and yield stability in modern spring barley cultivars. Genetics 168:435–446

Lee SH, van der Werf JHJ, Ben J. Hayes BJ, ME Goddard, Visscher PM (2008) Predicting unobserved phenotypes for complex traits from whole-genome SNP Data. PLoS Genetics 4(10):1000231

Mackay IJ, Powell W (2007) The significance and relevance of linkage disequilibrium and association mapping in crops. Trends Plant Sci 12:53–54

Malosetti M, van der Linden CG, Vosman B, van Eeuwijk FA (2007) A mixed-model approach to association mapping using pedigree information with an illustration of resistance to *Phytophthora infestans* in potato. Genetics 175:879–889

McDonald A, Riha S, DiTommaso A, DeGaetano A (2009) Climate change and the geography of weed damage: analysis of U.S. maize systems suggests the potential for significant range transformations. Agric Ecosyst Environ 130:131–140

Meteorological Office Hadley Centre Observation Data. http://www.metoffice.gov.uk/climate/uk/2001/

Patterson HD, Williams ER (1976) A new class of resolvable incomplete block designs. Biometrika 63:83–92

Patterson HD, Williams ER, Hunter EA (1978) Block designs for variety trials. J Agric Sci 90:395–400

Payne RW, Murray DA, Harding SA, Baird DB, Soutar DM (2007) GenStat for windows introduction, 10th edn. VSN International, Hemel Hempstead

Pidgeon JD, Ober ES, Qi A, Clark CJA, Royal A, Jaggard KW (2006) Using multi-environment sugar beet variety trials to screen for drought tolerance. Field Crops Res 95:268–279

Piepho HP (2009) Ridge regression and extensions for genomewide selection in maize. Crop Sci 49:1165–1176

Piepho HP, Möhring (2006) Selection in cultivar trials—is it ignorable? Crop Sci 46:192–201

Piepho HP, Möhring J, Melchinger AE, Büchse A (2007) BLUP for phenotypic selection in plant breeding and variety testing. Euphytica 161:209–228

R Development Core Team (2005) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Silvey V (1978) The contribution of new varieties to increasing cereal yield in England and Wales. J Natl Inst Agric Bot 14:367–384

Silvey V (1981) The contribution of new wheat, barley and oat varieties to increasing yield in England and Wales. J Natl Inst Agric Bot 15:399–412

Silvey V (1986) The contribution of new varieties to cereal yields in England and Wales between 1947 and 1983. J Natl Inst Agric Bot 17:155–168

Silvey V (1999) NIAB Recommended lists of cereal varieties: an aid to orderly marketing in the United Kingdom. Plant Varieties Seeds 12:23–42

Stobart R (2009) Oilseeds and pulses in rotation. http://www.hgca.com/publications/documents/5_-_Ron_Stobart_TAG.pdf

Storey JD (2002) A direct approach to false discovery rates. J R Stat Soc Ser B 64:479–498

Storey JD, Tibshirani R (2003) Statistical significance for genome-wide experiments. Proc Natl Academy of Sci 100:9440–9445

Wellington PS, Silvey V (1997) Crop and seed improvement. A history of the National Institute of Agricultural Botany 1919–1996. National Institute of Agricultural Botany, Cambridge

White J, Law JR, Mackay I, Chalmers KJ, Smith JSC, Kilian A, Powell W (2008) The genetic diversity of UK, US and Australian cultivars of *Triticum aestivum* measured by DArT markers and considered by genome. Theor Appl Genet 116:439–453

Whittaker JC, Thompson R, Denham MC (2000) Marker-assisted selection using ridge regression. Genet Res 75:249–252

Zhong S, Dekkers JCM, Fernando RL, Jannink J-L (2009) Factors affecting accuracy from genomic selection in populations derived from multiple inbred lines: a barley case study. Genetics 182:355–364