Project Report No. 496 July 2012

Adapting wheat to global warming

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or ‘ERYCC’ – Earliness and Resilience for Yield in a Changing Climate

by

Sarah Clarke[1], Roger Sylvester-Bradley[2], John Foulkes[3], Denise Ginsburg[2], Oorbessy Gaju[3], Peter Werner[4], Peter Jack[5], Ed Flatman[5] and Lucy Smith-Reeve[6]

[1]ADAS Gleadthorpe, Meden Vale, Nottinghamshire NG20 9PD
[2]ADAS Boxworth, Battlegate Rd, Boxworth, Cambridgeshire CB23 4NN
[3]Division of Plant and Crop Sciences, University of Nottingham, School of Biosciences, Sutton Bonington, Leicestershire LE12 5RD
[4]KWS UK Ltd., 56 Church Street, Thriplow, Royston, Hertfordshire SG8 7RE
[5]RAGT Seeds Ltd., Grange Rd, Ickleton, Saffron Walden CB10 1TA
[6]Limagrain UK Ltd., Woolpit Business Park, Windmill Avenue, Woolpit,
Bury St Edmunds, Suffolk IP30 9UP

This is the final report of a 51 month project (RD-2005-3214) which started in July 2007. The work was funded through the Defra Sustainable Arable LINK programme (LK0992) and a contract for £109,000 from HGCA.

HGCA is the cereals and oilseeds division of the Agriculture and Horticulture Development Board.

ABBREVIATIONS

AGDM	Above-ground Dry Matter
CGR	Crop GrowthRate
CP	Construction Phase (Growth stage 31-61)
CV%	Coefficient of variation
DM	Dry Matter
EFI	Ear Fertility Index (equivalent to Spike Fertility Index)
EP	Extended Photoperiod
EPI	Ear Partitioning Index (equivalent to Spike Partitioning Index)
ERYCC	Earliness and Resilience for Yield in a Changed Climate
FP	Foundation Phase (Growth stage 10-31)
GM2	Grains per m^2
GN	Grain number per m^2
GS	Growth Stage as described by Tottman (1987)
h	Hour
h^2	Heritability
HI	Harvest Index
Lam DM	Lamina (leaf blade) Dry Matter
Lam PI	Lamina DM Partitioning Index
N	Nitrogen
NHI	Nitrogen Harvest Index
NL	National List
NP	Normal Photoperiod
PC	Principal Component
PH	Plant Height at harvest
Ppd	Photoperiod insensitivity gene(s) (see Table 4)
PP	Production Phase (Growth stage 61-87)
Rht	Reduced height gene(s) (see Table 4)
RL	HGCA Recommended List
RUE	Radiation-use Efficiency (biomass per unit radiation interception)
SD	Standard Deviation
SFI	Spike Fertility Index
SPI	Spike Partitioning Index
S7SD	Single Seed Descent
t/ha	Tonnes per Hectare
TGW	Thousand Grain Weight
Vrn	Vernalisation gene(s) (see Table 4)
WSC	Water Soluble Carbohydrates

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1. ABSTRACT

In future years, UK wheat is likely to be grown under earlier and more frequently stressed conditions due to climate change. In this project, 64 UK, French and other elite varieties (the 'ERYCC panel') released between 1953 and 2008 were characterised to inform breeders of trait sources and trends associated with adaptation of wheat to these conditions. Dates of key growth stages, yield stability traits (e.g. stem reserves, ear fertility) and yield determining traits were measured in nine experiments in Eastern England between 2008 and 2010, augmented by data from a further six experiments between 2007 and 2010. Specific additional experiments tested the 64 varieties' responses to vernalisation (using a breeder's vernalisation chamber) and photoperiod (using daylength extension lamps in the field), and the varieties were typed for major genes controlling height and responses to vernalisation and photoperiod.

Results showed that breeders have increased yield potential by ~0.5 t per hectare per decade through the past half century, and that they continue to do so. Yield increases have been associated with improvements in the numbers of grains per ear and soluble stem reserves, i.e. traits developed during the construction phase (stem extension to flowering) of plant development. The increase in the number of grains per m^2 found was associated with an extended foundation phase (sowing to stem extension), increased ears per m^2 and a faster crop growth rate pre-flowering, but a short construction period.

Vernalisation requirements of the varieties related well to their numbers of copies of the *Vrn1* gene, so this could become useful in predicting vernalisation requirements of wheat. As for photoperiod requirements, there were significant differences in responses of varieties which could partly be explained by *Ppd* genes, but responses changed significantly between seasons so further understanding is required before photoperiod responses of varieties could be predicted usefully.

The ERYCC panel showed significant diversity in yield-determining traits which may be exploited in breeding for current and future climates: multiplication of trait maxima gave a 'potential yield' of 18 t/ha. Three multi-trait doubled-haploid (DH) mapping populations (the 'ERYCC populations') were developed so that (through future work) genetic markers may be identified for important yield-determining traits, and so that their interdependencies can be examined. Crosses were between Oakley as the common parent (having high yields due to high grains per ear, and a long production phase) and (i) Gatsby (contrasting in ears per m^2 and grains per ear), (ii) Battalion (contrasting in development pattern), and (iii) Exsept (contrasting in ear size traits).

2. SUMMARY

2.1. Background and aim

Through the 21st Century, the UK climate is likely to change significantly, with important implications for crop production. Average temperatures may increase by 4 or 5°C, with the greatest warming in the summer; annual precipitation is likely to increase with more rain in the winter and less in the summer, and there are likely to be more frequent extreme weather events. The wheat varieties in these new conditions will need to mature earlier and cope with stresses better, and they must also yield more to support an increasing global population.

Therefore, the aim of this project was to identify, source and characterise traits that will enable plant breeders to adapt UK wheat germplasm to earlier and more frequently stressed production conditions arising through climate change.

This was addressed through: assembling a panel of 64 current and recent elite varieties from the UK and abroad, characterising these for phenology (e.g. key growth stages), yield stability traits (e.g. stem reserves, ear fertility), and yield components; genotyping them for candidate genes affecting height and responses to photoperiod and vernalisation; and then validating these photoperiod and vernalisation responses by experiment to understand the extent to which they determine the development of the varieties. This varietal information was then used to design and develop three mapping populations for further analysis in subsequent research.

2.2. Materials and methods

2.2.1. Material used in the project

The 64 varieties chosen became known as ‘the ERYCC panel’ (Earliness & Resilience for Yield in a Changed Climate); they can be split into three subsets: ‘Historical’ varieties released between 1953 and 1996, varieties with phenological traits of interest from UK, France and Mexico, and ‘modern / control’ varieties.

Each subset comprises both bread-making and feed varieties (including soft ‘biscuit’ wheats). For some analyses, subsets known as ‘landmark’ varieties were identified (bold in Table 1), defined as those that had ever been grown on a significant proportion of the UK wheat area (>15% and >5% for feed and bread-making varieties, respectively).

Table 1. The ERYCC panel of 64 wheat varieties used in this project, split into 'Historical', 'Phenology' and 'Modern/controls' subsets, with associated codes used throughout the report. Landmark varieties are in bold.

Historical	Code	Phenology	Code	Modern	Code
Avalon	46	Alixan	44	Access	4
Beaver	9	Andalou	10	**Alchemy**	19
Cappelle Desprez	**47**	Apache	42	Ambrosia	17
Equinox	1	Bacanora	64	Battalion	37
Galahad	45	Buster	55	Brompton	29
Haven	48	Cadenza	58	**Claire**	16
Hobbit	59	Caphorn	43	**Consort**	36
Maris Huntsman	**51**	Cezanne	49	Deben	25
Hustler	60	**Cordiale**	2	Dover	8
Longbow	61	Exotic	12	**Einstein**	15
Maris Widgeon	62	Exsept	14	Gladiator	28
Mercia	57	Gatsby	32	Glasgow	18
Norman	54	Hyperion	33	Gulliver	34
Rialto	13	Mendel	23	**Hereward**	41
Riband	53	Mercato	24	Humber	6
Savannah	50	Paragon	52	Istabraq	20
Virtue	63	Recital	40	**Malacca**	7
		Royssac	11	Marksman	38
		Sankara	22	Mascot	30
		Soissons	21	Musketeer	39
		Spark	56	**Oakley**	5
		Timber	35	**Robigus**	3
				Solstice	27
				Xi19	26
				Zebedee	31

2.2.2. Phenotyping experiments

The phenotypic characteristics of the full ERYCC panel were assessed at each of three sites (Norfolk, Cambridgeshire, North Yorkshire) in each of three seasons (harvests 2008-2010). In 2007, three additional experiments in Suffolk and Cambridgeshire tested 49 varieties of the ERYCC panel through Sustainable Arable LINK project LK0986 and these were characterised for pre-harvest and harvest characters. Also, in the three seasons 2008-2010 the full ERYCC panel was tested in Suffolk for growth stages, yield and thousand grain weight. Each of the 15 experiments was of a two-way latin square design with two replicates.

Dates of key growth stages (GS; Tottman, 1987) were recorded and the thermal durations (base 0°C) of the foundation (GS10-31), construction (GS31-61) and production (GS61-87) phases were calculated. Plants were sampled at GS61 and pre-harvest to determine dry weights of plant components, stem water soluble carbohydrates (WSC) and nitrogen contents. Plots were combine harvested, moisture content determined and grain yield, adjusted to 85% dry matter (DM) was calculated.

2.2.3. Genotyping material

Genotyping for known genes controlling height (*Rht*), photoperiod sensitivity (*Ppd*) and vernalisation (*Vrn*) was carried out on all 64 varieties by RAGT Seeds and at the John Innes Centre (by D Laurie).

2.2.4. Vernalisation experiment

An experiment was carried out in 2010-11 at KWS UK Ltd. under conditions used for ‘single seed descent’. All 64 varieties (replicated twice) were grown as single plants in module trays; trays were treated for 0, 1, and up to 9 weeks in a vernalisation chamber, then on 14 Dec 2010, were all moved to a heated glasshouse lit to give a 18h daylength. The dates of GS39 and GS61 were recorded for each plant, along with leaf and node numbers.

2.2.5. Photoperiod extension experiments

All 64 varieties were tested under normal photoperiod (NP) and extended photoperiod (EP) in each of three growing seasons (2008-09, 2009-10, 2010-11) in field experiments at Thriplow, Cambridge. EP provided a 16h photoperiod from the shortest day (22nd Dec.) until two weeks after GS31. Dates of GS31, 39, 59 and 61 were recorded; the experiment terminated after GS61. Due to heavy rabbit grazing, only GS33 and 61 dates were recorded in the 2009-10 experiment.

2.2.6. Data analysis

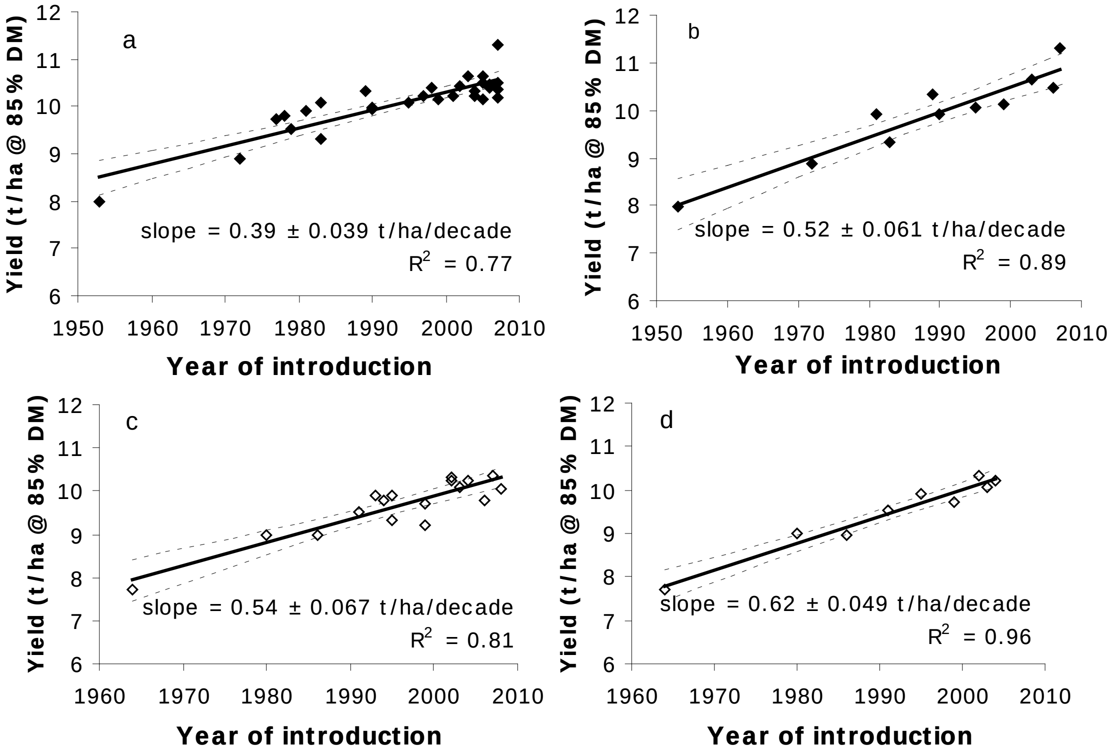
Individual experiments were analysed using analysis of variance in Genstat (VSN International). Cross-site analysis was carried out using weighted analysis of variance. Regression analysis was then carried out on weighted means over all experiments.

2.3. Results

2.3.1. Phenotyping experiments

Trends with year of introduction

The overall relationship between yield and year of introduction was highly significant ($P<0.001$; $R^2 = 0.36$), with an average rate of yield improvement over time of 0.39 t/ha/decade; there was no evidence that the rate was slowing. The rate of increase for just UK feed varieties was the same (Summary Figure 1.a), but when the data were further restricted to ‘landmark’ varieties the slope was greater (Summary Figure 1.b). Regression analysis of all or just ‘landmark’ UK bread-making varieties showed steeper increases with year of introduction than with feed varieties (Summary Figure 1.c,d).



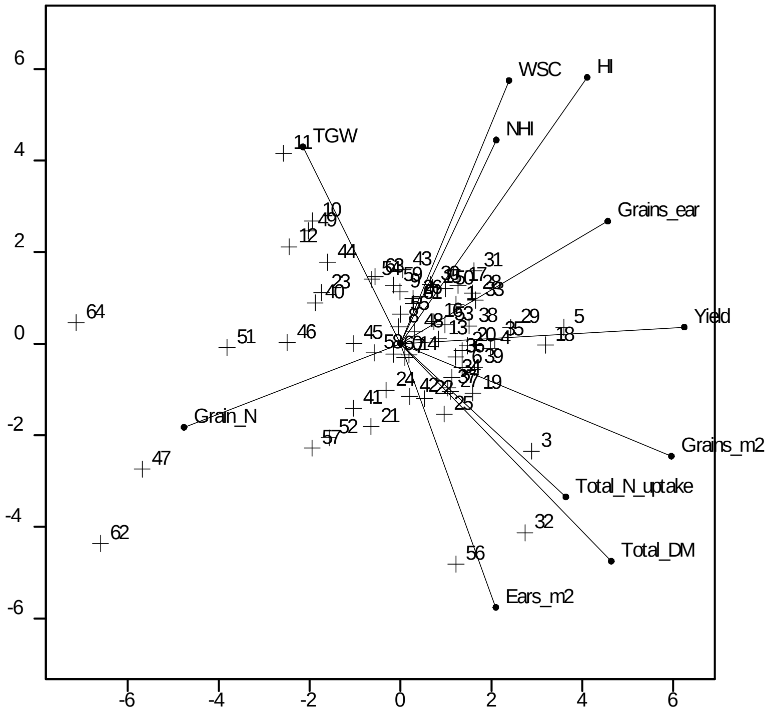
Summary Figure 1. Weighted mean grain yields (t/ha @ 85% DM) of: all UK feed (a) and bread-making (c) varieties; and 'landmark' feed (including soft biscuit wheat) (b) and bread-making (d) varieties, introduced between 1964 and 2008, and grown in 15 experiments in Eastern and North East England between 2007 and 2010. Linear trends, 95% confidence limits, standard of the trends and variance accounted for are given on each graph.

Further analysis showed that in both feed and bread-making varieties harvest index increased with year of introduction, but this increase appeared to be slowing. There was also an increase in crop biomass in the feed, but not the bread-making varieties. In both sets of varieties, there were no effects of year of introduction on thousand grain weight, so yield increases had arisen through grains per m^2; the number of grains per ear had increased significantly and there was a significant increase in the number of ears per m^2 in the feed varieties, but this was not found in bread-making varieties. There were significant increases in N capture and N harvest index with year of introduction in both the feed and bread-making varieties, but grain N% continued to decrease as yields increased.

When the determination of grains per m^2 was examined, crop growth rate (feed varieties only) appeared to increase after ca. 1985, whereas increases in ear partitioning (both feed and bread-making varieties) along with decreases in stem partitioning occurred before ca. 1985. There was no trend in ear fertility (grains per g ear DM) and there were no trends in plant development with year of introduction.

Varietal variation in yield and yield components

A principal component biplot was used to illustrate the relationships between yield and it's components, and to identify the varieties responsible for these relationships (Summary Figure 2). This shows variety 5 (Oakley) having the highest yield as it is furthest along the yield axis, and variety 64 (Bacanora) being lowest-yielding. The yield vector (line) was closer (i.e. more closely related) to the number of grains per m^2 than to TGW (Summary Figure 2). Variation amongst the varieties can be examined in the same way, for example, Gatsby (32) has a high number of ears per m^2 and total crop biomass, but it has a low TGW and below average HI (Summary Figure 2). Varieties with higher TGW were generally French bread-making varieties e.g. 10 (Andalou), 44 (Alixan), 49 (Cezanne); these also had higher than average grain N concentrations but lower than average yields (Summary Figure 2). These varieties were also earlier than most with below average durations of the foundation, construction and production phases.



1	Equinox	33	Hyperion
2	Cordiale	34	Gulliver
3	Robigus	35	Timber
4	Access	36	Consort
5	Oakley	37	Battalion
6	Humber	38	Marksman
7	Malacca	39	Musketeer
8	Dover	40	Recital
9	Beaver	41	Hereward
10	Andalou	42	Apache
11	Royssac	43	Caphorn
12	Exotic	44	Alixan
13	Rialto	45	Galahad
14	Exsept	46	Avalon
15	Einstein	47	Cappelle Desprez
16	Claire	48	Haven
17	Ambrosia	49	Cezanne
18	Glasgow	50	Savannah
19	Alchemy	51	Huntsman
20	Istabraq	52	Paragon
21	Soissons	53	Riband
22	Sankara	54	Norman
23	Mendel	55	Buster
24	Mercato	56	Spark
25	Deben	57	Mercia
26	Xi19	58	Cadenza
27	Solstice	59	Hobbit
28	Gladiator	60	Hustler
29	Brompton	61	Longbow
30	Mascot	62	Maris Widgeon
31	Zebedee	63	Virtue
32	Gatsby	64	Bacanora

Summary Figure 2. Principal component biplot showing positions of weighted means for varieties 1-64 of the ERYCC panel in relation to vector lines for yield and its components.

Another biplot showed grains/m^2 to be positively correlated with foundation phase duration but, surprisingly, not with construction phase duration. There were however significant associations of grains/m^2 with days from GS10 to GS61, crop growth rate (GS10-61), spike partitioning index (SPI) and spike fertility index (SFI); the strongest of these were with spike partitioning index and spike fertility index; varieties 56 (Spark) and 32 (Gatsby) had particularly high spike fertility indices.

Effects of major genes

Effects of major genes (*Ppd* and *Rht*) on yield and yield components were highly significant ($P<0.01$; although note there were low numbers of varieties with certain genotypes): *Ppd1* or *Ppd2* genotypes were associated with lower yields and fewer grains per m^2, shorter foundation phase and increased TGW, ear fertility index and grain N. These results are as expected since varieties with a *Ppd1* or *Ppd2* genotypes are generally the French bread-making varieties identified as having these traits at the outset.

The *Rht* genotypes significantly ($P<0.05$) increased all yield components except total crop biomass which was reduced. *Rht1* or *Rht2* varieties were associated with higher yields, increased number of grains per m^2, a higher harvest index, a higher concentration of stem water soluble carbohydrates, a higher number of grains per ear, a higher N harvest index but a lower grain N. There were no effects of *Rht* genes on the duration of the foundation or construction phases.

2.3.2. Vernalisation experiments

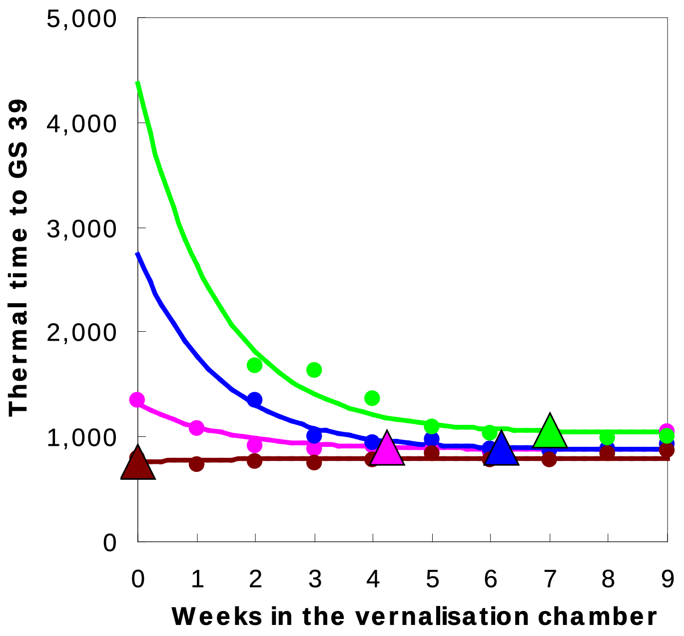
Generally, as the number of weeks that varieties spent in the vernalisation chamber increased, the thermal time it took to reach GS39 reduced; the thermal time to GS39 had minimised for all varieties after 6-7 weeks of treatment (and patterns were similar when GS61 was examined). Treatment effects were summarised by fitting parallel exponential curves, and examples of contrasting fitted responses are shown in Summary Figure 3. Here,

$$\text{thermal time to GS39} = a + b \times R^x$$

where x is the number of weeks of vernalisation treatment, a gives an estimate of the minimum thermal time needed to complete development to GS39 after reproductive development has been triggered (equivalent to inherent earliness), b is the effect on thermal time to GS39 of nil time in the vernalisation chamber (i.e. responsiveness to vernalisation), and R is a fitted parameter (common to all varieties; 0.4811) that describes the ‘shape’ of the vernalisation response, and enables calculation of vernalisation requirement (V_{Tmin}; in weeks) using the expression

$$V_{T\min} = \log_R\left(\frac{20}{b}\right)$$

where 20 was a value set to give sensible values for V_{Tmin}. This fitting process accounted for 91.5% of variation in the data.



Summary Figure 3. Example exponential curves fitted to thermal times to GS39 (°C days) as they were affected by weeks of vernalisation for Cadenza (brown), Claire (pink), Malacca (blue) and Hereward (green). Circles, experimental means; triangles, calculated vernalisation requirements.

The minimum time that varieties took to reach GS39 (*a*), differed significantly and ranged from 758 to 997^{o}C days. Vernalisation requirements ranged from nil to nearly 8 weeks, and varieties separated into four groups which tended to correlate with the *Vrn1* gene copy number as determined by genotyping at the John Innes Centre.

2.3.3. Photoperiod extension experiments

On average, plants reached key growth stages (GS) earlier in the 2011 experiment than the 2009 experiment. The average duration of the construction period (GS31 to 61) was 75°C days shorter in 2009 than 2011. Extending the photoperiod to 16 hours brought forward all growth stages by an average of 7 to 13 days ($P<0.001$). Variety 64 (Bacanora) was always the earliest to reach every growth stage, whether under extended or normal photoperiod. However, the photoperiod effect for most varieties differed with growth stage and year, as indicated by significant interactions between photoperiod and variety in all experiments.

Extended photoperiods significantly reduced the average number of leaves on a mainshoot in both 2009 (by 1.51; $P = 0.023$) and 2011 (by 1.76; $P = 0.037$) and this was the main basis of advancement of GS39. However, whilst the average phyllochron (thermal time between emergence of successive leaves) was unaffected in 2009 (at 112°C days), phyllochrons tended to be longer in 2011, and were prolonged by photoperiod extension.

An unbalanced analysis of variance showed significant ($P<0.05$) effects of major photoperiod genes (*Ppd1* and *Ppd2*) on thermal time to GS31, GS39, GS61 as well as the phyllochron in 2009 and 2011. Generally, *Ppd1* reduced the thermal time to key growth stages compared to *ppd*, and the extended photoperiod effect on the time to GS39 was generally reduced where *Ppd1* was present.

2.3.4. Modelling

Data collected in support of the HGCA RL on Latest Safe Sowing Dates and Speed of Development to GS31 proved inadequate to distinguish the response of a variety to vernalisation from its response to photoperiod. Also, the Sirius Wheat Calculator used to model UK varieties in New Zealand gave unsatisfactorily late predictions of flowering (GS61) in the UK. It was concluded that development of satisfactory growth stage predictions for UK varieties under UK conditions will depend on specific tests designed to show varietal vernalisation and photoperiod responses separately. It was shown that tests of vernalisation responses could be interpreted to give vernalisation requirements expressed in ‘vernal time’, an index that could then be used to interpret field data, hence to help interpret varietal responses to photoperiod extension. This offers a potential means of achieving more accurate growth stage predictions for wheat in the UK.

2.4. Conclusions and research suggestions

The main conclusions that can be drawn from this project are as follows:

1. Creation of the ERYCC panel of 64 varieties enabled effective analysis of wheat improvement in the UK; this panel is now being used in several further projects (e.g. LINK project LK09125: New wheat root ideotypes for yield performance in reduced input agriculture).
2. The yield potential of varieties continues to be increased by breeders at about 0.5 t/ha per decade through increases in the number of grains/m^2 (grains per ear and ears per m^2). However, these increases are not being translated into increased farm yields. Rates of genetic yield improvement need to increase 3 or 4 fold if UK wheat production is to play its part in meeting predicted global food demands.
3. High yields were not associated with the duration of the construction period (GS31-61), but were associated with traits developed during this period e.g. grains per m^2, stem WSC.
4. Genetic gains in grains/m^2 in the sets of landmark cultivars were associated:
    a. For feed cultivars: with increased spike partitioning associated with increased grains / ear and harvest index (up to about 1990), then (after 1990) an extended foundation phase associated with increased ears /m^2 and total biomass; an increased crop growth rate pre-anthesis was also associated with continued increases in grains / ear.

    b. For bread-making cultivars: with an extended foundation phase and increased ear partitioning up to about 1985, then post 1990 with increased spike fertility index linked to increased ear DM per m^2 and grains / ear.

5. Nitrogen capture and nitrogen partitioning to grain showed gradual increases over recent decades but (with fixed N supplies as in these experiments) grain N concentration of landmark bread-making varieties showed a continuing decline. Thus, bread-making quality must be achieved through higher fertiliser N applications by farmers. Alternatives are breeding for better quality protein at the same N%, and / or changing bread-making requirements for protein.
6. The varieties tested in this project showed significant variation in traits that may be used for breeding for a future climate. Multiplication of maxima for ears /m^2, grains/ear and TGW gave a yield of 18 t/ha, 60% more than the maximum yielding variety Oakley. Genetic control of these and other traits can be further understood through analysis of the Oakley x Gatsby, Oakley x Battallion and Oakley x Exsept mapping populations developed through this project.
7. The vernalisation requirements of varieties could be predicted to a significant extent by copy number of the *Vrn1* gene on chromosome 5A.
8. The significant variation in response to photoperiod among varieties could partly be explained by *Ppd* genes, but it appeared to interact significantly with season.

It is recommended that the following further research would be worthwhile:

1. The mapping populations developed in this project should be analysed for yield determining traits and their genetic determinants. Promising lines or markers should then enable breeders to enhance yield progress.
2. Wider use of vernalisation experiments and modelling (such as were used here) should be investigated, to improve predictions of latest safe sowing dates and speed of development of UK wheat varieties.
3. The photoperiod experiment should be extended to test the causes of seasonal interactions, and should allow for new understanding of the different vernalisation requirements for each variety.
4. Further modelling should be carried out to integrate understanding of vernalisation and photoperiod responses, and to embrace effects on leaf emergence and phyllochrons, so that the dates of culm leaf emergence can be predicted, to allow better planning of spray application windows.

3. TECHNICAL DETAIL

3.1. Project Objectives and Background

3.1.1. Project objectives

To identify, source and characterise traits that will enable plant breeders to adapt UK wheat germplasm to earlier and more frequently stressed production conditions arising through global warming, and specifically to:

1. Characterise (by phenotyping) current and recent elite materials from the UK and abroad for phenology, yield stability traits (e.g. stem reserves, ear fertility), and yield components.
2. Characterise (by genotyping) current and recent elite materials from the UK and abroad for candidate genes affecting phenology traits (e.g. photoperiod and vernalisation responses).
3. Determine under field conditions the photoperiod sensitivity of current elite germplasm, and the effects of photoperiod on earliness and duration of the crop construction phase.
4. On the basis of findings from Objectives 1, 2 and 3, develop mapping populations in elite UK backgrounds segregating for phenology and partitioning, in preparation for subsequent research, and
5. Develop quantitative physiological approaches to assist breeders in devising ideotypes and selecting parental materials that will optimise wheat phenology for warmer climates.

3.1.2. Background

By the end of the 21st Century, the UK climate is likely to have changed significantly, with important implications for crop production. The average temperature is likely to have increased, perhaps by as much as 5.5°C, with the greatest warming in the summer; annual precipitation is likely to increase with more rain in the winter and less in the summer, and there are likely to be more frequent extreme weather events (Alcamo *et al.*, 2007). Conditions are likely to be even more difficult in Southern Europe, with less precipitation, and more frequent droughts and heat-waves (Alcamo *et al.,* 2007). This means that Europe will be more reliant on countries like the UK to grow a larger proportion of the food required, so well-adapted, higher yielding wheat crops are needed.

Well-adapted to these future UK conditions means maturing earlier and coping with stresses better (Foulkes *et al*., 2004; Richter & Semenov, 2005), although this goal may not be easy to achieve. Foulkes *et al.* (2004) analysed the repercussions of advancing reproductive development and maturity by ~10 days in UK wheats by comparing *Ppd1* and *ppd1* near-isogenic lines. In a Mercia background (at 8-9 t/ha) the yield effect was neutral. However, shoot number, canopy size, internode number, height, stem reserves (water soluble carbohydrates: WSC) and water capture all decreased with earliness, and it is likely that such effects will need to be avoided or counteracted if earliness is to be yield-neutral in modern higher-yielding backgrounds.

Ideally, however, the earliness of varieties would be accompanied by higher yields. Genetic gains in wheat worldwide have historically been achieved by improvements in harvest index (HI) and grain number per square meter (GN), with little change in total biomass or individual grain weight. The semi-dwarf varieties introduced in the 1960s and 1970s contributed large increases in GN and HI associated with more fertile florets per ear as a consequence of increased assimilate partitioning to the ear during the pre-flowering period (Fischer, 1983; Calderini *et al*., 1995; Miralles *et al*., 2000). The study of Austin *et al*. (1989) on UK varieties introduced from 1908 to 1986 showed HI to be associated with yield progress, with only a slight, non-significant increase in above-ground dry matter (DM). Improved HI was associated with altered DM partitioning in favour of the ear and higher GN with the introduction of the *Rht2* semi-dwarf allele in the modern group of varieties (1981–1986). Higher GN resulted mainly from more grains per ear, and further studies have found that semi-dwarf wheat varieties showed more fertile florets per ear as a consequence of increased assimilate partitioning to the ear during the pre-flowering period (Fischer, 1983; Calderini *et al*., 1995; Miralles & Slafer, 1995).

Other experiments on historic sets of varieties worldwide have shown that grain yield improvement is highly associated with HI and GN in wheat (Canevara *et al*., 1994; Sayre *et al*., 1997; Brancourt-Hulmel *et al*., 2003; Peltonen-Saino *et al*., 2007). Current evidence suggests that grain sink strength remains a critical yield-limiting factor (Fischer, 1985; Abbate *et al*., 1995; Miralles *et al*., 2000; Borras *et al*., 2004; Miralles & Slafer, 2007) and that improving the balance of sink over source is a promising approach for raising yield and post-anthesis Radiation Use Efficiency (RUE; biomass per unit radiation interception) (Reynolds *et al*. 2001, 2005).

The period before the start of the grain-filling is very important for the determination of grain number in wheat. Despite some uncertainty about the actual beginning and the end of this critical period, it is generally accepted that it occurs between late booting and flowering in wheat (Slafer *et al*., 1999; Foulkes *et al*., 2009), i.e. during rapid ear growth, pre-anthesis. Greater ear growth during the critical period is associated well with higher grain number in wheat (Calderini *et al*. 1997; Reynolds *et al*. 2001; Fischer, 2007).

Ear growth from initiation to flowering is concurrent with growth of internodes, culm leaves, and roots that will support grain formation after flowering; hence we call this the ‘construction’ phase. In addition to reduced stem growth, increased RUE during the construction phase may directly cause increases in grain number, which then in turn may enhance RUE in the post-anthesis period as a result of improved grain sink strength. A positive association between RUE during the period from the onset of stem elongation to flowering and each of GN and yield was observed in winter wheat amongst a set of varieties released from 1972 and 1995 in the UK (Shearman *et al*., 2005).

However, there has been no systematic analysis of changes in source and sink determining traits in UK winter wheat varieties introduced since 1995.

Successful manipulation of wheat development to both accommodate the stresses likely to arise through climate change and to achieve an optimum balance between source and sinks for assimilate will depend upon a good understanding of the control of plant development. Indeed simulation models of wheat growth and yield are fundamentally dependent on good predictions of plant development, since this is what dictates the duration of growth in successive phases of the life cycle, hence the distribution of assimilates between organs. There is a large literature on plant development in wheat and other species (e.g. Chouard, 1960; Angus *et al*., 1981; Amasino, 2004; Yan & Wallace, 1998). In summary, the progress from seed through leaf and shoot production, internode production, flowering, grain-filling and back to a viable seed is governed throughout by temperature, but initiation of reproductive development commonly also requires experience of cold temperatures (vernalisation: 0-15°C) and / or exceedance of a ‘critical’ photoperiod. Light intensity, nutrition, water supply and pathogens have only minor effects on reproductive development. Wheat development has been modelled in relation to temperatures and daylengths (Jamieson *et al*., 2007), but not with comprehensive success (McMaster *et al*., 2008). As yet there also has been little success in quantitative modelling of plant development from the burgeoning knowledge of plant genetics, including genetical controls of circadian rhythms as well as plant responses to temperatures and daylengths (Trevaskis *et al*., 2007). Thus, improvement in the predictability of key growth stages from genetical, daylength and weather information will be crucial, both in developing varieties suited to changed climates and in planning growth-stage-linked crop management decisions according to weather variation from season to season.

Sylvester-Bradley *et al.* (2008) considered the life cycle of wheat to be divided into three main phases: ‘foundation’ from seed germination to the start of stem extension (GS31), ‘construction’ until flowering (GS61), and ‘production’ until maturity (GS92). Each appears to last 900 to 1,200°C days (base temperature 0°C) with winter wheat under UK conditions. However, the key stages of GS31 and GS61 are not considered predictable from weather and a knowledge of germplasm except in the crudest terms; breeders and agronomists commonly inspect crops to anticipate these stages. Varietal variation is reported in the HGCA Recommended List through ‘Latest Safe Sowing Dates’, ‘Ripening’ (days difference from a control) and ‘Speed of development to GS31’, all of which depend directly on empirical observations. Flowering dates are not reported, and there are no specific tests of vernalisation and photoperiod responses, such as might allow projections of varietal behaviour in changed climates.

Recent wheat breeding in the UK has increased genetic diversity (Donini *et al*. 2000), and so has probably increased physiological diversity. Particular introgressions include *Rht1* (e.g. Robigus,

Gatsby), and introductions from *Triticum dicoccoides* (e.g. Shamrock, Gulliver) and *Aegilops ventricosa* (e.g. Hyperion, Battalion). Superficial observation suggests that current high yielding varieties show significant variation in physiology, e.g. phenology (Cordiale is distinctly early), heights, stem types (hollow v. solid), grain sizes, etc. Thus, the basic hypothesis to be addressed here is that:
a) current elite adapted wheat varieties from UK, France and elsewhere offer ample untapped physiological diversity, which could be harnessed to address the new breeding objectives presented by climate change.

This project anticipates and has prepared mapping populations for subsequent research which should address more specific hypotheses that:
a) recombination of vernalisation, photoperiod, and earliness *per se* genes in UK wheat can provide appropriate and reliable foreshortening of its development to minimise the combined risks of exposure to frost and late stresses under global warming, and
b) changes in DM partitioning can be developed, especially with increased CO_2, which negate detrimental effects of foreshortened DM growth and summer warming on grain productivity.

Hence the project described here incorporated experiments to test differences in yield determination between historical and modern wheat varieties, and between early and normal UK varieties. The focus of the phenotyping was on phenology, on ear formation at flowering, and on grain yield and its components. Observations on phenology were augmented by specific experiments testing varietal differences in responses to vernalisation (using a breeder's vernalisation chamber) and photoperiod (using daylength extension lamps in the field). Varieties were typed for major genes e.g. controlling height and responses to vernalisation and photoperiod, and a modelling task assessed the extent to which varietal differences in phenology were predictable from genetical and response data relating to vernalisation and photoperiod responses.

3.2. Materials and methods

3.2.1. Material used in the project

A panel of 64 wheat varieties was characterised in each experiment in this project. The majority of the varieties (49) had been chosen as having phenology and yield resilience traits of interest for use in the sister Sustainable Arable LINK project 'Improving water use efficiency and drought tolerance in UK winter wheats' (HGCA Project 3233; LK0986; Ober *et al.*, 2012). Further varieties were added and substituted, primarily to extend the historical range and the variation in phenology; thus the 64 varieties can be split into three subsets (Table 2)

1. ‘Historical’ (17 varieties) – UK elite varieties released between 1953 and 1996.
2. ‘Phenology’ (24 varieties) – UK, French and CIMMYT varieties with phenological traits of interest.
3. ‘Modern/Controls’ (23 varieties) – recent and current UK varieties as well as French elite varieties and advanced breeders’ lines.

The ‘year of introduction’ for each variety was expressed as the first year when it would have been harvested in National List (NL) trials, plus 3 to allow for Recommended List testing. Subsets comprised both bread-making and feed (including soft ‘biscuit’ wheats) varieties. For analysis of breeding progress, subsets of nine bread-making and eleven feed varieties were used, termed ‘landmark’ varieties. ‘Landmark’ varieties were those that had been grown on a significant proportion (>15% for feed varieties or >5% for bread varieties) of the UK wheat area for at least 1 year (Table 3).

Table 2. The 64 varieties used throughout the project split into ‘Historical’, ‘Phenology’ and ‘Modern/controls’ subsets, with associated codes used throughout the report.

Historical	Code	Phenology	Code	Modern	Code
Avalon	46	Alixan	44	Access	4
Beaver	9	Andalou	10	Alchemy	19
Cappelle Desprez	47	Apache	42	Ambrosia	17
Equinox	1	Bacanora	64	Battalion	37
Galahad	45	Buster	55	Brompton	29
Haven	48	Cadenza	58	Claire	16
Hobbit	59	Caphorn	43	Consort	36
Maris Huntsman	51	Cezanne	49	Deben	25
Hustler	60	Cordiale	2	Dover	8
Longbow	61	Exotic	12	Einstein	15
Maris Widgeon	62	Exsept	14	Gladiator	28
Mercia	57	Gatsby	32	Glasgow	18
Norman	54	Hyperion	33	Gulliver	34
Rialto	13	Mendel	23	Hereward	41
Riband	53	Mercato	24	Humber	6
Savannah	50	Paragon	52	Istabraq	20
Virtue	63	Recital	40	Malacca	7
		Royssac	11	Marksman	38
		Sankara	22	Mascot	30
		Soissons	21	Musketeer	39
		Spark	56	Oakley	5
		Timber	35	Robigus	3
				Solstice	27
				Xi19	26
				Zebedee	31

Table 3. ‘Landmark’ bread-making and feed (including soft ‘biscuit’ wheats) variety subsets with year of introduction and maximum contributions to the UK wheat area derived from national seed certification statistics (available from NIAB TAG).

Bread or Feed variety	Variety name	Year of introduction	Maximum proportion of UK wheat area grown on (%)
Feed	Cappelle Desprez	1953	>70
Feed	Maris Huntsman	1972	16
Feed	Norman	1981	20
Feed	Galahad	1983	25
Feed	Riband	1989	36
Feed	Beaver	1990	15
Feed	Consort	1995	26
Feed	Claire	1999	27
Feed	Robigus	2003	19
Feed	Alchemy	2006	18
Feed	Oakley	2007	15
Bread	Maris Widgeon	1964	>5
Bread	Avalon	1980	29
Bread	Mercia	1986	26
Bread	Hereward	1991	9
Bread	Rialto	1995	9
Bread	Malacca	1999	13
Bread	Solstice	2002	11
Bread	Einstein	2003	15
Bread	Cordiale	2004	8

3.2.2. Experimental methods

Phenotyping experiments

The phenotypic characteristics of 64 varieties were determined in nine core experiments carried out at three sites in Eastern and North East England in three seasons (harvest years 2008-2010). Sites were at Langton, near Malton, North Yorkshire; Newton, near Cambridge; and Terrington, near King’s Lynn, Norfolk. Soil types were clay loam at Langton, sandy at Newton and silty clay loam at Terrington.

The nine core experiments were augmented by a further six experiments carried out between 2007 and 2010. In 2007, three experiments tested 49 varieties in Sustainable Arable LINK project LK0986 (Ober *et al*., 2012) and characterised pre-harvest and harvest characters only (Table 4). Sites were on clay loam near Framlingham, Suffolk, on clay loam over gravel at Grantchester near Cambridge, and on sandy loam at Woolpit near Bury-St.-Edmunds, Suffolk. In 2008-2010 three further experiments tested all 64 varieties on a sandy loam at Clopton near Bury St. Edmunds, Suffolk. A subset of measurements was carried out on these experiments (Table 4).

Each experiment was of a two-way latin square design with two replicates. Plot sizes were at least 12 m^2, and at least 9m^2 for Clopton. Experiments were generally drilled between late September and late October each season, although Woolpit (2007) was drilled in early November. The plots were managed according to the protocol for Recommended List trials (available via the HGCA website; see Appendix 1 for details) and experiments were harvested between early August and early September each season (see Appendix 1 for details).

Assessments

All assessments carried out on the phenotyping experiments are described below. The subset of assessments carried out in each experiment can be found in Table 4.

Growth stages

The dates at which each plot reached the following decimal growth stages (GS; Tottman, 1987) were assessed as follows:

- *GS10 (first leaf through coleoptile)* – the experiment was visited at 2-3 day intervals from ~120 day degrees after sowing. The date when the first leaf was visible for the majority of the expected seedling population was recorded for each plot.
- *GS31 (first node detectable)* – the experiment was visited at least twice a week when GS31 was thought to be approaching. Five plants per plot were dug or pulled up and the main shoot identified. The first node stage was detected by feeling the stem, and splitting the stem if necessary. The date of this growth stage was recorded slightly differently in different years.

  In 2008, the date for this growth stage was when at least three of the five main shoots had an internode at least 1 cm long, or (if earlier) a length from stem base to apex of at least 2 cm.

  In 2009, the assessments continued until all 5 plants had reached the growth stage.

  In 2010, the assessments continued until all 5 plants had reached the growth stage on two visits in succession.

  In all three years, relationships were fitted to the data to determine the date at which 50% of the plants in each plot had achieved GS31. In the Langton 2009 experiment, a number of varieties had already reached GS31 when the assessment was carried out. Because it was not possible to determine when the varieties had reached GS31 accurately, the GS31 data for this experiment was excluded from the analysis.
- *GS39 (flag leaf ligule just visible)* – the experiment was visited at least twice a week when GS39 was thought to be approaching. For each plot, the date was recorded when 50% of shoots (judged to be viable) had a flag leaf ligule just visible. If the median flag ligule had already extended above the penultimate leaf ligule since the last visit, the GS39 date was adjusted by 1 day per cm sheath extension. The visits were repeated until all plots had at least 50% of shoots at or beyond GS39.
- *GS59 (ear completely emerged)* – the experiment was visited at least twice a week when GS59 was thought to be approaching. For each plot, the date was recorded when 50% of shoots (judged to be fertile) had an ear that is completely emerged (i.e. the collar is above

the flag-leaf ligule). This assessment was repeated at subsequent visits until all plots had at least 50% of shoots with their ears emerged.

- *GS61 (start of flowering)* - the experiment was visited at least twice a week when GS61 was thought to be approaching. For each plot the date was recorded when the ear had started to flower (anthers had exserted from the central spikelets of the ear) on 50% of shoots. The assessment was repeated at subsequent visits until all plots had at least 50% of shoots flowering.
- *GS87 (grain at ‘hard dough’, 45% moisture content)* – the experiment was visited at least twice a week when GS87 was thought to be approaching. When the middle grains in ears of the most advanced variety reached GS87 (i.e. when squeezed between the finger and thumb, grain contents are dry and cannot be squeezed out but a fingernail impression remains), 10 randomly-selected ears were sampled from every plot, and placed immediately in a sealed paper bag of known weight. The fresh weight was recorded, and then the dry weight recorded after drying for 24 hours at 80ºC. The moisture content was calculated and the GS87 date determined by assuming that for every 1% moisture content away from 45% moisture a sample was, it was 1 day away from GS87. On the 5 treatments with highest ear moisture content, the ear moisture determination was repeated 3-5 days later. It should be noted that in a number of cases, grain moisture contents were significantly below 45% (range of 15 – 55%), so although moisture contents will have indicated differences in maturity, it is possible that for these plots the relationship between the moisture content and the number of days away from adjustment for GS87 date was not accurate.

Table 4. Assessments carried out in each of the phenotyping experiments, including Growth Stages (GS), growth analyses and harvest assessments.

Site	Harvest year	No. varieties tested	GS10	GS31	GS39	GS59	GS61	GS87	Phyllo-chron	Height	GS61 growth analysis	Fertile ear counts	Spikelets per ear	Pre-harvest growth analysis	Combine yield	Thousand grain weight	Grain/straw N analyses
Framlingham	2007	49										✓		✓	✓	✓	
Grantchester	2007	49										✓		✓	✓	✓	
Woolpit	2007	49										✓		✓	✓	✓	
Clopton	2008	64	✓	✓	✓	✓	✓	✓							✓	✓	
Langton	2008	64	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Newton	2008	64	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Terrington	2008	64	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Clopton	2009	64	✓	✓		✓				✓			✓		✓	✓	
Langton	2009	64	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Newton	2009	64	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓
Terrington	2009	64	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Clopton	2010	64	✓	✓		✓	✓								✓		
Langton	2010	64	✓	✓	✓	✓	✓	✓			✓	✓		✓	✓	✓	✓
Newton	2010	64	✓	✓	✓	✓	✓			✓	✓	✓		✓	✓	✓	✓
Terrington	2010	64	✓	✓	✓	✓	✓			✓	✓	✓	✓	✓	✓	✓	✓

Leaf emergence and leaf number

For each plot, six representative plants were marked and their youngest fully emerged leaf was tagged on two dates:

1. when most plants had three fully-emerged leaves (and the first leaf could still be identified)
2. when most plants had seven fully-emerged leaves (and the previously tagged leaf could still be identified).

by placing a tag around the youngest leaf with ligule visible, and recording the number of that leaf (where the first leaf at crop emergence is leaf 1). The proportion emerged of the next, partially-emerged leaf lamina was also recorded.

At GS 39 (flag leaf emergence), the number of leaves that had emerged since the last leaf tag was attached was counted. These assessments allowed the calculation of final leaf number and, in conjunction with assessment date and temperature data, phyllochron (the average interval in thermal time between emergence of successive leaves on the main shoot).

Growth analysis at GS61

To allow for adjustment of measurements to GS61 date for each variety, samples were taken on three occasions; all varieties were sampled within 2 days of Claire reaching GS61, and a subset of three varieties was sampled approximately a week before and a week after the main sampling.

At each sampling date, grab samples of around six shoots from five objectively chosen positions per plot were taken to give a sample of 30 shoots. A representative subsample of 5 shoots was then taken, the ears and leaf laminae removed, the stems dried at 80°C for 16 hours and then submitted for lab analysis of water-soluble carbohydrates (g/kg). Soluble carbohydrates were extracted from the ground sample by shaking with water, filtering, reacting the filtrate with Anthrone reagent, and measuring the concentration of carbohydrate photometrically.

The remaining samples were separated into three components: leaf lamina, leaf sheath plus stem, and ears, and dry weights determined. To express measurements at GS61 on a land area basis, the value per shoot was multiplied by the number of fertile ears per m^2 determined at harvest (see below).

Fertile ear counts, spikelet counts and height

Before harvest, the row widths within plots in each experiment were recorded accurately. In six randomly chosen areas of each plot, the total number of fertile ears along 0.5m lengths of 2 adjacent rows was recorded. At each of the six sampling points, the height (cm) from ground level to the top of a median ear was determined. The total number of spikelets (fertile and infertile) on that ear was also recorded. Comparison of fertile ear count data with ears per m^2 back-calculated from combine yield data (yield, g/m^2, divided by grain weight, g/ear) showed unsatisfactory and variable accuracy and precision, hence the combine-related estimate was used in the analysis instead of the counts.

Lodging

Just before harvest, the percentage area of each plot that was leaning (10-45^o from vertical) or lodged (46-90^o from vertical) was recorded.

Pre-harvest sampling

Six sampling points were selected per plot. At each point, approximately 10 shoots were cut from a group of adjacent stem bases at ground level, and then combined to give a total of approximately 60 shoots per plot.

For each plot sample, the numbers of fertile shoots, infertile shoots and secondary tillers were recorded. The ears were removed from the fertile shoots and the ears and straw dried separately in an oven at 80^o C for 24 hours, or until no further weight loss occurred. Dry weights of the ear and straw samples were measured. The ears were threshed and the dry weight of the grain determined. Thousand grain weight (TGW) was determined by counting a known weight of grain (ca. 40g). Straw samples were sent for nitrogen (N) analysis by oxidative combustion (LECO; Dumas method). Grain samples were sent for N analysis by either Near Infra-Red reflectance or oxidative combustion.

Grain yield

Plots were combine harvested and weighed, moisture contents determined and grain yield determined, adjusted to 85% dry matter (DM). TGW was determined by counting a known weight of grain (ca. 40g). It should be noted that grain yields include grain from secondary tillers. Secondary tillering was a significant issue in 2007, and tests at Framlingham indicated that back tillers contributed up to 18% of the total yield.

Genotyping

Genotyping was carried out on all 64 varieties by RAGT Seeds[1]. First, DNA was extracted from leaf tissue using the method described on the MASWheat website (http://maswheat.ucdavis.edu/protocols/general_protocols/DNA_extraction_003.htm), which is based on the method by Pallotta *et al.* (2003). PCR markers were microsatellites or gene-derived and obtained from either Graingenes (http://wheat.pw.usda.gov/GG2/index.shtml) or MASWheat (http://maswheat.ucdavis.edu/protocols/index.htm), except for those with the prefix wmm

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[1] For technical detail, contact Peter Jack [PJack@ragt.fr]

(proprietary to RAGT seeds). PCR amplification and electrophoretic separation was as described on the MASWheat website (http://maswheat.ucdavis.edu/protocols/general_protocols/SSR_Protocol.htm).

Relationships between phenotypes and major genes are described in the report. The nomenclature used in the report is the ‘previous notation’ column in Table 5. Major gene results and other genetical information for all 64 varieties can be found in Appendix B.

Vernalisation experiment

An experiment was carried out in 2010-11 under controlled conditions at KWS UK Ltd., Thriplow, Cambridge to investigate the vernalisation requirements of the 64 varieties described in Section 3.2.1 above.

Every week for 10 weeks, each variety was sown as a single seed in one (non-edge) cell of a single seed descent (SSD) tray (8 x 13 cell trays). Edge cells were all sown to a control variety (Humber). Two replicate trays were used for each vernalisation treatment, with different randomisations in each tray. Immediately after sowing, the two trays were put into a cold room (4°C) for 2 nights to break dormancy and ensure even emergence of all seeds. After taking out of the cold room, the seed was germinated in a warm (20-24°C) glasshouse under artificial light set to a 13h day. After 1 week after sowing, the trays were moved to a vernalisation room run at 4°C when dark for 16h, rising to 6°C when lit for 8h. When all 10 repeat sowings had been made and the week of germination was complete for the final sowing (14th December 2010), all 20 trays for the 10 sowings (ranging from 9 to 0 weeks in vernalisation) were moved into a glasshouse and arranged in two randomised blocks on one bench. The glasshouse was set at 21°C and an 18h day (day length increased to 19h by the end of the experiment on 7th April 2011), with the intended temperature falling to 14°C in the 8h dark period.

The dates of GS39 (flag leaf ligule just visible) and GS61 (start of flowering) were recorded for each plant, if this occurred before 7th April. The total number of main shoot leaves was measured at GS39. This included both culm leaves and older, dead leaves (still intact due to the non-disturbance of the plants).

Table 5. A description of the phenotype, previous notation (used in this report), current notation, the number of varieties with each genotype, and example varieties associated with all *Vrn*, *Ppd* and *Rht* genotypes mentioned in this report. A full set of major gene information for all 64 varieties can be found in Appendix B.

Phenotype	Previous notation	Current notation*	No.	Example varieties
Vernalisation sensitive, winter	*vrn1*	*vrn-A1*[#]	61	Hereward, Soissons
Vernalisation insensitive, spring	*Vrn1*	*Vrn-A1a*	3	Paragon, Xi19
Photoperiod sensitive	*ppd3*	*Ppd-A1b*	64	Oakley, Claire
Photoperiod insensitive	*Ppd3*	*Ppd-A1a*	0	(none in ERYCC panel)
Photoperiod sensitive	*ppd2*	*Ppd-B1b*	62	Oakley, Claire
Photoperiod insensitive	*Ppd2*	*Ppd-B1a*	2	Mendel, Recital
Tall	*rht1*	*Rht-B1a*	56	Maris Huntsman, Cadenza
Reduced height	*Rht1*	*Rht-B1b*	8	Oakley, Robigus
Photoperiod sensitive	*ppd1*	*Ppd-D1b*	54	Oakley, Claire
Photoperiod insensitive	*Ppd1*	*Ppd-D1a*	10	Soissons, Bacanora
Tall	*rht2*	*Rht-D1a*	16	Maris Huntsman, Cadenza
Reduced height	*Rht2*	*Rht-D1b*	48	Consort, Claire

* McIntosh et al. (2003)

[#] the letter after the hyphen signifies the genome: A, B or D.

[#] there were 7 varieties with 3 copies of Vrn-A1 (e.g. Hereward), 45 varieties with 2 copies (e.g. Malacca), 6 varieties with 1 copy (winter; e.g. Claire), 4 varieties with 1 copy (spring; e.g. Cadenza) and 2 varieties with copy numbers unresolved (i.e. Longbow & Humber). .

Photoperiod extension experiments

An experiment was carried out in each of three growing seasons (2008-09, 2009-10, 2010-11) at Thriplow, near Cambridge, to investigate the photoperiod sensitivity of the 64 varieties described in Section 3.2.1 above.

Experiments were drilled on 20th October 2008, 4th November 2009 and 22nd October 2010 (see Appendix 1 for further site details). Two photoperiod treatments were applied – extended photoperiod (EP) and natural photoperiod (NP). The EP treatment provided a 16h photoperiod from the shortest day (22nd December) until two weeks after GS31 (around 23rd May each season).

Figure 1. Arrangement of lighting for photoperiod extension experiments at Thriplow.

There were two replicates of the two photoperiod treatments in main plots, making a total of four main plots. Main plots were arranged in a two by two square, with main treatments allocated systematically (plots of the same treatment diagonally opposite). Each main plot had 64 variety sub-plots, comprising one sub-plot of each variety. A sub-plot was three rows wide (0.6 m) by 1.1 m long. Sub-plots were arranged in pairs, each pair being an area of 1.2 m wide (6 rows) by 1.1 m long. Pairs of sub-plots were separated from other pairs of sub-plots by a distance of 0.4 m in each direction.

In each main plot, the 64 subplots were arranged in a 'square' of 8 x 8 sub-plots, randomised to take out row or column effects. Main plots of treatment EP had lights above each pair of sub-plots, over the boundary between the two plots. The light was supplied from 25W clear glass tungsten bulbs suspended 1m above the centre of plot-pairs at 37.5 cm intervals (Figure 1). These bulbs increased the temperature at the plant level very slightly when they were switched on (+0.2°C; giving +0.9% thermal time at the average temperature in spring 7°C), but not enough to significantly affect the relative differences between the light effects of the EP treatment. NP main plots were separated from EP main plots by at least 3m. Observations of guard plots showed that treatment effects were not detectable beyond 3m.

Assessments

Assessments carried out in 2008-09 and 2010-11.

The following assessments were carried out in the 2008-09 and 2010-11 seasons only:

- *GS31 (first node detectable)* – the experiment was visited at least twice each week when GS31 was thought to be approaching. Five plants per plot were dug or pulled up and the main shoot identified. It was determined whether the first node was 'detectable' by feeling the stem, and splitting the stem if necessary. The date of this growth stage was recorded slightly differently each year. In 2008-09, the date for this growth stage was recorded when all five main shoots had an internode at least 1 cm long, or (if earlier) a length from stem base to apex of at least 2 cm. In 2010-11, the assessments continued until all 5 plants had reached the growth stage on two visits in succession. In both years, relationships were fitted to the data to determine the date at which 50% of the plants in each plot had achieved GS31.
- *GS39 (flag leaf ligule just visible)* – the experiment was visited at least twice each week when GS39 was thought to be approaching. For each plot, the date was recorded when 50% of shoots (judged potentially fertile) had a flag leaf ligule just visible. If the median flag leaf ligule had already extended above the penultimate leaf ligule since the last visit, the GS39 date was adjusted by 1 day per cm sheath extension. The visits were repeated until all plots had at least 50% of shoots at or beyond GS39.
- *GS59 (ear completely emerged)* - the experiment was visited at least twice each week when GS59 was thought to be approaching. For each plot, the date was recorded when 50% of shoots (judged to be fertile) had an ear completely emerged (i.e. the collar was above the flag-leaf ligule). This assessment was repeated at subsequent visits until all plots had at least 50% of shoots with their ears emerged.
- *GS61 (start of flowering)* - the experiment was visited at least twice each week when GS61 was thought to be approaching. For each plot the date was recorded when the ear had started to flower (anthers have exserted from the central spikelets of the ear) on 50% of all ears. Assessments were repeated at subsequent visits until all plots had at least 50% of ears flowering.

- *Leaf emergence and leaf number -* For each plot, six plants were selected within one row. A plastic cane was placed next to each selected plant to assist in locating the plant at each subsequent assessment. Leaves were tagged on two dates:
    - when most plants had three fully-emerged leaves (and the first leaf could still be identified)
    - when most plants had seven fully-emerged leaves (and the previously tagged leaf could still be identified).

  On both dates a leaf tag was placed around the youngest, fully expanded leaf, i.e. youngest leaf with ligule visible, and the number of the tagged leaf recorded (where the first leaf at crop emergence is leaf 1). The proportion emerged of the next, partially-emerged leaf lamina was also recorded.
- At GS 39 (flag leaf emergence), the number of leaves that had emerged since the last leaf tag was attached was counted. These assessments allowed the calculation of final leaf number and, in conjunction with assessment date and temperature records, phyllochron.

The experiments were terminated once the GS61 assessments were complete.

Assessments carried out in 2009-10

Soon after emergence, the 2009-10 experiment suffered from significant rabbit grazing. Therefore, because of the potentially confounding affects of this grazing, it was decided to abandon the majority of assessments. However, the EP treatment was still applied and the following assessments were made:

- *GS33 (third node detectable)* – the experiment was visited at least twice a week when GS33 was thought to be approaching. The main shoot was identified on 5 plants per plot. GS33 was identified when the internode to the first node was more than 1cm, and the next 2 internodes were more than 2cm each. The plot was deemed to have reached GS33 when the main stem of at least 50% of the plants had reached GS33.
- *GS61 (start of flowering)* - as above.

The experiment was terminated once GS61 assessments were complete.

3.2.3. Data analysis

Data were analysed using a number of methods, but all using Genstat (VSN International). Individual experiments were analysed using analysis of variance. Cross-site (where site = site/season) analysis was carried out on either all experiments, or only the experiments where particular measurements had been taken. This was done using a weighted analysis of variance, where the data at each site was weighted by the reciprocal of the coefficient of variation (CV%) of the data for that measurement at that site. Note that multiplication of weighted means of yield components will give mean yields that differ (slightly) from the reported yields (which are also weighted means). Regression analysis was then carried out on the resulting weighted means, often using subgroups such as the landmark bread-making and feed varieties (for explanation of landmark varieties see above). Unbalanced analysis of variance was used to examine genotype effects on different variates. Biplots were produced using Genstat, based on the method of Gower and Hand (1996). Yield data were analysed for superiority using the method of Lin and Binns (1988) which calculates a coefficient indicating the variety's *in*stability. For each variety, this is the sum of the squares of the differences between its mean in each environment and the mean of the best variety there, divided by twice the number of environments.

3.3. Results

3.3.1. Characterising varieties (phenotyping experiments)

Weather

At every site, the 2008 harvest season had the mildest winter (December – February) of all the experimental seasons (5.6^{o}C winter average over all sites; Table 6) with 2010 the coldest winter (2.2^{o}C winter average over all sites). The springs (March - May) of 2009 and 2010 were a lot drier than that of 2008 (Table 7), with Langton and Terrington experiencing the driest spring of the project in 2009 (42.7 and 38.9 mm total spring rainfall, respectively) and Clopton and Newton experiencing the driest spring in 2010 (46.8 and 28.0 mm total spring rainfall, respectively; Table 7)

Table 6. Average quarterly temperature at each experimental site in each of the three core harvest seasons (2008 – 2010). Autumn is September to November, etc.

Site	Quarter	Average temperature (^{o}C) 2008	2009	2010
Clopton	Autumn	10.6	10.0	11.9
	Winter	5.7	3.1	2.3
	Spring	7.0	8.6	7.7
	Summer	15.5	15.7	15.4
Langton	Autumn	10.6	9.9	10.9
	Winter	5.2	3.4	1.8
	Spring	6.5	8.0	7.1
	Summer	14.4	14.5	14.2
Newton	Autumn	11.3	10.4	12.3
	Winter	6.2	3.3	2.4
	Spring	7.6	8.4	8.4
	Summer	15.8	16.6	16.4
Terrington	Autumn	11.2	10.0	11.8
	Winter	5.4	3.6	2.2
	Spring	7.2	8.8	7.6
	Summer	15.6	15.9	16.2

Table 7. Total quarterly rainfall and total annual rainfall at each experimental site in each of the three core harvest seasons (2008 – 2010). Autumn is September to November, etc.

Site	Quarter	Total Rainfall (mm) 2008	2009	2010
Clopton	Autumn	101.8	166.5	168.1
	Winter	122.5	130.9	187.3
	Spring	132.1	47.8	46.8
	Summer	245.5	161.3	223.8
Clopton Total		601.9	506.5	626.0
Langton	Autumn	137.8	191.1	216.7
	Winter	211.1	149.4	218.4
	Spring	144.5	42.7	82.0
	Summer	306.6	267.1	158.3
Langton Total		800.0	650.3	675.4
Newton	Autumn	91.4	135.7	133.0
	Winter	110.1	106.3	140.1
	Spring	108.4	46.4	28.0
	Summer	185.2	142.7	150.0
Newton Total		495.1	431.1	451.1
Terrington	Autumn	105.6	183.4	159.5
	Winter	133.3	115.1	191.9
	Spring	119.5	38.9	56.7
	Summer	224.8	271.7	211.8
Terrington Total		583.2	609.1	619.9

Yield and its determinants

Experimental results

The average yield over all experiments was 9.77 t/ha @ 85% DM (Table 8). This is less than the average yield from Recommended List trials in the East of England over the same period (10.6 t/ha @ 85% DM), but the experiments reported here contained lower-yielding older varieties and non-UK varieties. On average, over sites, the year resulting in the highest yields was 2008, and 2010 gave, on average, the lowest yields, with Clopton 2008 giving the highest average site yield (13.63 t/ha) and Newton 2010 the lowest (7.32 t/ha; Table 8). There were significant ($P<0.05$) effects of variety on yield in all 15 experiments, although there was less variation within the 2010 experiments than in other years. There was also a significant ($P<0.001$) site by variety interaction when a cross-site analysis was carried out. However, the rankings of varieties were similar among experiments. In 8 of the 15 experiments, variety 5 (Oakley) was the highest yielding variety and in 11 of the 15 experiments, variety 64 (Bacanora) was the lowest yielding variety (Table 8). Heritability (h^2; the relative contribution of genetic (G) effects and genetic x environment (E) interactions on a trait; G + G.E) for yield over all experiments was 0.21.

Grain yield was the only assessment that was carried out on all 15 experiments. However, measurements of the components of yield were carried out in 12 of the 15 experiments, and thousand grain weight (TGW) was measured in 14 of the 15 experiments. The highest-yielding site (Clopton 2008) also gave the biggest thousand grain weight, on average (56.6g; Table 8), but high yields were not associated with large TGWs across all sites. There were significant ($P<0.001$) effects of variety on TGW at all sites and a significant ($P<0.001$) site by variety interaction was found from cross-site analysis. Variety 12 (Exotic) gave the highest TGW in 10 of the 14 experiments where it had been measured, with an average TGW of over 60 g in 3 of the experiments (Table 8). Variety 64 (Bacanora), often the lowest yielding variety, also gave the lowest TGW in 4 of the 14 experiments, but varieties 32 (Gatsby) and 56 (Spark) also gave the lowest TGW in a number of experiments (Table 8), much lower than the benchmark 43 g given in the HGCA Wheat Growth Guide (Sylvester-Bradley *et al*. 2008). However, these varieties also gave the highest number of ears per m^2 in a number of experiments (Table 8), so their yields were not low. On average over all experiments, the numbers of ears per m^2 was 397, lower than the benchmark of 460, but numbers were very variable, from an average of 286 at Newton 2010 to 556 at Woolpit 2007 and Newton 2008. This may have been because the ears per m^2 data were calculated from the combine yields. There were again significant ($P<0.05$) effects of variety on the number of ears/m^2 in every experiment and there was a significant variety by site interaction. This was also the case for the number of grains per ear, although this measure showed the highest heritability ($h^2 = 0.58$) of the three yield components, TGW, grains/ear and ears/m^2 (Table 8).

The overall average crop biomass at harvest was 14.7 t/ha @ 100% DM, and averages for each experiment reflected grain yields (Table 8). However, unlike with yield, the effect of variety on crop biomass was not significant in the 2010 experiments, and variety 5 (Oakley) did not have the highest biomass in any of the experiments, because it tended the give high harvest indices with the highest harvest index in 2 of the 12 experiments where it was measured (Table 8). The varieties with the highest crop biomass were, in 5 of the 9 experiments, 32 and 56 (Gatsby and Spark); these also gave high numbers of ears per m^2. Variety 64 (Bacanora), often the lowest yielding variety, also gave the lowest crop biomass in 5 experiments. Harvest index exceeded the benchmark of 51% in 11 of the 12 experiments, with an overall average of 53.2% (Table 8). There were significant ($P<0.01$) effects of variety on harvest index in all experiments, and either variety 47 (Capelle Desprez) or 62 (Maris Widgeon), the two oldest and tallest varieties tested, always gave the lowest harvest index. Harvest index was much more heritable ($h^2 = 0.52$) than crop biomass ($h^2 = 0.19$).

Nitrogen (N) uptake and partitioning were examined in the 9 core experiments between 2008 and 2010 (Table 9). Overall average N uptake was 210 kg/ha, but site averages ranged from 144 kg/ha at Newton 2010 to 288 kg/ha at Newton 2008 (Table 9). There were significant ($P<0.05$) variety effects on total N taken up in only 3 of the 9 experiments (Newton 2008, Newton 2009, Terrington 2009) and heritability was low ($h^2 = 0.11$). This contrasts with the grain N concentration, for which there were significant effects of variety in 8 of the 9 experiments (only Langton 2008 did not show significant differences), and where heritability was much higher (h^2 = 0.42; Table 9). The heritability of N harvest index was 0.33 (Table 9), and was significantly (P<0.05) affected by variety in 5 of the 9 experiments; as with the total and straw N uptakes, none of the 2010 experiments showed significant variety effects on N harvest index.

On average, GS10 occurred on 1st November, GS31 on 17th April, GS39 on 18th May, GS59 on 3rd June, GS61 on 7th June and GS87 on 18th July (Table 10). There were significant (P<0.05) effects of variety on dates of all growth stages in all experiments, apart from GS59 at Newton 2008, and the heritabilities of most growth stages were similar (0.30 to 0.39), apart from GS10 (h^2 = 0.02) which was more dependent on drilling date. There was anything from 13 (Newton 2008) to 38 (Terrington 2009) days between the first and last variety to reach GS31. Variety 64 (Bacanora) was frequently the earliest to reach any growth stage (Table 10) and had the shortest foundation phase (GS10-31) in 6 of 11 experiments (Table 11), but did not generally have the shortest construction (GS31-61) or production (GS61 – 87) phase durations. The French varieties included (e.g. 10 Andalou, 42 Apache, 49 Cezanne) also tended to reach growth stages early, and had below average durations of development phases. However, it was more common for varieties to reach growth stages at the average date or later, with the variation in the dates of growth stages of UK varieties much smaller than if non-UK varieties were included. There were significant (P<0.05) differences among varieties in all experiments when each of the development phase durations were examined, but the heritability of the development phase durations were lower than those of the growth stages, with the heritability of the construction phase the highest (h^2 = 0.28; Table 11).

On average over 6 experiments in 2008 and 2009, the average number of leaves that developed on the main shoots was 10.6, associated with an average phyllochron of 138 °C days per leaf (Table 11). There were significant (P<0.05) effects of variety on total leaf number in all experiments except Langton 2009, and variety effects (P<0.05) on phyllochron were found in all experiments except Langton 2008 and Newton 2008. The average phyllochron generally appeared lower in the 2009 experiments (127 °C days) than the 2008 experiments (149 °C days; Table 11), but this may have been due to the slightly different assessment method used between the two years. Varieties 14 (Exsept) and 20 (Istabraq) gave the highest phyllochrons in two experiments each, with the highest phyllochron of 14 (Exsept) measured as 189 °C days and the highest phyllochron of 20 (Istabraq) measured as 155 °C days (Table 11). The low-yielding, early variety, 64 (Bacanora), gave the shortest phyllochron identified in any experiment (101 °C days; Terrington 2009) and also had the lowest total number of leaves in all three 2008 experiments (Table 11).

Crop growth analysis at anthesis was carried out at GS61 on 9 experiments between 2008 and 2010 (Table 12). Leaf, ear and stem DM measured on a per shoot basis showed significant

(P<0.05) differences among varieties at all sites and Water Soluble Carbohydrates (WSC) per shoot at all but Newton 2008, but when the whole crop biomass was examined on a per area basis, differences among varieties were generally less significant and were not significant at Newton 2009, Langton 2010 and Newton 2010. The same was true when WSC was examined on an area basis. When WSC was examined on a % DM basis, significant variety effects were found at most sites, but not Langton 2008, Newton 2010 or Terrington 2010. The leaf and stem DMs per shoot at GS61 were also more heritable (h^2 = 0.51 and 0.50, respectively) than crop biomass per area (h^2 = 0.39; Table 12). Crop height measured at this stage was found to be the most heritable trait of any measured in this project (h^2 = 0.62), with heights ranging, on average, from 64 to 110 cm (Table 12). The tallest varieties were generally varieties 47 (Capelle Desprez) and 62 (Maris Widgeon), and the shortest were varieties 8 (Dover) and 64 (Bacanora).

Overall, although there were significant variety by site interactions found with cross-site analyses of all traits measured during this project, variety rankings were generally similar between sites. Therefore, weighted means over sites are used to examine traits and relationships in the following sections of this report.

Table 8. Summary of the mean, minimum and maximum yield, crop biomass, harvest index, thousand grain weight (TGW), and numbers of grains/ear and ears/m^2 for each experiment plus the overall mean and heritability (h^2; G + G.E). The summary includes standard deviations (SD) and the number codes of extreme varieties (var.).

			Yield (t/ha)			**Crop biomass (t/ha)**			**Harvest Index (%)**			**TGW (g)**			**No. grains/ear**			**No. ears/m^2**	
Site	**Year**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**
Framlingham	2007	8.83	10.62	6.54	13.89	16.26	9.53	54.1	58.6	42.6	45.1	62.9	40.2	45.6	55.4	33.2	370	475	272
		(0.87)	(3)	(47,11)	(1.32)	(3)	(11)	(2.6)	(12)	(47)	(4.4)	(12)	(32)	(5.9)	(30)	(10)	(48.1)	(42,32)	(11)
Grantchester	2007	8.39	9.76	5.31	16.14	20.24	11.75	44.4	52.4	34.6	35.4	43.3	26.2	46.4	58.7	33.9	445	658	331
		(0.78)	(5)	(47)	(1.66)	(32)	(11)	(3.5)	(11)	(47)	(3.4)	(49)	(3)	(5.2)	(35)	(10)	(68.9)	(32)	(47)
Woolpit	2007	9.99	12.19	7.87	16.3	19.64	12.40	52.2	57.1	44.2	34.9	41.6	30.3	44.7	54.8	30.4	556	861	416
		(0.96)	(5)	(11)	(1.64)	(34)	(11)	(2.6)	(44)	(47)	(2.5)	(10)	(35)	(5.5)	(16)	(24)	(85.9)	(21)	(46)
Clopton	2008	13.63	16.52	9.06							56.6	72.4	43.9						
		(1.41)	(5)	(64)							(4.7)	(12)	(64)						
Langton	2008	9.85	12.32	7.07	15.56	18.37	12.50	53.9	58.6	39.9	44	54.7	35.4	46.4	55.5	30.7	416	554	337
		(1.16)	(5)	(47)	(1.72)	(29)	(40)	(3.3)	(5)	(62)	(3.8)	(12)	(64)	(6.3)	(18)	(47)	(61.4)	(56)	(53)
Newton	2008	11.67	13.49	7.67	19	22.17	13.61	52.3	61.4	37.2	45.9	55.2	35.5	39.8	48.4	25.9	556	885	404
		(1.23)	(5)	(64)	(1.72)	(6)	(64)	(4.3)	(26)	(62)	(3.9)	(12)	(64)	(6.2)	(40)	(56)	(92.4)	(56)	(46)
Terrington	2008	10.72	12.73	7.61	17.06	20.60	12.95	53.4	58.8	39.7	45.9	59.5	38.9	50.9	61.0	36.3	396	616	297
		(1.18)	(5)	(64)	(1.68)	(32)	(64)	(3.3)	(5)	(62)	(3.7)	(12)	(32)	(6.2)	(30)	(62)	(59.4)	(56)	(11)
Clopton	2009	12.16	14.02	7.66							48.1	61.1	39.0						
		(1.19)	(6)	(64)							(3.9)	(12)	(56)						
Langton	2009	10.04	11.46	6.27	15.13	18.13	10.36	56.4	67.4	42.4	50.3	59.9	41.6	43.1	50.0	34.4	394	556	211
		(1.08)	(50)	(64)	(1.41)	(56)	(64)	(4)	(31)	(62)	(3.8)	(54)	(64)	(4.5)	(43)	(62,24)	(64.6)	(56)	(41)
Newton	2009	9.57	11.24	5.85	14.99	18.48	10.54	54.3	59.8	37.9	50.1	58.6	40.3	44.4	52.7	30.5	315	478	257
		(1.05)	(56,31)	(64)	(1.41)	(56)	(64)	(3.8)	(9)	(62)	(4)	(12)	(56)	(5)	(29)	(62)	(45.2)	(56)	(64)
Terrington	2009	8.62	10.25	5.39	14.08	17.74	10.03	52.1	56.0	39.2	44.5	55.2	36.8	54.4	64.8	39.6	307	447	246
		(0.83)	(32)	(64)	(1.25)	(32)	(64)	(3.2)	(1)	(62)	(3.7)	(12)	(56)	(7.1)	(13)	(62)	(37.6)	(32)	(54)
Clopton	2010	9.99	11.05	7.14															
		(0.74)	(5)	(64)															
Langton	2010	9.68	11.75	6.75	14.08	15.75	12.32	56.5	62.6	45.0	48.8	55.0	41.9	42.1	51.3	27.2	404	508	313
		(1.05)	(5)	(64)	(1.25)	(40)	(16)	(3.3)	(33)	(64)	(3.1)	(10)	(56)	(4.8)	(29)	(64)	(51.5)	(32)	(14)
Newton	2010	6.05	7.24	4.28	9.15	10.96	6.64	56.3	60.5	48.0	41.1	49.7	30.3	44.1	51.7	33.0	286	393	209
		(0.89)	(25)	(64)	(1.32)	(25)	(44)	(2.9)	(44)	(47)	(3.5)	(12)	(32)	(4.4)	(28)	(12)	(42.8)	(32)	(19)
Terrington	2010	7.32	8.28	5.17	10.91	12.76	9.36	52	56.0	41.9	40.4	49.8	32.3	48.7	58.0	35.0	325	409	238
		(0.71)	(27)	(64)	(1.14)	(35)	(11)	(2.7)	(10)	(62)	(3.2)	(12)	(32)	(5.4)	(35)	(64)	(44.1)	(42)	(47)
	Mean	9.77	11.53	6.64	14.69	17.59	11.00	53.2	59.1	41.1	45.1	56.0	36.61	45.8	55.2	32.5	397	570	294
	h^2	0.21			0.19			0.52			0.29			0.58			0.26		

Table 9. Summary of the mean, minimum and maximum grain, straw and total N uptake, grain and straw N concentration, and N harvest index measured pre-harvest for each experiment plus the overall mean and heritability (h^2; G + G.E). The summary includes standard deviations (SD) and the number codes of extreme varieties (var.).

		Total N uptake			**Grain N (%)**			**Grain N offtake (kg/ha)**			**Straw N(%)**			**Straw N uptake (kg/ha)**			**N Harvest Index (%)**		
Site	**Year**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**
Framlingham	2007																		
Grantchester	2007																		
Woolpit	2007																		
Clopton	2008																		
Langton	2008	211 (33.6)	277 (24)	156 (40)	1.95 (0.3)	2.88 (24)	1.55 (3)	163 (29.4)	236 (24)	118 (47)	0.673 (0.139)	0.984 (64)	0.494 (47)	48.1 (10.7)	63.7 (64)	30.6 (11)	77.1 (4.1)	84.0 (24)	68.0 (64)
Newton	2008	288 (27.6)	337 (6)	229 (64)	2.18 (0.18)	2.65 (64)	1.81 (5)	215 (19.2)	248 (27)	172 (64)	0.791 (0.136)	1.103 (25)	0.593 (12)	72.5 (19.9)	138.5 (25)	43.4 (7)	75 (5.3)	83.2 (7)	56.8 (25)
Terrington	2008	252 (24.9)	316 (14)	212 (49)	2.04 (0.18)	2.61 (64)	1.64 (20)	185 (18.9)	225 (14)	150 (62)	0.843 (0.122)	1.125 (40)	0.673 (29)	67.1 (12.8)	90.6 (62)	50.0 (11)	73.5 (3.9)	78.4 (29)	62.2 (62)
Clopton	2009																		
Langton	2009	225 (24)	272 (56)	176 (64)	2.14 (0.21)	2.72 (64)	1.65 (4)	181 (19.2)	210 (22)	144 (47)	0.666 (0.088)	0.805 (44)	0.550 (25)	43.9 (8.6)	63.1 (56)	30.7 (31)	80.6 (2.8)	85.4 (22)	75.2 (62)
Newton	2009	226 (19)	272 (56)	179 (64)	2.19 (0.17)	2.70 (64)	1.92 (5)	177 (14.9)	210 (56)	135 (64)	0.714 (0.054)	0.806 (53)	0.635 (20)	49 (8.2)	75.2 (62)	37.6 (9)	78.4 (2.8)	81.7 (9)	66.5 (62)
Terrington	2009	166 (18.3)	233 (38)	121 (64)	1.77 (0.17)	2.38 (38)	1.59 (32)	130 (16)	194 (38)	93 (64)	0.543 (0.071)	0.679 (9)	0.436 (52)	36.5 (5.7)	48.2 (43)	27.1 (32)	78 (2.8)	82.4 (38)	72.6 (62)
Clopton	2010																		
Langton	2010	204 (16.2)	233 (41)	177 (9)	2.05 (0.2)	2.56 (62)	1.63 (53)	167 (14.5)	192 (41)	142 (9)	0.597 (0.057)	0.688 (36)	0.511 (62)	36.5 (5.5)	47.0 (40)	29.4 (33)	82.1 (2.4)	85.6 (35)	75.8 (64)
Newton	2010	144 (20.4)	176 (39)	99 (19)	2.32 (0.18)	2.63 (56)	2.03 (60)	119 (17)	144 (39)	80 (19)	0.634 (0.048)	0.730 (55)	0.540 (62)	25.3 (4.6)	33.6 (34)	15.7 (44)	82.4 (2)	86.5 (44)	77.7 (64)
Terrington	2010	172 (13.8)	199 (27)	146 (64)	1.91 (0.1)	2.21 (62)	1.76 (53)	119 (11.5)	140 (27)	93 (64)	0.49 (0.038)	0.566 (64)	0.434 (15)	53.1 (6.2)	65.1 (50)	45.8 (39)	69.1 (3.1)	73.7 (39)	63.3 (64)
	Mean	210	257	166	2.06	2.59	1.73	162	200	125	0.661	0.831	0.540	48.0	69.4	34.5	77.3	82.3	68.7
	h^2	0.11			0.42			0.15			0.20			0.18			0.33		

Table 10. Summary of the mean, minimum and maximum date (Julian days) of key growth stages (GS) for each experiment, plus the overall mean and heritability (h^2; G + G.E). The summary includes standard deviations (SD) and the number codes of extreme varieties (var.). Where variety numbers are absent, this is because more than two varieties gave the same extreme.

			GS10			GS31			GS39			GS59			GS61			GS87	
Site	**Year**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**
Framlingham	2007																		
Grantchester	2007																		
Woolpit	2007																		
Clopton	2008	303 (1.5)	308	303	91 (7.5)	107 (56)	74 (49)	135 (6.7)	144 (9)	111 (64)	156 (5.1)	163 (9)	140 (64)	157 (4.7)	167 (9)	143 (64)	198 (7.7)	207 (9)	178 (64)
Langton	2008	308 (2.2)	312	305	108 (9.1)	122 (58)	93 (49)	148 (3.2)	152 (48)	143	159 (1.9)	162 (36)	154 (9)	168 (5.0)	177 (6)	158 (12)	209 (5.5)	216 (40)	196 (44)
Newton	2008	311 (1.1)	315	310	112 (3.5)	120 (26)	107	138 (4.2)	147 (14,56)	126 (64)	154 (4.5)	160	147 (53)	159 (4.0)	163	143 (64)	203 (4.5)	208 (50)	190 (49)
Terrington	2008	301 (0.9)	303	301	110 (4.7)	118 (5)	102 (13)	139 (4.9)	147	129	157 (4.9)	161	141 (64)	160 (4.8)	167	143 (64)	206 (3.9)	211 (9)	188 (64)
Clopton	2009	313 (1.2)	314	310 (52)	109 (4)	115 (26)	93 (64)				155 (4.6)	163 (4)	144 (40						
Langton	2009	350 (5.7)	357 (61)	333 (62)				145 (4.1)	151	138	164 (5.8)	169	149 (64)	167 (3.7)	173 (14)	158 (64,12)	208 (4.4)	215 (50)	196 (64)
Newton	2009	293 (0.7)	295	293	106 (4.8)	114 (37)	84 (64)	131 (4.6)	139 (19)	116 (64)	146 (4)	152 (14,56)	131 (64)	150 (3.4)	157 (55)	137 (64)	194 (4.5)	200 (48)	176 (64)
Terrington	2009	294 (0.8)	296	294	109 (5.6)	122 (60)	84 (64)	133 (4.3)	139 (25)	116 (64)	148 (4.9)	161 (64)	134 (39)	152 (3.1)	158	140 (64)	193 (5.6)	200 (50)	177 (64)
Clopton	2010	298 (1.9)	299	295	117 (3.6)	126 (26)	105 (10)				162 (3.5)	167 (36)	151 (40)	166 (6.4)	182 (6)	157			
Langton	2010	300 (1.9)	302	298	107 (4.2)	114 (52)	88 (64)	143 (2.3)	147	133 (64)	160 (3.5)	164	147 (64)	164 (2.9)	168	157	193 (4.7)	202 (50)	181 (44)
Newton	2010	307 (est.)			115 (5.2)	123 (33)	88 (64)	140 (2.8)	144 (36,48)	126 (64)	154 (3.9)	159 (19,48)	139 (64)	157 (3)	161	143 (64)			
Terrington	2010	295 (2.8)	299	292	108 (3.8)	116 (56)	102 (30)	139 (3.7)	142	123 (64)	153 (2.3)	156	140 (64)	156 (2.2)	158	144 (64)			
	Mean	306	309	303	109	118	93	139	145	126	156	161	143	160	166	148	201	207	185
	h^2	0.02			0.39			0.35			0.36			0.30			0.33		

Table 11. Summary of the mean, minimum and maximum duration (°C day) of the foundation (GS10 – 31), construction (GS31 – 61) and production (GS61 – 87) phases, the full life cycle (GS10 – 87), the mean phyllochron (°C day), and the number of main shoot leaves for each experiment, plus the overall mean and heritability (h^2; G + G.E). The summary includes standard deviations (SD) and the number codes of extreme varieties (var.). Where variety numbers are absent, this is because more than two varieties gave the same extreme.

Site	Year	Foundation			Construction			Production			Full life cycle			Phyllochron			Total leaf number		
		Mean (SD)	Max. (var.)	Min. (var.)	Mean (SD)	Max. (var.)	Min. (var.)	Mean (SD)	Max. (var.)	Min. (var.)	Mean (SD)	Max. (var.)	Min. (var.)	Mean (SD)	Max. (var.)	Min. (var.)	Mean (SD)	Max. (var.)	Min. (var.)
Framlingham	2007																		
Grantchester	2007																		
Woolpit	2007																		
Clopton	2008	929 (49.4)	1036 (56)	821 (40)	750 (47.1)	848 (34)	651 (21)	608 (67.2)	717 (50)	442 (44)	2284 (119.6)	2419 (1)	1968 (64)						
Langton	2008	974 (62.3)	1102 (14)	873 (9)	694 (79.7)	863 (11)	566 (52)	622 (85.6)	723 (41,20)	411 (11)	2286 (91.2)	2405 (36)	2074 (44)	172 (13.9)	189 (14)	139 (58)	9.4 (0.49)	10.3 (58)	8.0 (64)
Newton	2008	1109 (36.3)	1200 (26)	1058 (64)	630 (71.5)	737 (46)	464 (14)	671 (93.7)	870 (14)	487 (64)	2410 (77.8)	2508	2201 (49)	135 (5.8)	146 (20)	122 (48)	10.5 (0.49)	11.3 (48)	9.2 (64)
Terrington	2008	1113 (40.3)	1183 (25)	1046 (40)	674 (53.3)	810 (37)	546 (24)	696 (43.5)	790 (40)	567 (35)	2480 (68.2)	2572 (1)	2205 (64)	141 (8.9)	164 (14)	130 (30)	11 (0.57)	11.8 (47)	9.4 (64)
Clopton	2009	879 (45)	959 (52)	703 (64)															
Langton	2009							641 (50.5)	729 (50)	526 (8)	2002 (68.3)	2101 (62)	1816 (64)	137 (8.6)	155 (20)	122 (42)	8.7 (0.4)	9.4 (27)	8.0 (24)
Newton	2009	1042 (50)	1122 (37)	831 (64)	551 (49.5)	633 (55)	452 (42)	736 (58.1)	817 (57)	589 (64)	2328 (83.3)	2433 (48)	1983 (64)	126 (6)	137 (60)	115 (49)	11.5 (0.43)	12.3 (8,26)	10.8
Terrington	2009	1057 (59)	1211 (60)	818 (64)	546 (49.4)	695 (43)	405 (60)	666 (76.8)	763 (24)	466 (58)	2269 (96.4)	2395 (19,50)	1990 (64)	119 (5.8)	129 (1)	101 (64)	12.2 (0.49)	13.0 (16)	11.4 (49)
Clopton	2010	1060 (42.9)	1151 (26)	955 (10)	604 (93.7)	893 (11)	493 (64)												
Langton	2010	835 (37.7)	902 (56)	717 (64)	628 (35.1)	708 (1)	569 (49)	1053 (44.4)	1128 (10)	969	2513 (9)	2526	2506						
Newton	2010	992 (58)	1083 (33)	737 (64)	540 (43.7)	629 (1)	422 (12)												
Terrington	2010	959 (40.4)	1014 (42,20)	870 (59)	564 (33.6)	616 (30)	479 (40)												
	Mean	995	1087	857	618	743	505	712	831	573	2321	2420	2111	138	153	121	10.6	11.3	9.5
	h^2	0.18			0.28			0.08			0.11			0.13			0.08		

Table 12. Summary of the mean, minimum and maximum crop biomass (@ 100% DM), leaf, ear and stem DM, stem water soluble carbohydrates (WSC @ 100% DM), and crop height, all measured at GS61, plus the overall mean and heritability (*h^2*; G + G.E). The summary includes standard deviations (SD) and the number codes of extreme varieties (var.).

		Crop biomass (t/ha)			**Leaf DM (g/shoot)**			**Ear DM (g/shoot)**			**Stem DM (g/shoot)**			**WSC (g/m^2)**			**Height (cm)**		
Site	**Year**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**	**Mean (SD)**	**Max. (var.)**	**Min. (var.)**
Framlingham	2007																		
Grantchester	2007																		
Woolpit	2007																		
Clopton	2008																		
Langton	2008	10.1	12.8	7.0	0.512	0.652	0.358	0.422	0.815	0.253	1.51	2.048	0.889	223	302	114	80.1	117.5	66.9
		(1.56)	(13)	(64)	(0.072)	(35)	(64)	(0.12)	(11)	(42)	(0.263)	(13)	(64)	(50.8)	(48)	(64)	(9.3)	(62)	(8)
Newton	2008	11.4	14.2	7.7	0.443	0.614	0.294	0.351	0.543	0.188	1.275	1.690	0.831	189	246	117	87.2	126.0	76.0
		(1.69)	(27)	(64)	(0.061)	(14)	(64)	(0.075)	(40)	(56)	(0.205)	(13)	(64)	(42.7)	(3)	(7)	(9.1)	(47)	(64)
Terrington	2008	10.4	13.6	6.4	0.555	0.678	0.398	0.476	0.668	0.320	1.61	2.179	1.102	183	243	131	77.4	90.5	69.4
		(1.65)	(56)	(64)	(0.064)	(54)	(56)	(0.082)	(1,11)	(32)	(0.259)	(13)	(64)	(33.5)	(48)	(60)	(6.4)	(6)	(54)
Clopton	2009																69.4	98.7	54.8
																	(8.4)	(62)	(64)
Langton	2009	9.5	12.2	4.5	0.433	0.556	0.322	0.469	0.627	0.248	1.517	2.091	0.983	204	296	67	76.6	115.7	63.4
		(1.7)	(29)	(41)	(0.059)	(14)	(24)	(0.094)	(64)	(57)	(0.267)	(58)	(12)	(48.2)	(41)	(29)	(9.8)	(62)	(8)
Newton	2009	8.9	10.7	6.7	0.53	0.696	0.373	0.502	0.688	0.257	1.809	2.216	1.419	203	276	128	80.8	126.2	66.3
		(1.08)	(62)	(64)	(0.074)	(54)	(56)	(0.113)	(54)	(42)	(0.226)	(62)	(56)	(40.8)	(18)	(56)	(11)	(47)	(8)
Terrington	2009	8.9	11.4	6.3	0.491	0.629	0.318	0.485	0.688	0.278	1.882	2.487	0.747	216	347	88	74	106.0	65.0
		(1.2)	(32)	(64)	(0.072)	(23)	(56)	(0.11)	(64)	(60)	(0.35)	(13)	(64)	(56.7)	(45)	(64)	(7.7)	(47)	(10)
Clopton	2010																		
Langton	2010	10.9	13.6	8.5	0.507	0.686	0.330	0.541	0.712	0.304	1.664	2.036	1.226	218	335	138			
		(1.61)	(32)	(18)	(0.09)	(14)	(35)	(0.096)	(59)	(56)	(0.222)	(51)	(56)	(52.8)	(34)	(18)			
Newton	2010	7.2	9.8	5.2	0.39	0.471	0.245	0.726	1.048	0.484	1.414	1.752	1.071	130	181	91	66.7	101.0	57.0
		(1.19)	(12)	(19)	(0.058)	(39)	(21)	(0.123)	(12)	(56)	(0.17)	(51)	(21)	(26.1)	(17)	(19)	(8.4)	(47)	(24)
Terrington	2010	9.2	11.1	6.7	0.459	0.936	0.303	0.664	0.881	0.434	1.735	2.096	1.243	184	236	111	71.5	109.4	57.9
		(1.18)	(4)	(40)	(0.104)	(4)	(40)	(0.109)	(10)	(56)	(0.2)	(58)	(42)	(35)	(32)	(47)	(9)	(47)	(8)
	Mean	9.6	12.2	6.6	0.480	0.658	0.327	0.515	0.741	0.307	1.602	2.066	1.057	194	274	109	76.0	110.1	64.1
	h^2	0.39			0.51			0.37			0.50			0.43			0.62		

How variety yields and yield components have changed with date of introduction

When regression analysis was carried out on the yields of all varieties tested in the 15 experiments against their year of introduction, significant (P<0.05) positive linear relationships were found for 13 of the 15 experiments (Table 13). No improvements were found by fitting quadratic relationships. The sites where there was no significant relationship between yield and year of introduction were both carried out in 2010 and were Clopton (P = 0.053; R^2 = 0.04) and Newton (P = 0.099; R^2 = 0.05) (Table 13). On average over all sites, 2010 gave the lowest yields, with a fitted yield for year 2000 (the yield of a variety introduced in 2000 AD, predicted from the data) of 8.31 t/ha, compared to an average year 2000 fitted yield over all experiments in all years of 9.86 t/ha.

Where significant relationships were found, the yield improvement with date of introduction varied from 0.186 t/ha/decade (s.e. = 0.078) at Langton in 2010 to 0.633 t/ha/decade (s.e. = 0.076) at Newton in 2008 (Table 13). The average slope of all significant relationships was 0.440 t/ha/decade.

Table 13. Slopes and intercepts (yield in 2000) of variety yields fitted to their year of variety introduction and a summary of percent area lodged at harvest for in each of fifteen variety trials. Experiments had 49 varieties in 2007 and 64 in 2008, 2009 and 2010.

Year	**Site**	**Parameters for Yield Trends**					**Leaning plus lodging**		
		Yield in 2000 (fitted)	*se*	*Change in yield (slope)*	*se*	*R^2* #	*Mean*	*Max*	*Min*
		(t/ha@85% DM)		*(t/ha/decade)*		(%)	*(%)*	*(%)*	*(%)*
2007	Framlingham	8.77	0.079	0.461	0.0840	28	60	100	3
	Grantchester	8.35	0.072	0.607	0.0756	54	-	-	-
	Woolpit	9.97	0.112	0.372	0.1170	14	1	28	0
2008	Clopton	13.80	0.118	0.517	0.0988	19	-	-	-
	Langton	10.00	0.094	0.463	0.0789	31	-	-	-
	Newton	11.88	0.091	0.633	0.0760	39	21	97	0
	Terrington	10.92	0.087	0.606	0.0728	42	2	45	0
2009	Clopton	12.30	0.101	0.400	0.0845	20	-	-	-
	Langton	10.20	0.085	0.498	0.0708	36	1	15	0
	Newton	9.69	0.089	0.370	0.0740	19	0	0	0
	Terrington	8.74	0.067	0.357	0.0559	29	7	100	0
2010	Clopton	10.03	0.067	0.110	0.0562	4	0	0	0
	Langton	9.74	0.095	0.186	0.0775	7	1	40	0
	Newton	6.09	0.082	0.113	0.0678	5	0	0	0
	Terrington	7.40	0.059	0.249	0.0497	26	12	100	0

#trends at Clopton 2010 and Newton 2010 are not statistically significant.

Lodging occurred in a number of experiments, with the most significant lodging occurring at Framlingham in 2007 (Table 13). Since it was generally older, taller varieties that suffered more from lodging, effects of lodging on the slopes of the relationships were investigated. It was found that although excluding these varieties from the analysis did result in a slightly reduced slope, the effect was not significant so these varieties were retained in the analysis.

Following cross-site analysis to produce weighted mean yields for all varieties, the overall relationship between yield and year of introduction was highly significant ($P<0.001$; $R^2 = 0.36$), with the rate of yield improvement over time of 0.39 t/ha/decade. However, as described in Section 4.1, the 64 varieties included UK, European and International varieties bred for a number for purposes. Therefore, further analysis was restricted to UK varieties, and bread-making and feed subsets were examined separately.

When the yield trend with year of introduction was examined for all UK feed varieties (30 varieties introduced between 1953 and 2008), the slope was the same as when all varieties had been examined (0.39 t/ha/decade), but the variation accounted for was higher (Figure 2.a; $R^2 = 0.77$). The feed variety subset was then restricted further to include only 'Landmark' varieties (11 varieties; for explanation of landmark varieties see Section 3.2.1), in order to represent varieties which were widely adopted by growers. The relationship between yield and year of introduction for the Landmark feed varieties was steeper than that of all feed varieties at 0.52 t/ha/decade and accounted for more of the variation ($R^2 = 0.89$; Figure 2.b).

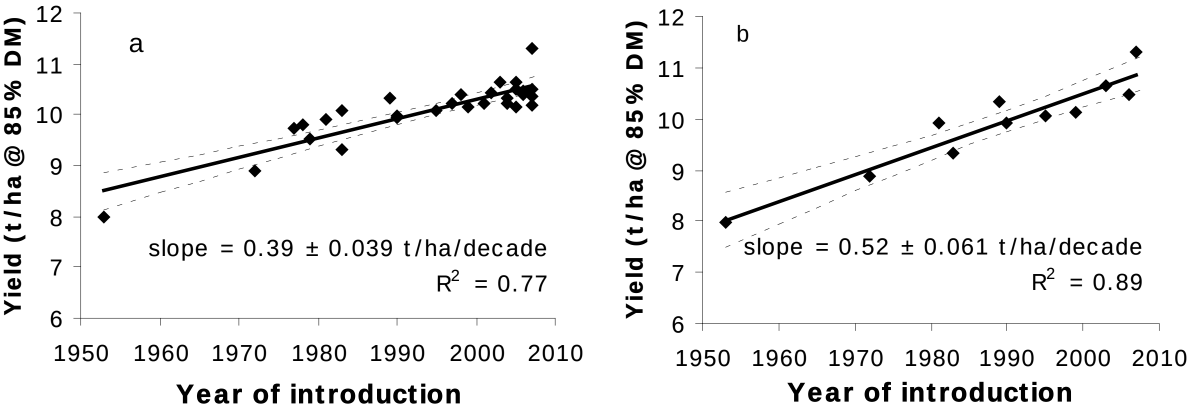


Figure 2. Weighted mean grain yields (diamonds) of: a. all UK feed varieties; and b. 'landmark' feed (including soft 'biscuit' wheats) varieties, introduced between 1953 and 2007, and grown in 15 experiments in Eastern and North East England between 2007 and 2010. Linear trends (black line), 95% confidence limits (dotted lines), mean trends, their standard errors and variance accounted for are all shown.

Carrying out the same regression analysis using all UK bread-making varieties (17 varieties introduced between 1964 and 2008) gave a steeper increase than the feed variety analysis (0.54 t/ha/decade; Figure 3.a). Further restricting the bread-making subset to include just the 9 Landmark varieties meant the rate of yield improvement increased to 0.62 t/ha/decade with 96% of the variation accounted for (Figure 3.b). However, the fitted yield for year 2000 of the Landmark bread-making varieties was 10.01 t/ha, 0.48 t/ha less than that of the Landmark feed varieties.

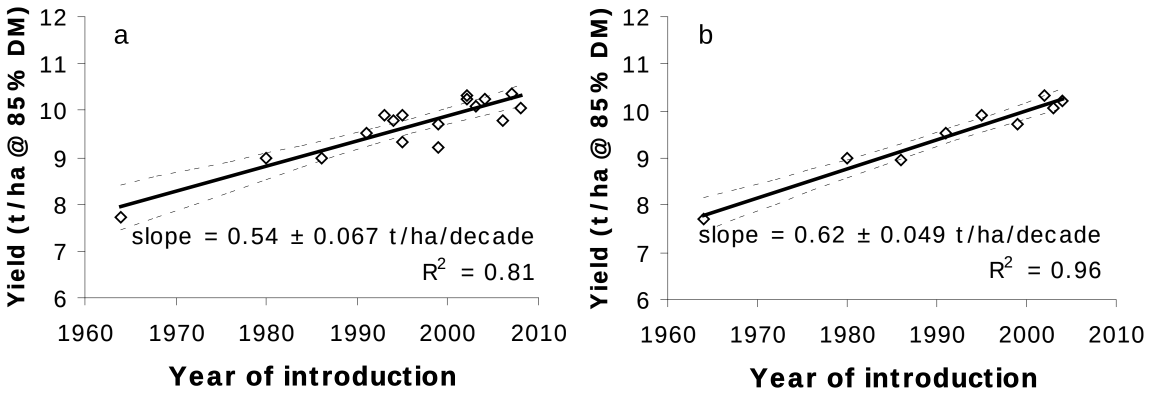


Figure 3. Weighted mean grain yields (diamonds) of: a. all UK bread-making varieties; and b. 'landmark' bread-making varieties, introduced between 1964 and 2008, and grown in 15 experiments in Eastern and North East England between 2007 and 2010. Linear trends (black line), 95% confidence limits (dotted lines), mean trends, their standard errors and variance accounted for are all shown.

Further analysis was carried out to determine which components of yield had improved to cause the yield trends in both the feed and bread-making varieties. Yield can be analysed using different approaches; it can be thought of as the product of total crop biomass (t/ha @ 100% DM) and harvest index, or as the product of the number of ears per m^2, the number of grains per ear and the individual grain weight (equivalent to TGW). The weighted means of these components were calculated using a cross-site analysis excluding Clopton, where the majority of these measurements, apart from thousand grain weight, had not been collected.

In the case of the Landmark feed varieties, there was a linear increase of 0.31 t/ha/decade in the total biomass (t/ha @ 100% DM) of the crop (Figure 4.d), and an increase in harvest index which appears to be slowing (Figure 4.e); a quadratic curve fitted significantly better than a linear relationship with year of introduction. The alternative analysis showed the yield trend to be due to a highly significant ($P<0.001$) increase in the number of grains per ear with year of introduction (R^2 = 0.74) with an increase of over 2 grains per ear per decade (Figure 4.b). The number of fertile ears also increased significantly with year of introduction, by 12.7 ears/m^2/decade, although this relationship was not as strong as that of the number of grains per ear (R^2 = 0.43; Figure 4.c). There was no relationship between thousand grain weight and the year of introduction (Figure 4.a).

A further approach to yield analysis is to consider the life cycle in three phases (foundation, construction and production), to examine the duration and growth rates of construction and production, and then to regard yield as the outcome of production growth, plus a redistributed portion of construction growth, often explained by WSC at GS61 (Beed *et al*. 2007). Foundation and construction phases will be considered in Section 0. However, there were no relationships between the duration of the production phase (GS61-87) or dates of GS61 or 87 and the year of introduction (Figure 7.a-c.). A similar result was found when all 64 varieties were examined so it can be inferred that the yield trends were related to increased growth rates (see Section 0) in the construction or production phases and to redistribution (see below).

When the yield components of the Landmark bread-making varieties were examined, it was found that, unlike the feed varieties, there was no significant relationship between total crop biomass and year of introduction (Figure 5.d) and, as with feed varieties, the increase in harvest index appeared to be slowing with a quadratic curve fitting better than a linear relationship (R^2 = 0.91; Figure 5.e). The only component where there was a significant relationship with the year of introduction was the number of grains per ear, which increased by just over 3 grains/ear/decade (R^2 = 0.60; Figure 5.b). As with the feed varieties, there were no relationships between the duration of the production phase (GS61-87) or dates of GS61 or 87, and the year of introduction (Figure 7).

Grain yield can also be analysed in terms of N uptake and distribution; the total N taken up by the crop is multiplied by the N harvest index and then the product is divided by the grain N concentration. These components were measured in 9 of the 15 experiments (Langton, Newton, Terrington, 2008-2010) and cross-site analysis gave weighted means. Regression analysis showed no significant relationship between total N uptake and the year of introduction in either the landmark feed (Figure 6.a) or bread-making (Figure 6.d) varieties, although there was some evidence in the feed varieties that total N uptake increased with year of introduction ($P = 0.055$). In both the landmark feed and bread-making varieties, there were significant ($P<0.05$) positive relationships between N harvest index and year of introduction (Figure 6.b, e), although the rate of increase of N harvest index in bread-making varieties appears to be slowing, as a quadratic curve fitted significantly better to this relationship than a linear relationship. As would be expected from an increasing N harvest index but no increase in the total amount of N taken up by the crop, grain N concentrations were found to be decreasing linearly over time in both the landmark feed and bread-making varieties (Figure 6.c, f). However, the decline was steeper for the feed varieties (0.071% N reduction per decade) than bread-making varieties (0.063% N reduction per decade). When converted to protein concentrations (N*5.7) this decline equates to decreases of 0.40% and 0.36% protein per decade for feed and bread-making varieties, respectively.

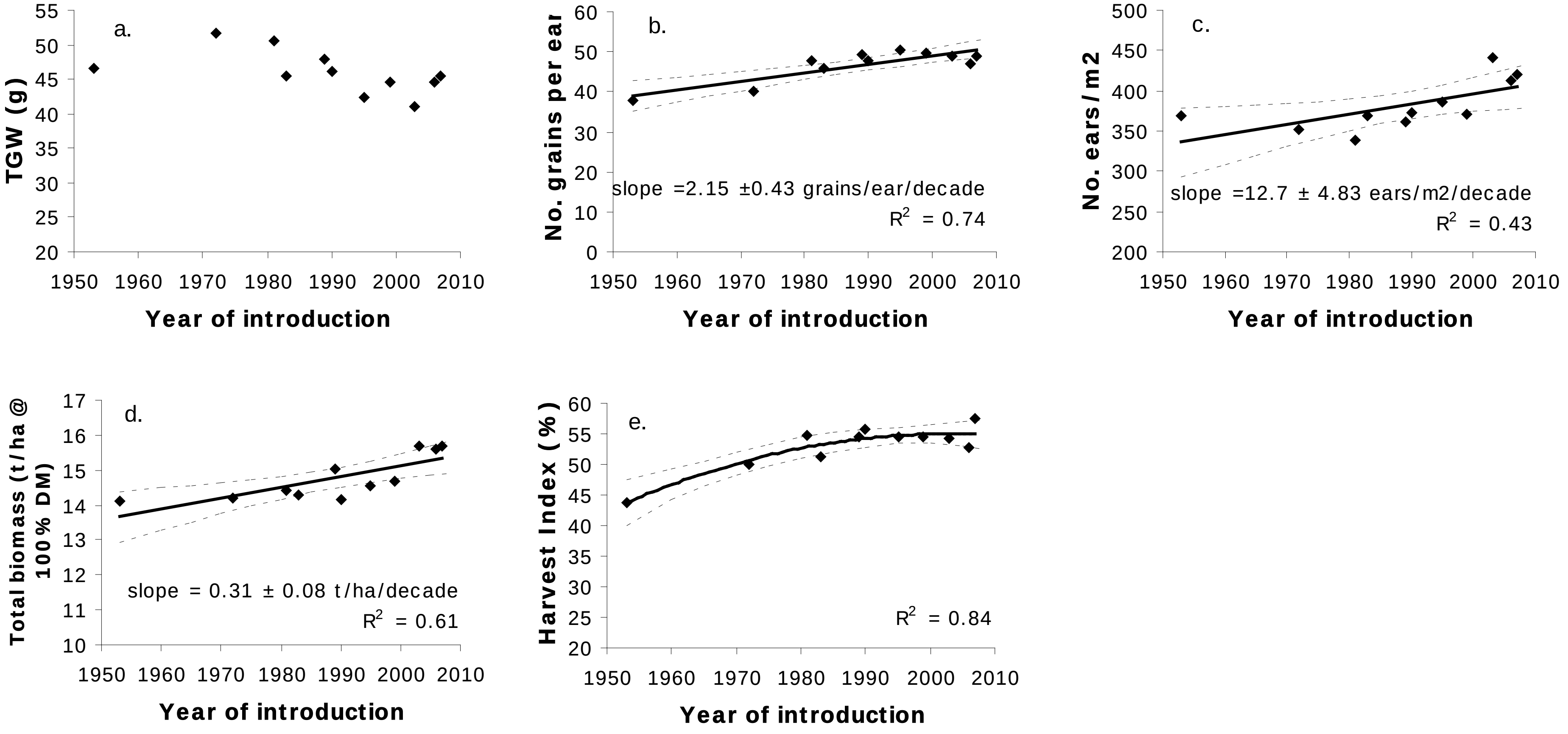


Figure 4. Weighted means (diamonds) of: a. thousand grain weight (TGW; g); b. number of grains per ear; c. number of ears per m^2; d. total crop biomass (t/ha @ 100% DM); and e. harvest index (%), of 'landmark' feed (including soft 'biscuit' wheats) varieties, introduced between 1953 and 2007, and grown in 15 experiments in Eastern and North East England between 2007 and 2010. Best-fit relationships (black lines), 95% confidence limits (dotted lines), mean trends (if linear), their standard errors and variance accounted for are shown.

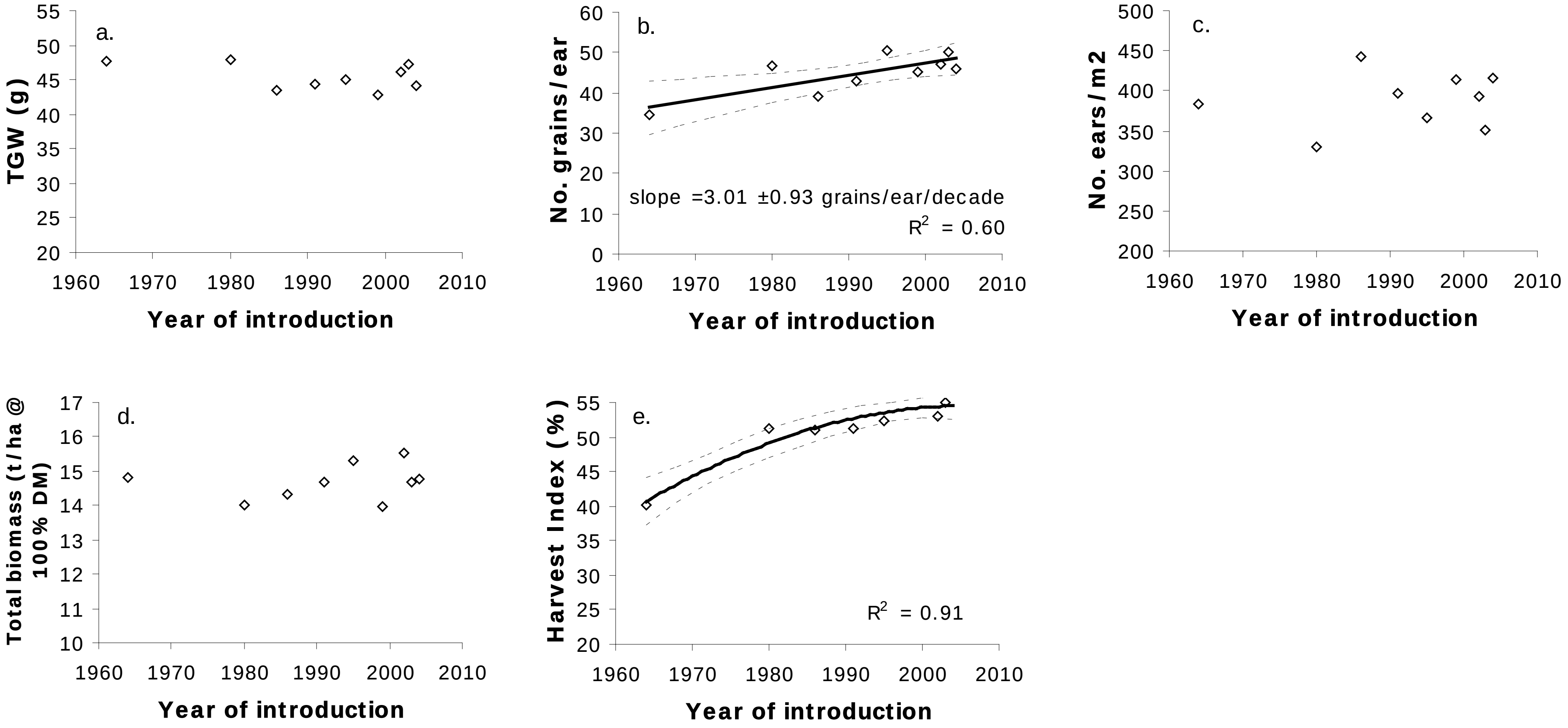


Figure 5. Weighted means (diamonds) of: a. thousand grain weight (TGW; g); b. number of grains per ear; c. number of ears per m^2; d. total crop biomass (t/ha @ 100% DM); and e. harvest index (%), of 'landmark' bread-making varieties, introduced between 1964 and 2008, and grown in 15 experiments in Eastern and North East England between 2007 and 2010. Best-fit relationships (black lines), 95% confidence limits (dotted lines), mean trends (if linear), their standard errors and variance accounted for are shown.

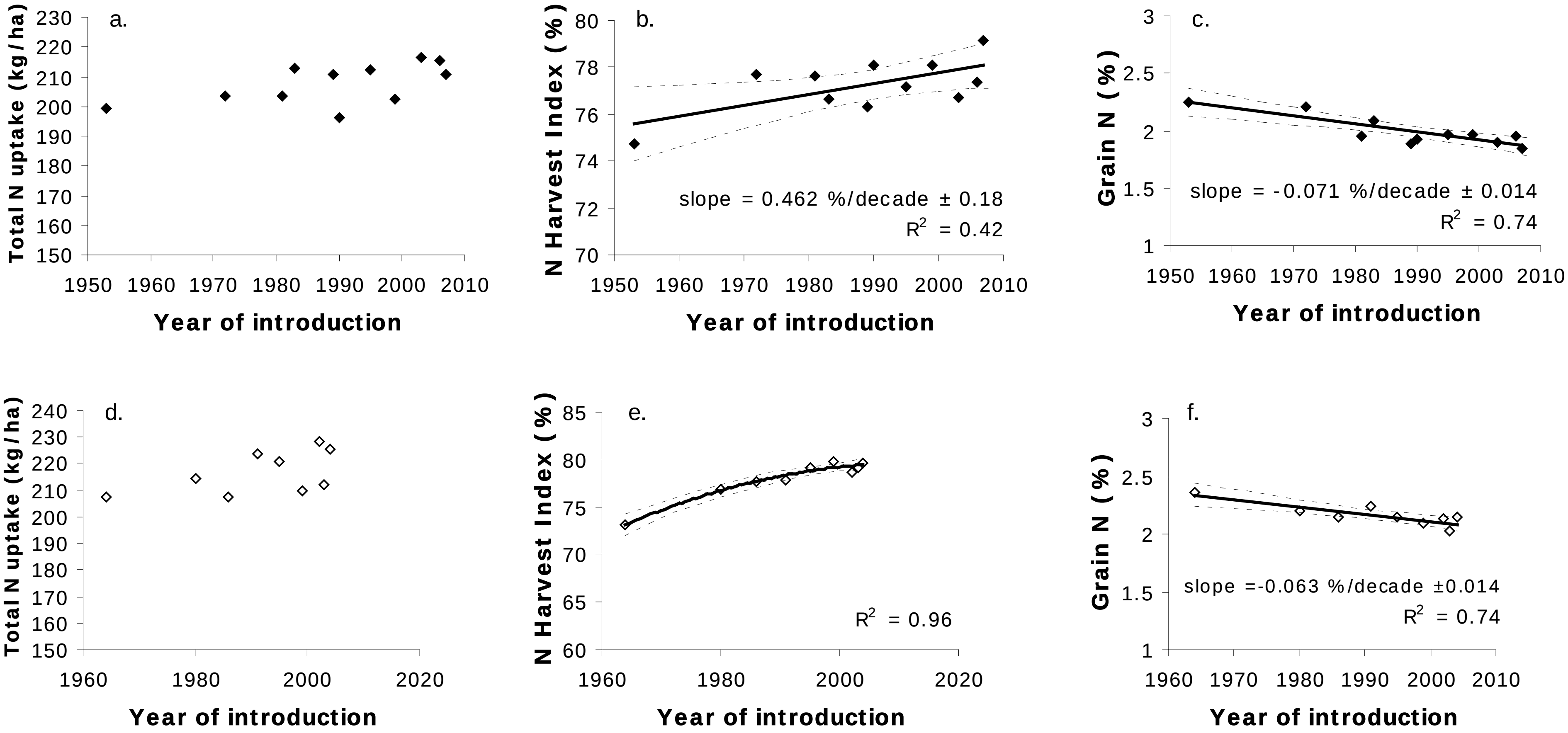


Figure 6. Weighted means (diamonds) of: a. and d. Total Nitrogen (N) taken up by the crop (kg/ha); b. and e. N harvest index (%); and c. and f. grain N (%), of 'landmark' feed (including soft 'biscuit' wheats) (a-c) and bread-making (d-f) varieties, introduced between 1964 and 2008, and grown in 9 experiments in Eastern and North East England between 2008 and 2010. Best-fit relationships (black lines), 95% confidence limits (dotted lines), mean trends (if linear), their standard errors and variance accounted for are shown.

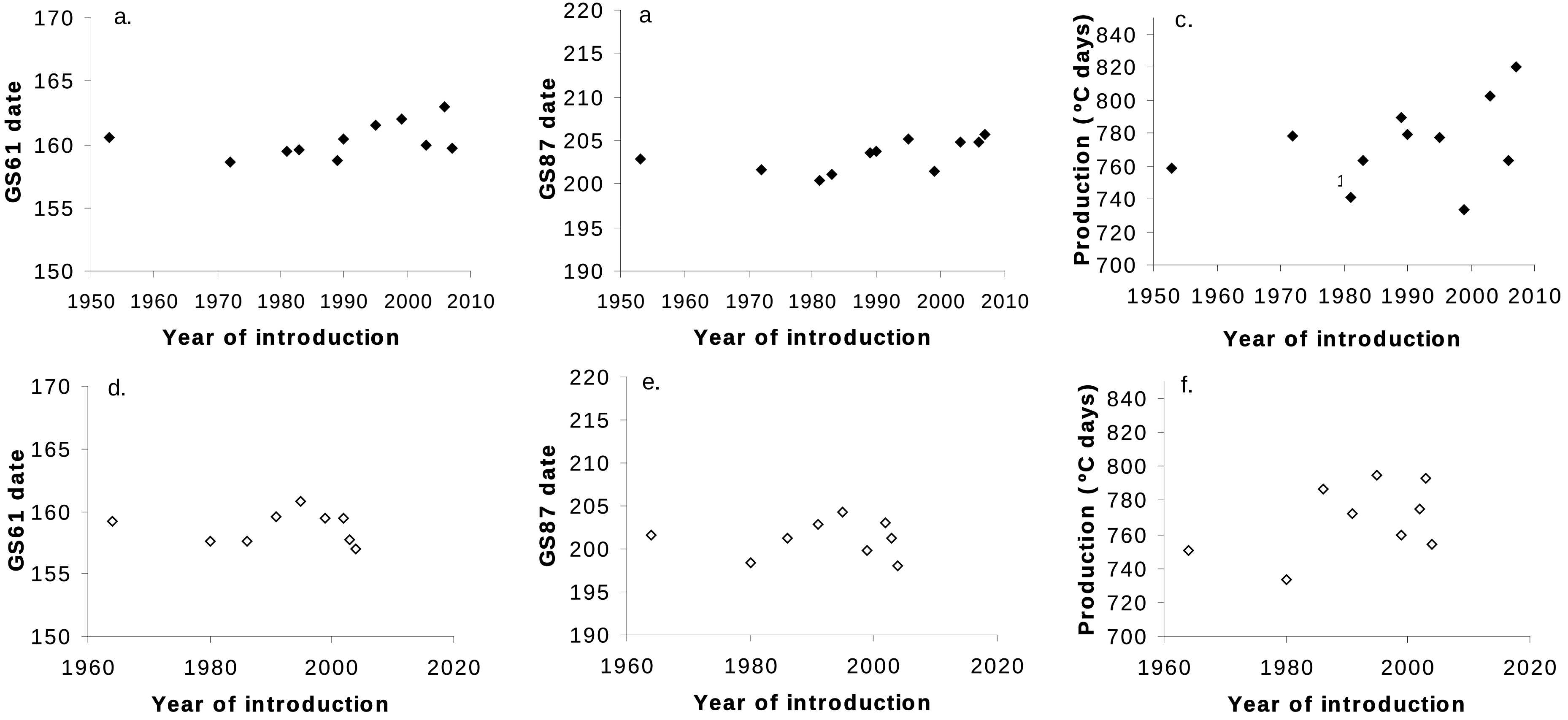


Figure 7. Weighted means (diamonds) of: a. and d. date of GS61 (Julian days); b. and e. date of GS87 (Julian days); and c. and f. duration of the production phase (GS61-87; ºC days), of ‘landmark’ feed (including soft ‘biscuit’ wheats) (a-c) and bread-making (d-f) varieties, introduced between 1964 and 2008, and grown in 9 experiments in Eastern and North East England between 2008 and 2010. No relationship was significant.

As well as N analyses, stem reserves (water soluble carbohydrates; WSC) were measured in the same 9 experiments at flowering. There were significant ($P<0.05$) positive relationships between WSC (g/kg) and year of introduction in all 64 varieties (data not shown), and in landmark feed varieties and landmark bread-making varieties (Figure 8). The relationship of the landmark bread-making varieties showed a linear increase of 14.6 g/kg WSC per decade ($R^2 = 0.59$; Figure 8.b.). The WSC of the landmark feed varieties also showed an increase, but this appears to be slowing as a quadratic relationship fitted better than a linear relationship (Figure 8.a.). When WSC was examined on a per area basis, similar increases were found, but there was no effect of year of introduction on the amount of WSC per stem (data not shown). These data in combination suggest that WSC has increased with year of introduction on a per stem basis and a per area basis mainly through increases in WSC concentration, but that the development of lighter (shorter) stems has been counter-balanced by an increase in stems per m^2.

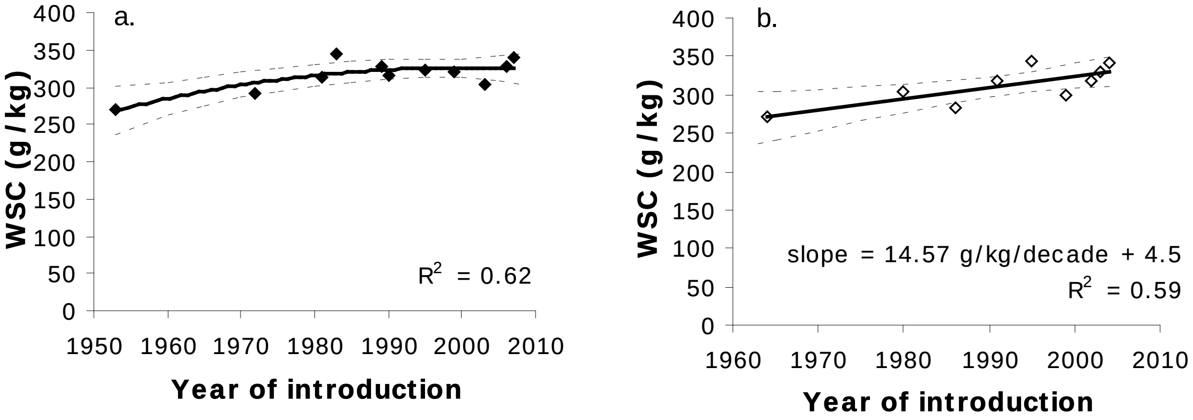


Figure 8. Weighted means of stem water soluble carbohydrates (WSC; g/kg) of ‘landmark’ feed (including soft ‘biscuit’ wheats) (a) and bread-making (b) varieties, introduced between 1964 and 2008, and grown in 9 experiments in Eastern and North East England between 2008 and 2010. Best-fit relationships (black lines), 95% confidence limits (dotted lines), mean trends (if linear), their standard errors and variance accounted for are shown.

Yield stability

Results above show that more recently introduced varieties gave higher yields on average. However, an important aim of breeding for the future, as well as increasing yields, may be to ensure that yields are stable over environments. Thus, two measures of stability were used to compare the varieties.

Firstly, coefficients of variation (CV) were calculated from the yields of each variety from all 12 experiments carried out in 2008-2010 (Figure 9). On average, the CV for a variety over these 12 experiments was 21.6%. Although variable, Figure 9 shows that varieties with higher yields tended to be less stable (higher CV). Variety 19 Alchemy, the 8th highest yielding variety, had the highest

CV at 25.9%, whilst the highest yielding variety (5 Oakley) gave a CV of 22.2%, only slightly higher than that of the lowest yielding variety 64 Bacanora (20.4%; Figure 9).

Secondly, a ‘superiority’ index of varieties was estimated using the method of Lin and Binns (1988). This index takes account of both the absolute yield and the yield stability over environments. A recent study (Jones *et al.*,2010; H. Jones, *pers. comm.*) used this method to investigate the superiority of 19 UK and European varieties released between 1934 and 2000 when grown in four organically- and four conventionally-managed experiments in England between 2005 and 2007. On average, yields at the organic sites were 44% lower than those at the conventional sites (Jones *et al.*, 2010), but variety superiority was better indicating smaller yield differences in variety performance among sites; the average index over the organic experiments was 0.53 and over the conventional experiments was 1.05. The range in variety superiority index was 0.03 to 4.10 at the conventional sites and 0.09 to 1.17 at the organic sites.

The superiority test was carried out on yield results from the 2008 – 2010 experiments, as not all 64 varieties were tested in 2007. The average stability coefficient was 0.29, lower (better) than that found in the conventional experiments from the work described above. The analysis showed that variety 5 (Oakley) was the best variety (lowest stability coefficient;) because it yielded highest in most experiments. Overall, the stability coefficients of the varieties mirrored the yield results, but there were some varieties whose stability coefficient indicated that it had a particularly stable performance over environments (Figure 10). For example, variety 44 (Alixan) gave a very similar yield (9.19 t/ha) to variety 45 (Galahad; 9.18 t/ha), but variety 45 gave a 0.12 lower (better) stability coefficient (Figure 10). Further up the yield scale, variety 4 (Access) and variety 6 (Humber) gave very similar yields (10.32 t/ha) but variety 4 gave a 0.09 lower (better) stability coefficient (Figure 10).

The apparent inconsistency between these two figures shows illustrates conflict between achieving both higher yields and very stable yields across different environments.

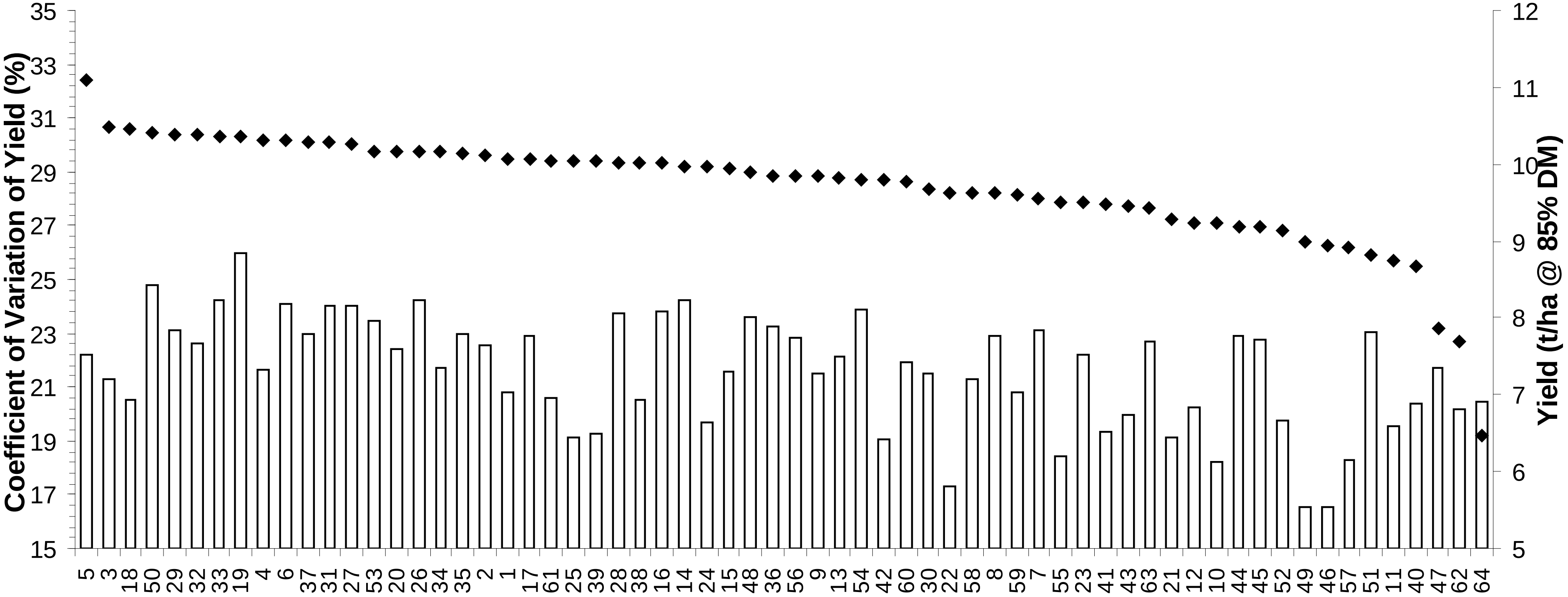


Figure 9. Yield standard deviations of 64 varieties grown in 12 experiments over 3 seasons (2008-2010) and associated weighted mean yields (black diamonds; t/ha @ 85% DM)

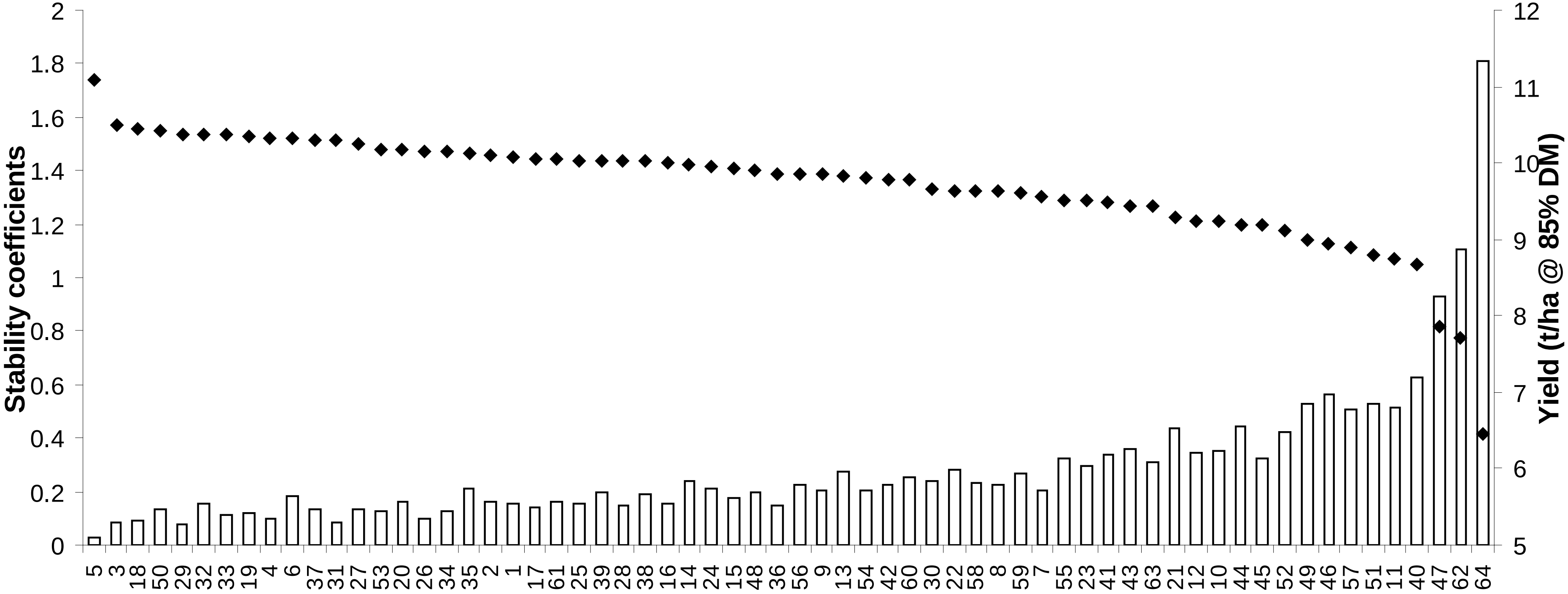


Figure 10. Stability coefficients (white bars; Lin & Binns, 1988) of 64 varieties grown in 12 experiments over 3 seasons (2008-2010) and associated weighted mean yields (black diamonds; t/ha @ 85% DM)

Yield determination

To further analyse how the yields of these varieties are made up, a biplot was constructed from the variety data for all yield components (Figure 11). A biplot results from principal component analysis and can be viewed as a multivariate analogue of a scatter plot. In this case, the data were normalised so that their variation could be viewed on a common scale. The x axis relates to the first principal component (which in this case relates closely to yield) and the y-axis relates to the second principal component. Yield and other variates are represented as vectors (or lines). If the vectors (i.e. lines) of two variates lie in the same orientation then there is high inter-variate correlation; if variate vectors lie at right-angles, then the variates are not correlated, and if variate vectors lie in opposite directions, the variates are inversely correlated. The positions of a variety point in relation to each variate vector relates to its value for that variate.

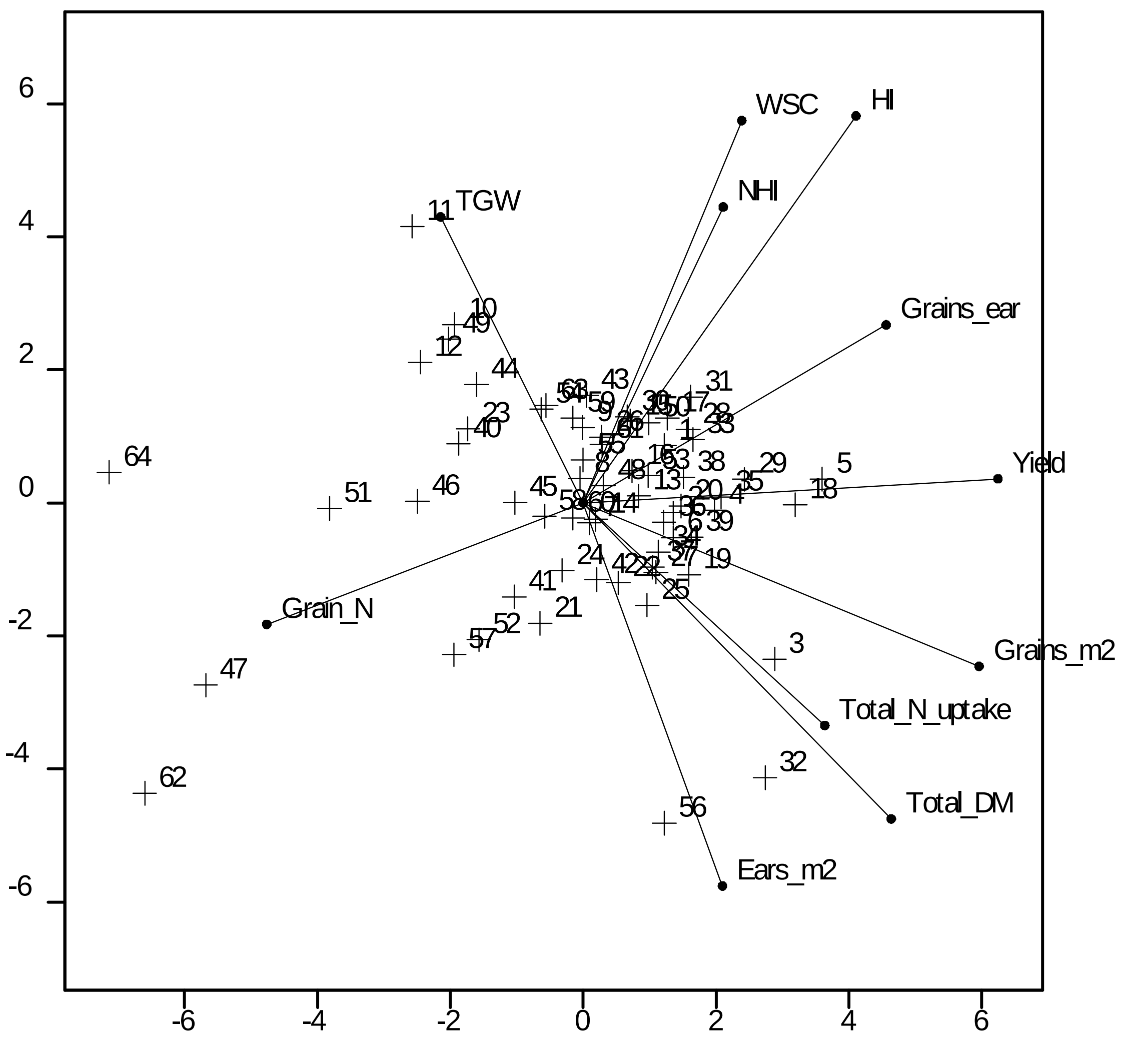
The first biplot (Figure 11) shows that variety 5 (Oakley) has the highest yield as it is furthest along the yield line, with the next two highest yielding varieties identified as 18 (Glasgow) and 3 (Robigus) and the lowest-yielding as 64 (Bacanora). The biplot shows sets of variate vectors that were closely correlated; WSC, harvest index and N harvest index was one set and total crop biomass and total N uptake was another (Figure 11). Although yield was not positively correlated very closely with another variate, it appeared from the biplot that it was more closely related to the numbers of grains per m^2 and per ear than the number of ears per m^2 or particularly TGW (Figure 11). Biplots of landmark feed and bread-making varieties showed similar relationships (Figure 12). Relationships were confirmed through plotting each of these variates against yield; there was no relationship between yield and TGW in either the 64 varieties, or when the landmark bread-making and feed varieties were examined separately. Relationships with grains per m^2 and grains per ear, were highly significant ($P<0.001$) and the relationship with ears per m^2 was significant ($P<0.05$) when all 64 varieties were examined, but not for the landmark feed and bread-making varieties (Figure 14). Since grain numbers are determined by anthesis, growth analysis data from anthesis are used in later sections of this report to explore more thoroughly the factors that determine the number of grains per m^2.

There did appear to be a strong negative relationship between yield and grain N% from the biplot, with bread-making varieties such as 62 (Maris Widgeon) having a high grain N% and low yield through a low harvest index (Figure 11, Figure 12). This was again confirmed through plotting grain N% against yield (Figure 15 e and f.) where highly significant ($P<0.001$) negative relationships were found for both the whole variety set and landmark varieties.

The biplot also shows how different varieties make up their yield. For example, variety 32 (Gatsby) has a similar yield to variety 31 (Zebedee) but they make up their yields rather differently. Gatsby has a high number of ears per m^2 and so it’s total crop biomass is high, but it has a low TGW and below average harvest index. Zebedee, in contrast, has a high harvest index, above average TGW and below average number of ears per m^2 (Figure 11). Unlike with the number of ears per m^2, there do not appear to be any varieties with particularly high numbers of grains per ear compared to the majority.

It appears that the varieties with higher TGW are generally French bread-making varieties e.g. 10 (Andalou), 11 (Royssac), 12 (Exotic), 44 (Alixan), 49 (Cezanne) which have higher than average grain N concentrations but lower than average yields (Figure 11). When varieties were further examined using a biplot of the durations of the three development phases and yield (Figure 16), these French varieties could again be seen as having below average yield, but they were also earlier than most with below average foundation, construction and production phase durations.

Biplot analysis of the development phases and yield of all 64 varieties showed that yield was closely related to the duration of the production phase and also the foundation phase, but not to the duration of the construction phase (Figure 16). When biplots were plotted for the landmark feed and bread-making varieties, however, yield did not appear to be as well related to the production phase duration but was closely related to the foundation duration (Figure 17). The relationships were investigated further by plotting each phase duration against yield (Figure 18). The best relationships were found between yield and foundation phase for both the 64 variety set and the bread-making and feed landmark varieties. There was also a significant ($P<0.05$) relationship between yield and production phase duration, although this was only significant when all 64 varieties were examined, and not for just the landmark varieties, despite an apparent relationship in the landmark feed varieties (Figure 18 e and f.) with variety 5 (Oakley) having the longest production duration. In both the production and foundation duration relationships for all 64 varieties, and the dates of growth stages associated with these phases, two varieties were later (Figure 19) and had longer durations (Figure 18) than would be expected from their yields. These varieties were 47 (Capelle Desprez) and 62 (Maris Widgeon), both old (pre 1965) UK varieties. When the construction phase duration was plotted against yield there was no relationship with all 64 varieties, but there was a significant ($P<0.05$) negative linear relationship with the landmark feed varieties (Figure 18 c and d.). If the dates of the growth stages used to calculate the duration of the construction period of all 64 varieties are examined (GS31 and 61; Figure 19 a and c.) significant ($P<0.001$) positive linear relationships are found with yield, and these relationships have the same slope. Thus, later developing varieties gave higher yields, but without any relationship with construction duration.



No.	Name	No.	Name	No.	Name	No.	Name
1	Equinox	17	Ambrosia	33	Hyperion	49	Cezanne
2	Cordiale	18	Glasgow	34	Gulliver	50	Savannah
3	Robigus	19	Alchemy	35	Timber	51	Maris Huntsman
4	Access	20	Istabraq	36	Consort	52	Paragon
5	Oakley	21	Soissons	37	Battalion	53	Riband
6	Humber	22	Sankara	38	Marksman	54	Norman
7	Malacca	23	Mendel	39	Musketeer	55	Buster
8	Dover	24	Mercato	40	Recital	56	Spark
9	Beaver	25	Deben	41	Hereward	57	Mercia
10	Andalou	26	Xi19	42	Apache	58	Cadenza
11	Royssac	27	Solstice	43	Caphorn	59	Hobbit
12	Exotic	28	Gladiator	44	Alixan	60	Hustler
13	Rialto	29	Brompton	45	Galahad	61	Longbow
14	Exsept	30	Mascot	46	Avalon	62	Maris Widgeon
15	Einstein	31	Zebedee	47	Cappelle Desprez	63	Virtue
16	Claire	32	Gatsby	48	Haven	64	Bacanora

Figure 11. Principal component biplot of weighted means of varieties (No. 1-64) indicating inter-relationships between yield and yield components. The 1st principal component (x-axis) explains 39.9% of the variation and the 2nd principal component (y-axis) explains 23.48% of the variation.

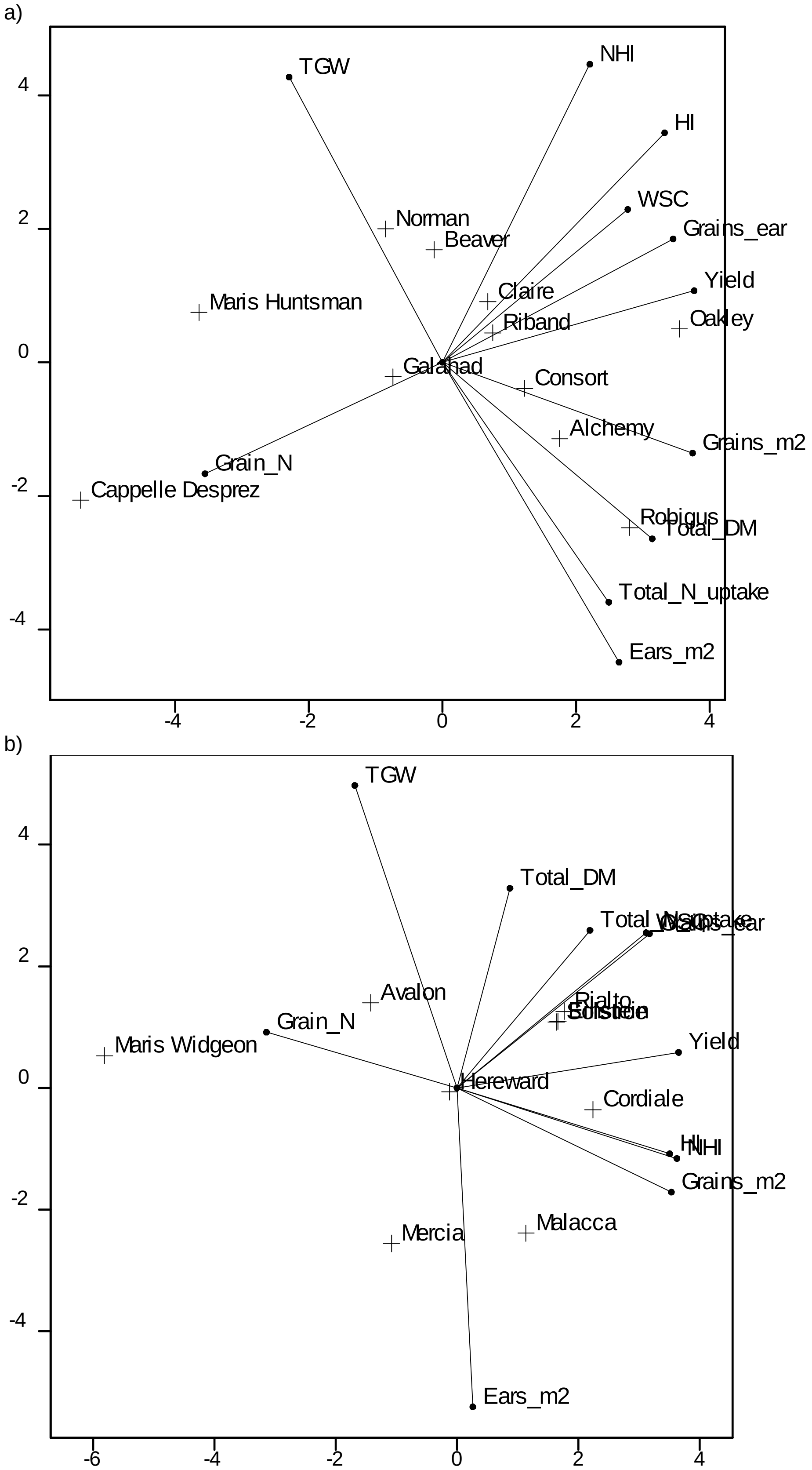


Figure 12. Principal component biplot of weighted means of: a) landmark feed (including soft ‘biscuit’ wheats) varieties (PC1 = 63.5%; PC2 = 18.7%) and b) landmark bread-making varieties (PC1 = 64.3%; PC2 = 21.7%) indicating inter-relationships between yield and yield components. In b, Einstein and Solstice are very close, as are the WSC and Grains/ear vectors.

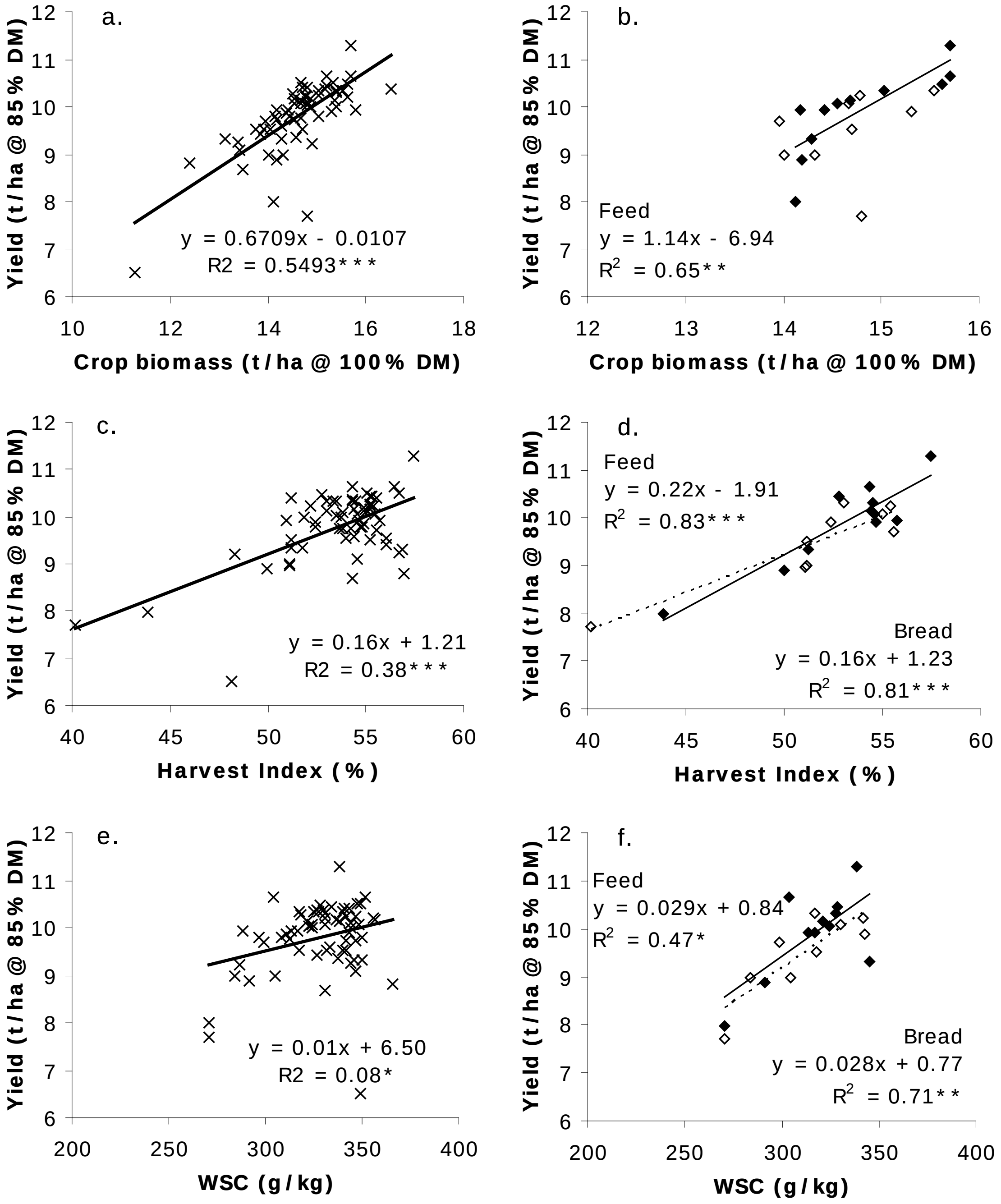


Figure 13. Relationships between weighted mean grain yields and weighted means of: a-b. total crop biomass (t/ha @ 100% DM), c-d. harvest index (%), e-f. stem water soluble carbohydrates (WSC; g/kg DM) for all 64 varieties (X) and for landmark feed (solid diamonds, solid line) and bread-making (open diamonds, dashed line) varieties.

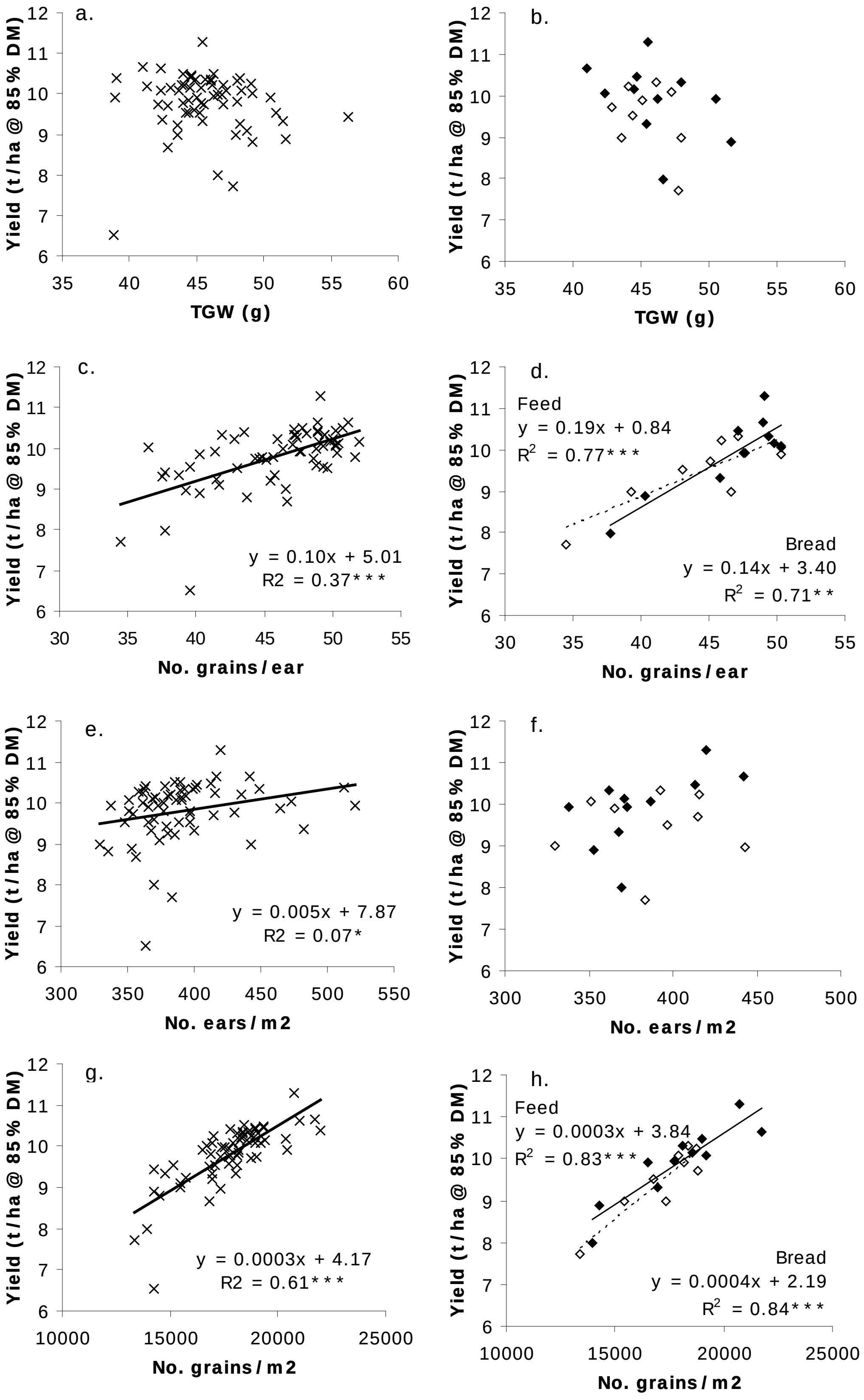


Figure 14. Relationships between weighted mean yields and weighted means of: a-b. thousand grain weight (TGW; g), c-d. grains/ear, e-f. ears/m^2, g-h. grains/m^2 for all 64 varieties (X) and for landmark feed (including soft 'biscuit' wheats) (solid diamonds, solid line) and bread-making (open diamonds, dashed line) varieties.

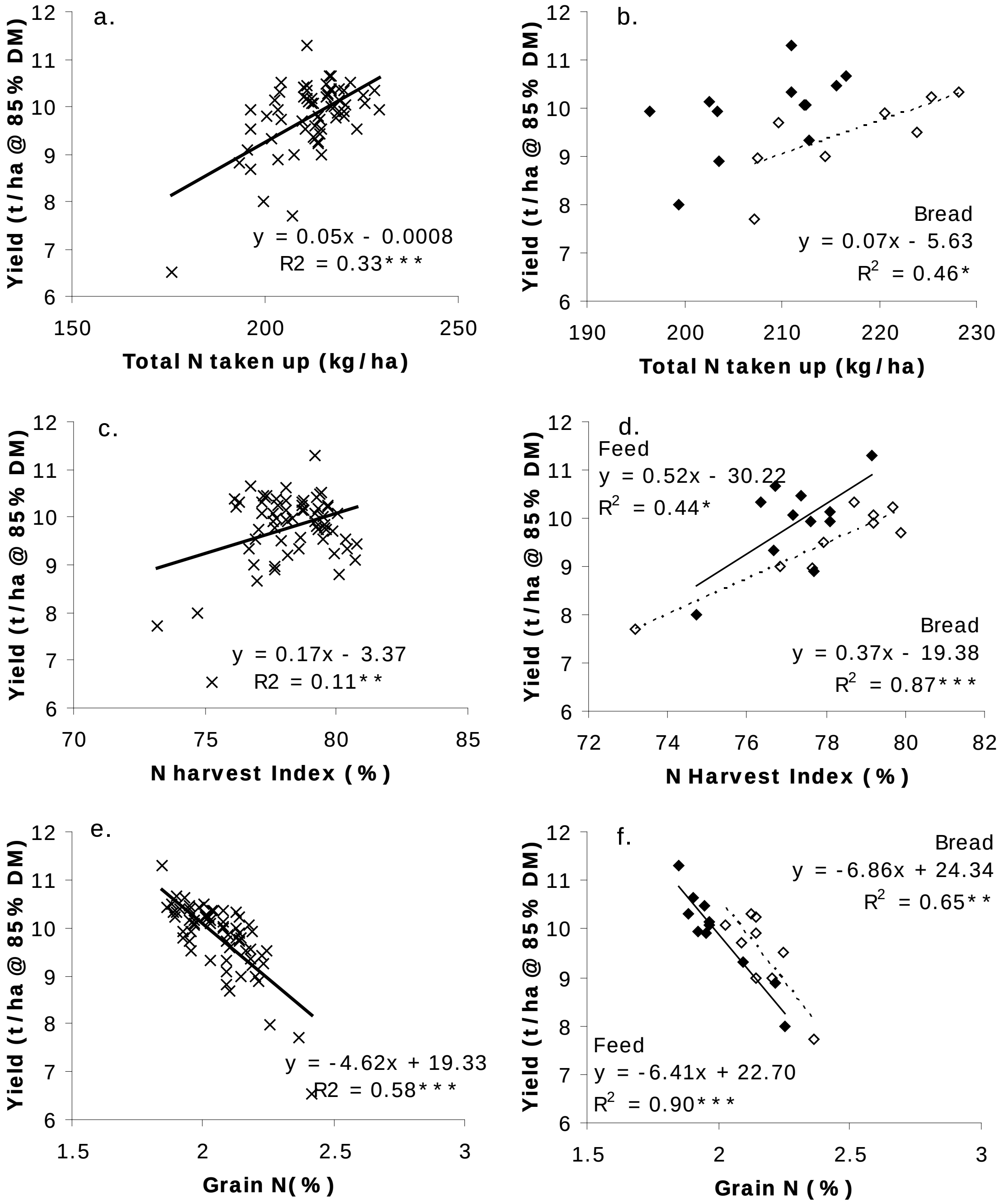
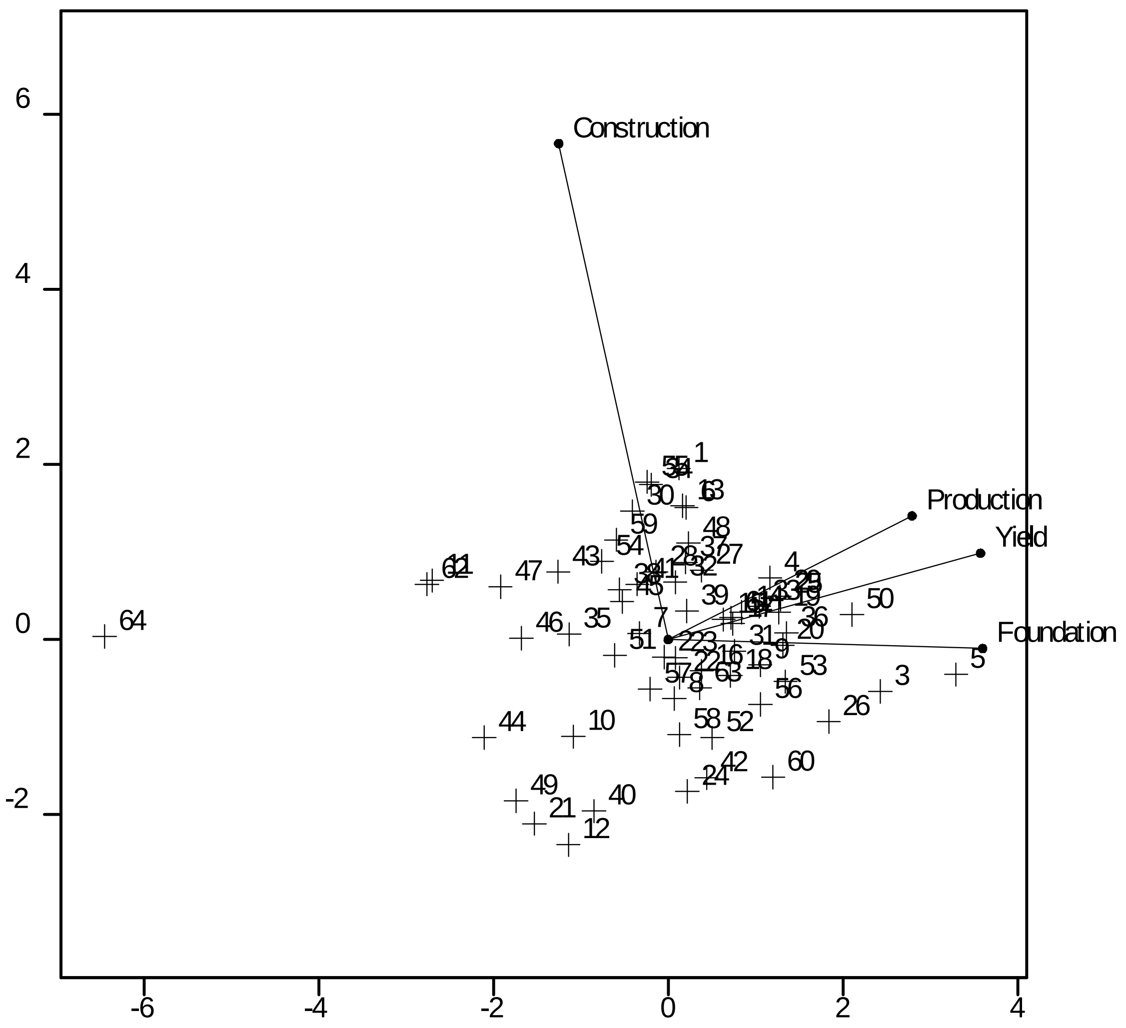


Figure 15. Relationships between weighted mean yields and weighted means of: a-b. total N uptake (kg/ha), c-d. N harvest index (NHI, %), e-f. grain N concentration (%) for all 64 varieties (X) and for landmark feed (including soft 'biscuit' wheats) (solid diamonds, solid line) and bread-making (open diamonds, dashed line) varieties.



No.	Name	No.	Name	No.	Name	No.	Name
1	Equinox	17	Ambrosia	33	Hyperion	49	Cezanne
2	Cordiale	18	Glasgow	34	Gulliver	50	Savannah
3	Robigus	19	Alchemy	35	Timber	51	Maris Huntsman
4	Access	20	Istabraq	36	Consort	52	Paragon
5	Oakley	21	Soissons	37	Battalion	53	Riband
6	Humber	22	Sankara	38	Marksman	54	Norman
7	Malacca	23	Mendel	39	Musketeer	55	Buster
8	Dover	24	Mercato	40	Recital	56	Spark
9	Beaver	25	Deben	41	Hereward	57	Mercia
10	Andalou	26	Xi19	42	Apache	58	Cadenza
11	Royssac	27	Solstice	43	Caphorn	59	Hobbit
12	Exotic	28	Gladiator	44	Alixan	60	Hustler
13	Rialto	29	Brompton	45	Galahad	61	Longbow
14	Exsept	30	Mascot	46	Avalon	62	Maris Widgeon
15	Einstein	31	Zebedee	47	Cappelle Desprez	63	Virtue
16	Claire	32	Gatsby	48	Haven	64	Bacanora

Figure 16. Principal component biplot of weighted means for each variety (No. 1-64) indicating inter-relationships between yield and foundation (GS10 – 31), construction (GS31 – 61) and production (GS61-87) phases of plant development. The 1st principal component (x-axis) explains 50.3% of the variation and the 2nd principal component (y-axis) explains 24.2% of the variation.

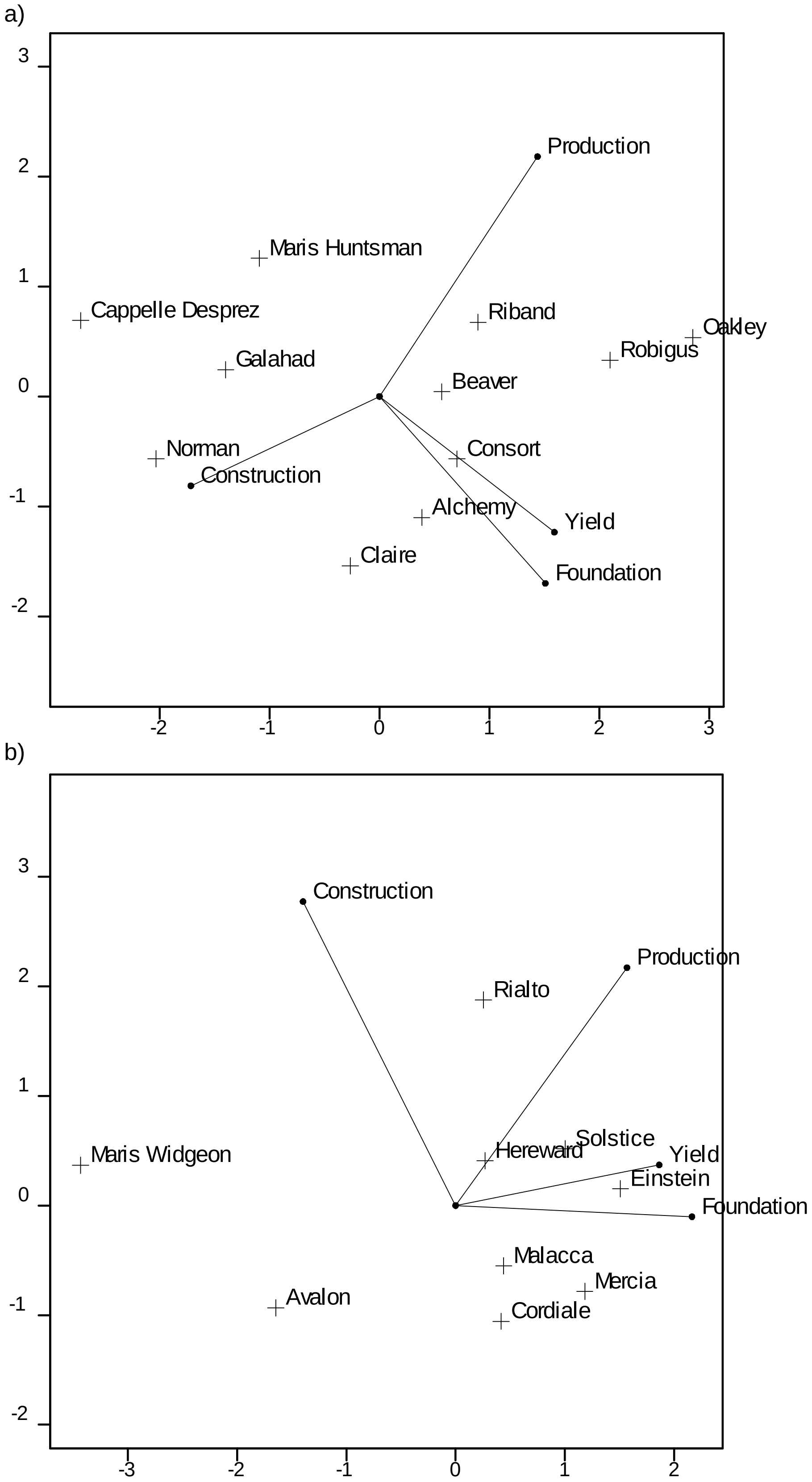


Figure 17. Principal component biplot of weighted means for: a) landmark feed (including soft ‘biscuit’ wheats) varieties (PC1 = 63.5%; PC2 = 18.7%) and b) landmark bread-making varieties (PC1 = 61.5; PC2 = 21.9%) indicating inter-relationships between yield and foundation (GS10 – 31), construction (GS31 – 61) and production (GS61- 87) phases of plant development.

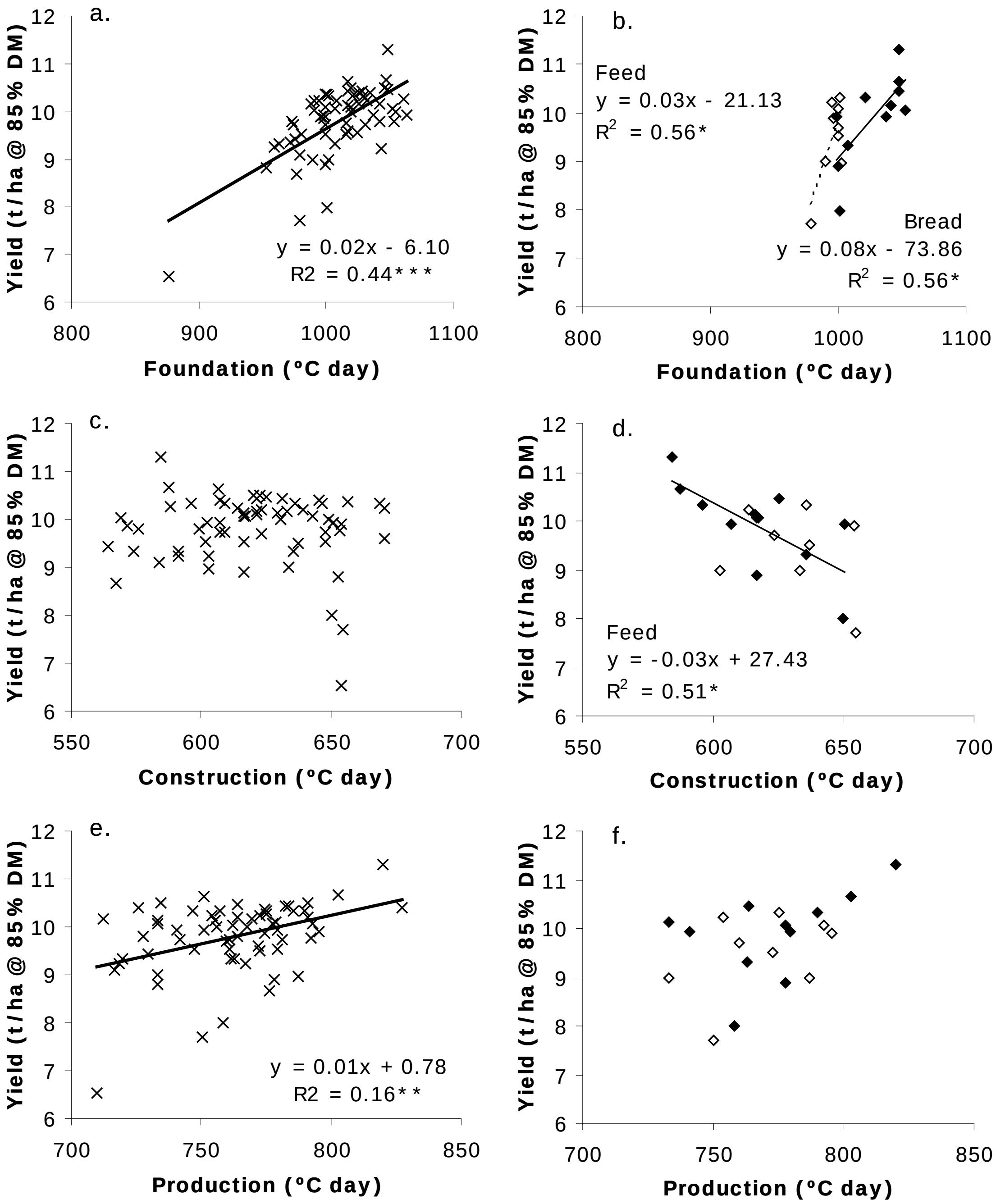


Figure 18. Relationships between weighted mean yields and weighted means of: a-b. foundation phase duration (^{o}C day), c-d. construction phase duration (^{o}C day), e-f. production phase duration (^{o}C day) for all 64 varieties (X) and for landmark feed (including soft 'biscuit' wheats) (solid diamonds, solid line) and bread-making (open diamonds, dashed line) varieties.

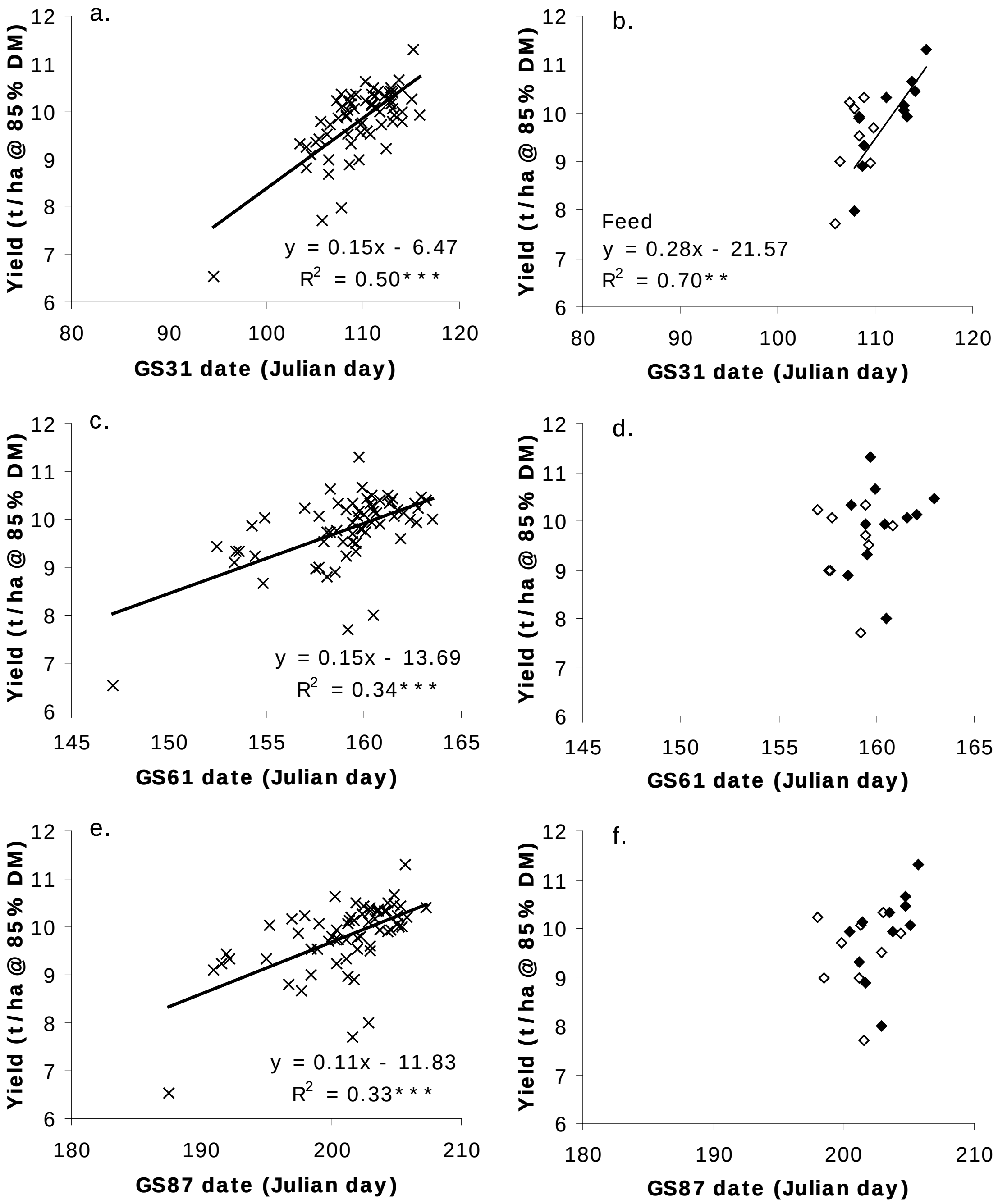


Figure 19. Relationships between weighted mean yields and weighted means of: a-b. GS31 date (Julian days), c-d. GS61 date (Julian days), e-f. GS87 date (Julian days) for all 64 varieties (X) and for landmark feed (including soft ‘biscuit’ wheats) (solid diamonds, solid line) and bread-making (open diamonds, dashed line) varieties.

Relationship between yield and major genes

An unbalanced cross-site ANOVA was carried out in order to investigate the effects of major genes controlling photoperiod sensitivity (*Ppd*) and reduced height (*Rht*) on yield and yield components (Table 14). Results should be treated with caution because of the low numbers of varieties with certain genotypes. However, the analysis detected highly significant ($P<0.01$) effects of *Ppd1* and *Ppd2* on all yield components apart from stem WSC. *Ppd1* or *Ppd2* alleles were associated with lower yields and grain numbers per ear, and increased TGW and grain N (Table 14). These results are as expected since varieties with *Ppd1* or *Ppd2* alleles are generally the French bread-making varieties identified as having these traits at the outset.

The *Rht2* allele related positively ($P<0.05$) to all yield components except total crop biomass. *Rht1* and *Rht2* varieties were associated with higher yields, a higher harvest index, a higher concentration of stem water soluble carbohydrates, a higher number of grains per ear, a higher N harvest index but a lower grain N (Table 14). *Rht1* led to a significantly higher number of ears per m^2 (432) than *rht* (tall controls) (414), but the *Rht2* allele was associated with the fewest ears (384 $/m^2$; Table 14.).

Table 14. Effects of *Ppd* and *Rht* genes on yield and yield components. Numbers of varieties with each allele and former annotation for these alleles are indicated in the first column. Different LSDs should be used when comparing genotypes as follows: min. rep. for comparing genotypes with the fewest varieties; Min.-max. for comparing genotypes with the most to those with the fewest varieties; max. rep for comparing genotypes with the most varieties.

Genotype (no. varieties)	**Yield (t/ha)**	**Total Biomass (t/ha)**	**HI (%)**	**WSC (g/kg)**	**TGW (g)**	**Grains per ear**	**Ears per m^2**	**N uptake (kg/ha)**	**NHI (%)**	**Grain N (%)**
ppd (53)	9.96	14.85	53.3	330	43.9	46.95	391	208.3	78.5	2.04
Ppd1 (9)	9.15	13.57	54.3	342	46.0	40.68	405.	201.3	80.2	2.16
Ppd2 (1)	9.55	14.06	53.8	343	49.8	39.79	387	211.8	80.2	2.21
Ppd3 (1)	*	*	*	333	*	*	*	189.9	77.7	2.09
LSD (max. rep.)	0.067	0.107	0.26	4.6	0.26	0.389	4.6	1.91	0.28	0.016
LSD (min.-max.)	0.148	0.235	0.57	12.5	0.58	0.858	10.2	5.18	0.75	0.044
LSD (min. rep.)	0.193	0.306	0.75	17.9	0.76	1.117	13.3	7.44	1.08	0.063
rht (8)	9.02	14.60	48.9	289	44.1	40.19	414	207.1	77.7	2.19
Rht1 (8)	9.59	14.56	53.0	335	42.5	43.10	432.	201.8	78.4	2.07
Rht2 (47)	9.97	14.63	54.2	338	44.6	47.16	384	207.8	79.0	2.04
LSD (max. rep.)	0.072	0.121	0.24	4.7	0.29	0.415	4.7	2.05	0.30	0.017
LSD (min.-max.)	0.083	0.141	0.28	5.1	0.34	0.487	5.6	2.26	0.33	0.019
LSD (min. rep.)	0.099	0.169	0.34	6.1	0.42	0.582	6.6	2.68	0.39	0.022

Analysis of grains per m^2 based on measurements at anthesis

It has been shown that the number of grains per unit land area in wheat crops is strongly associated with the DM accumulated in the ear at around anthesis, as described above.

The following model analyses the physiological basis of grain number:

GN = days (GS10-GS61) x CGR x EPI x EFI Eqn 1

where GN = grains/m^2; CGR = crop growth rate in the phase from crop emergence (GS10) to anthesis (GS61) (g/m^2/d); EPI = ear partitioning index (fraction of above-ground DM at GS61 in the ear); and EFI = ear fertility index (grains to ear DM ratio at anthesis, grains/g).

This approach will be used in the following analysis to examine the physiological basis of genetic variation GN amongst the 64 varieties and genetic gains in GN with breeding over recent decades.

The results reported in this section are based on average performance across a sub-set of 8 site-seasons in 2008-10 where the full set of measurements at anthesis was carried out. The relationships between this dataset and the full data set (15 sites-seasons in 2007-10; Figure 20) were both very close ($R^2 > 0.97$), whether comparing amongst all 64 varieties or either of the groups of landmark varieties. Therefore, it is reasonable to assume that the current analysis of anthesis data should explain the basis of the genetic variation found in the full dataset. A further check was carried out for the relationship between DM per ear at anthesis and chaff DM per ear at harvest across all 15 site-seasons. The spike partitioning and ear fertility indices in the following analysis were calculated using ear DM measured at anthesis, so it is important that the latter relates to harvest performance. The relationship (Figure 1.24) indicates the level of confidence that can be placed in anthesis data explaining ear fertility traits. The means of anthesis and harvest measures were similar; however, the slope was <1.0, so anthesis ear DM appeared to over- or under-estimate final chaff DM to some extent, possibly associated with earlier / later flowering varieties. However, since there was no trend for flowering date with year of release, any small errors are unlikely to affect relationships between anthesis growth parameters and year of release.

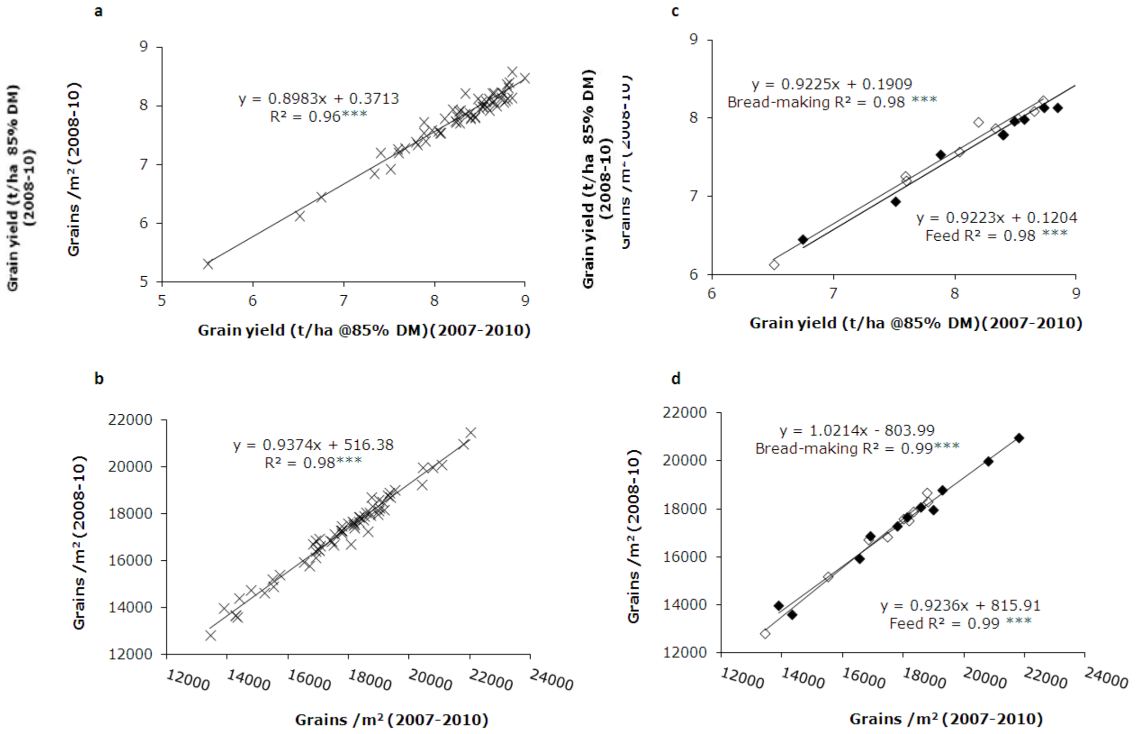


Figure 20. Comparison of mean grain yield or grains/m^2 in 8 site-seasons (2008-10) on the y-axis and 15 site-seasons (2007-10) on the x-axis, for (a and b) all 64 varieties (x) and (c and d) landmark feed (including soft 'biscuit' wheats) (◆) and bread-making (◇) varieties.

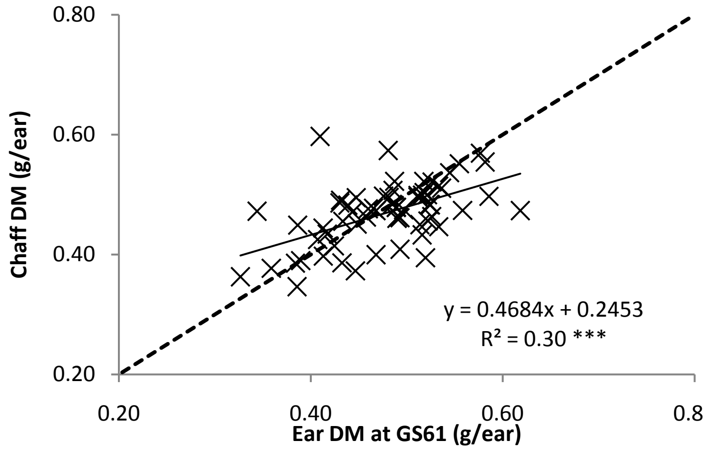


Figure 21. Comparison of DM per ear at anthesis and chaff DM per ear at harvest in 15 site-seasons for 64 varieties.

Grain number and its determinants at anthesis: trends with year of introduction

Confirmation of trends in grain yield and grain number for the dataset with anthesis measurements

Just to confirm the analysis already described, analysis of the eight site-seasons with anthesis data showed very similar linear trends in grain yield with year of introduction (0.32 t/ha per decade amongst all 64 varieties and of 0.41 and 0.49 t/ha per decade in the feed and bread-making landmark varieties) (Figure 22). The same trends were also shown in grains/m^2 (feed: 1,323 grains/m^2 per decade, $R^2 = 0.92$, $P<0.001$; bread-making: 1,231 grains/m^2 per decade, $R^2 = 0.78$, P<0.001), ears/m^2 (feed only: ca. 20 ears/m^2 per decade, R^2 = 0.69, apparent from about 1970 onwards), and grains/ear (feed: 2 grains/ear per decade, R^2 = 0.68, P<0.01; bread-making: 3.1 grains/ear per decade, R^2 = 0.59, P<0.01).

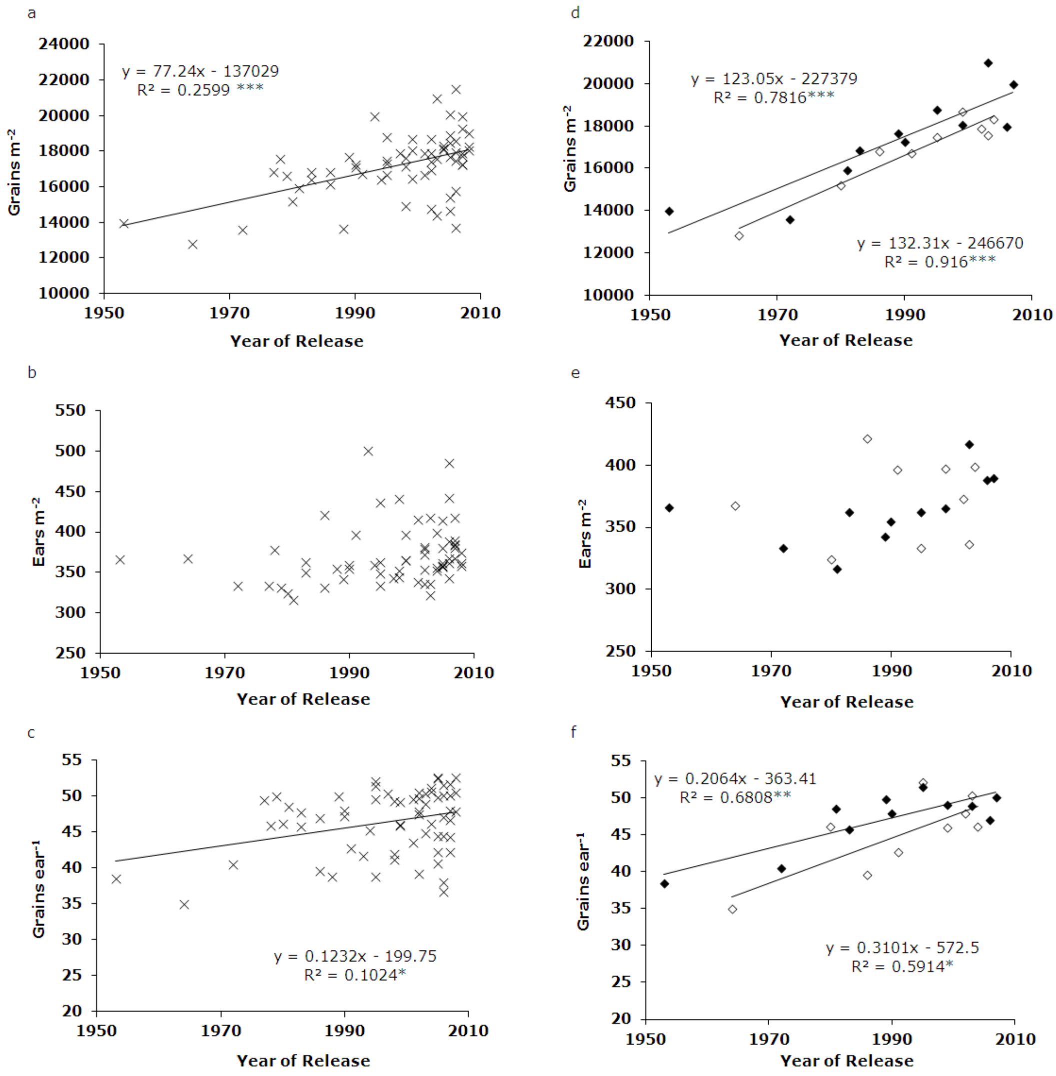


Figure 22. Mean values from 8 site-seasons confirming trends with year of introduction from 15 site-seasons in Figure 4 and Figure 5 in grain yield (a), grains/m^2 (b), ears/m^2 (c) and grains/ear (d) on year of introduction amongst 64 varieties; and e, f, g, and h, respectively, amongst landmark groups of feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties.

Spikelets/ear was measured at 5 sites, and showed no systematic change with year of introduction in either the feed or bread-making landmark varieties. However, there was an increase grains/spikelet in the bread-making landmark wheats (P<0.001), although not amongst the feed wheats (Figure 23).

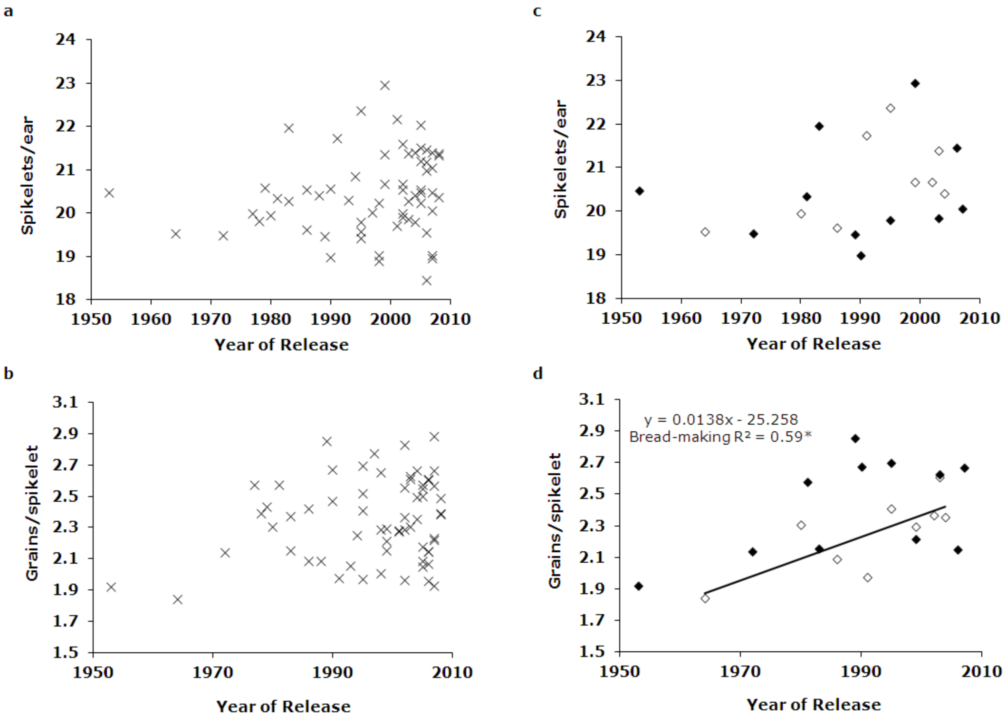


Figure 23. Trends with year of introduction in spikelets per ear (a) and grains per spikelet (b) amongst 64 varieties; and c and d, respectively, amongst landmark groups of feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Data values represent means across 5 site-seasons only.

Trends in development, growth and partitioning to anthesis

The range in the duration of the pre-anthesis phase from GS10 to GS61 was similar in the feed (222-225 days) and bread-making (221-223 days) groups of landmark varieties (Figure 24). Overall, the variation in the duration of this phase was only 4 days amongst all landmark varieties. A slightly greater range in CGR from GS10 to GS61 was apparent amongst the feed (18-23 g/m^2/d) compared to the bread-making varieties (18-21 g/m^2/d). The range in EPI at GS61 was similar in both landmark groups at 0.13-0.20 and 0.13-0.21, respectively; whereas an extended range for EFI was observed amongst the feed (88-122 grains/g) compared to the bread-making landmark varieties (86-108 grains/g).

The change in days from GS10 to GS61 was insufficient to detect a trend with breeding. For, CGR there was a non-linear increase with breeding in the feed varieties ($P<0.01$), with genetic gains apparent from ca. 1980 onwards and CGR increasing from about 19 to 22 g/m^2/d. For the bread-making landmark varieties there was no change with year of introduction. Genetic progress occurred in EPI in both landmark groups; in both cases the progress was non-linear, with EPI increasing to ca. 0.19 by ca. 1985, but EPI plateauing thereafter. Non-linear genetic progress in EFI was also observed in both landmark groups with genetic gains only apparent after ca. 1985. The main phase of genetic progress in EPI, therefore, was during the period of introduction of the semi-dwarf varieties, and for the EFI in the period since the introduction of the semi-dwarf varieties

There was no significant trend in above-ground biomass at anthesis with breeding in either the feed or bread-making landmark varieties (Figure 25) so the trends found for feed varieties at harvest (Figure 3) appear to have developed after anthesis. However, there were statistically significant differences in anthesis biomass amongst the varieties from 8.8–10.0 t/ha for feed and 8.8-10.7 t/ha for bread-making ($P<0.001$).

DM partitioning to the lamina at anthesis was on average the same in both groups of varieties at 0.19, and showed no change with year of introduction (Figure 26). Lamina DM was also, on average, similar between the two variety groups at 188 and 192 g/m^2, respectively. In contrast, stem DM partitioning at anthesis showed a non-linear decrease in the feed varieties with year of introduction decreasing from ca. 0.68 in 1953 to ca. 0.62 in the early 1980s and remaining stable thereafter. A trend for a decrease was apparent within the bread-making varieties but this was not statistically significant. These changes in stem partitioning were, therefore, mainly associated with the introduction of the semi-dwarf varieties. Stem DM per m^2 at anthesis showed an apparent trend to decrease from the earliest varieties (Cappelle Deprez and Maris Widgeon) but the regressions were not statistically significant for either the feed or bread-making varieties. Pooling the data from both groups gave a trend for a non-linear decrease stem DM with year of introduction (quadratic regression; $P = 0.06$) with stem DM decreasing up until the early 1980s and remaining stable thereafter.

The changes in EPI with year of introduction tended to reflect the changes in stem partitioning, because there was no decrease in lamina partitioning with year of introduction. In both landmark groups there were linear gains in ear DM per m^2 in the last decades of ca. 10 g/m^2 per decade.

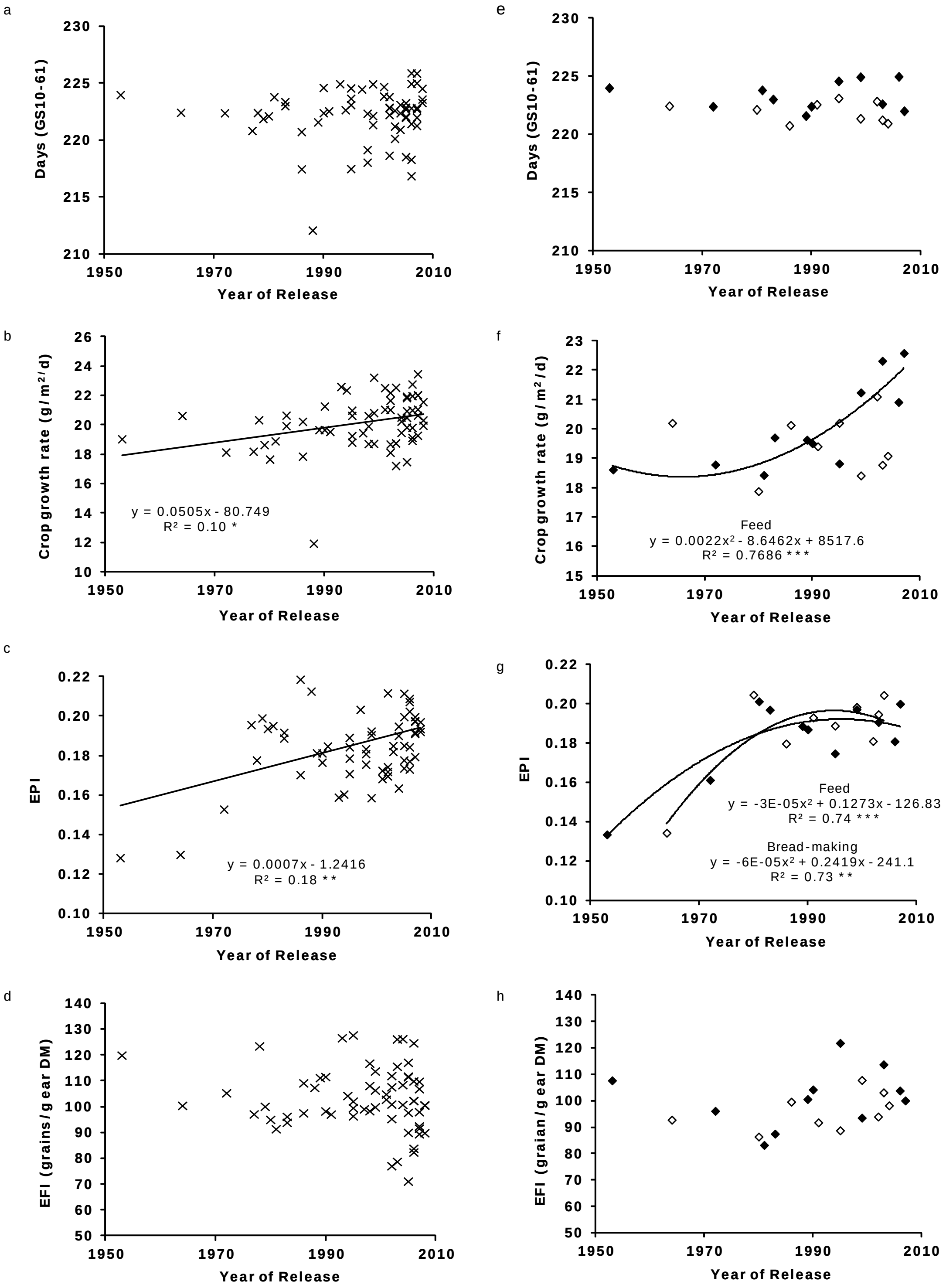


Figure 24. Trends with date of variety introduction in days from GS10 (emergence) to GS61 (anthesis) (a), crop growth rate GS10-GS61 (b), ear DM partitioning index at GS61 (c), and ear fertility index (EFI) at GS61 (grains per g ear DM) (d) for 64 varieties (x); and (e, f, g, and h) respectively, for landmark feed (including soft 'biscuit' wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

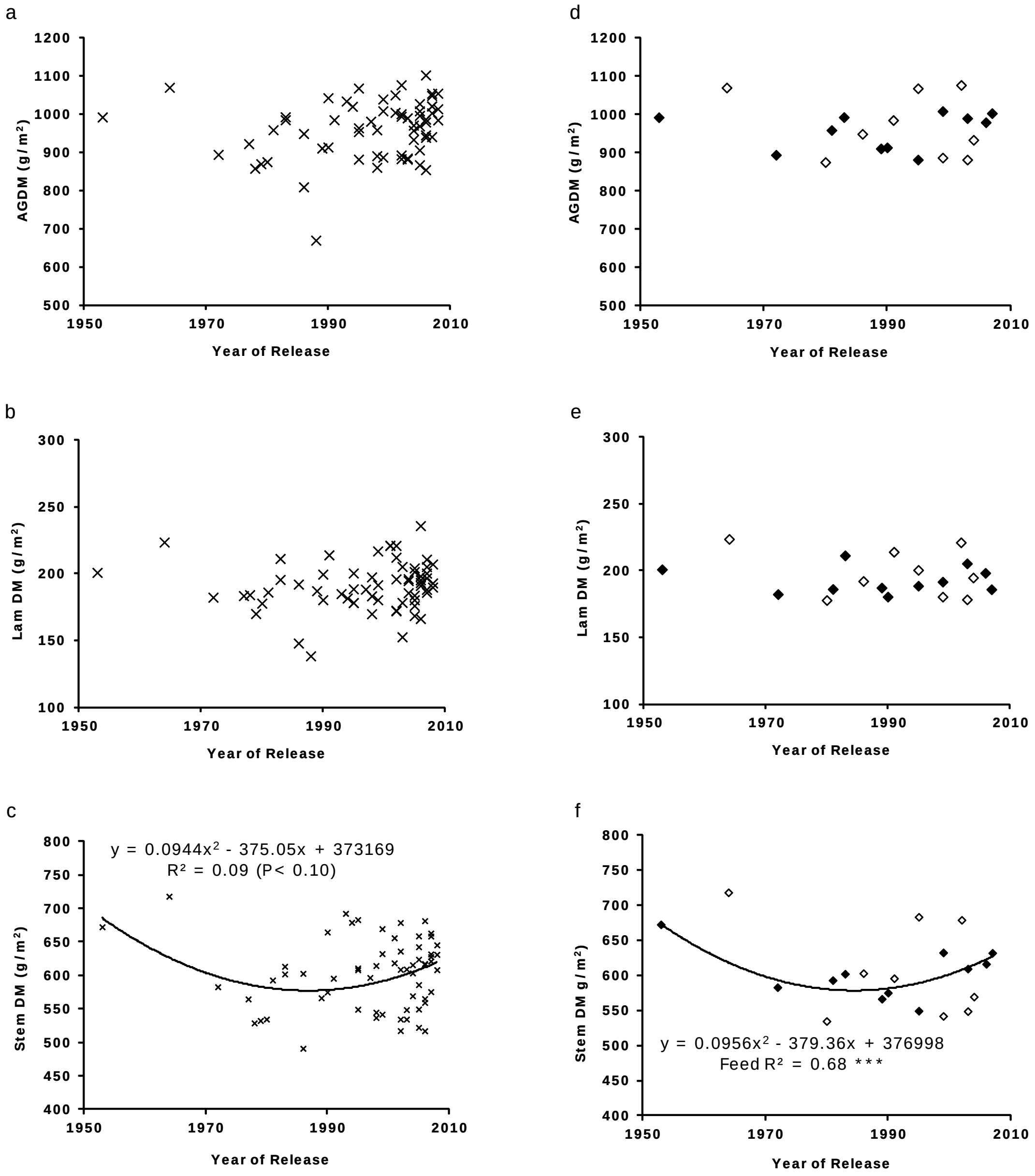


Figure 25. Trends with date of introduction in biomass (AGDM) at anthesis (GS61) (a), lamina DM at GS61 (b), and stem and leaf sheath DM at GS61 (c) amongst 64 varieties (x); and d, e, and f, respectively, amongst landmark feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

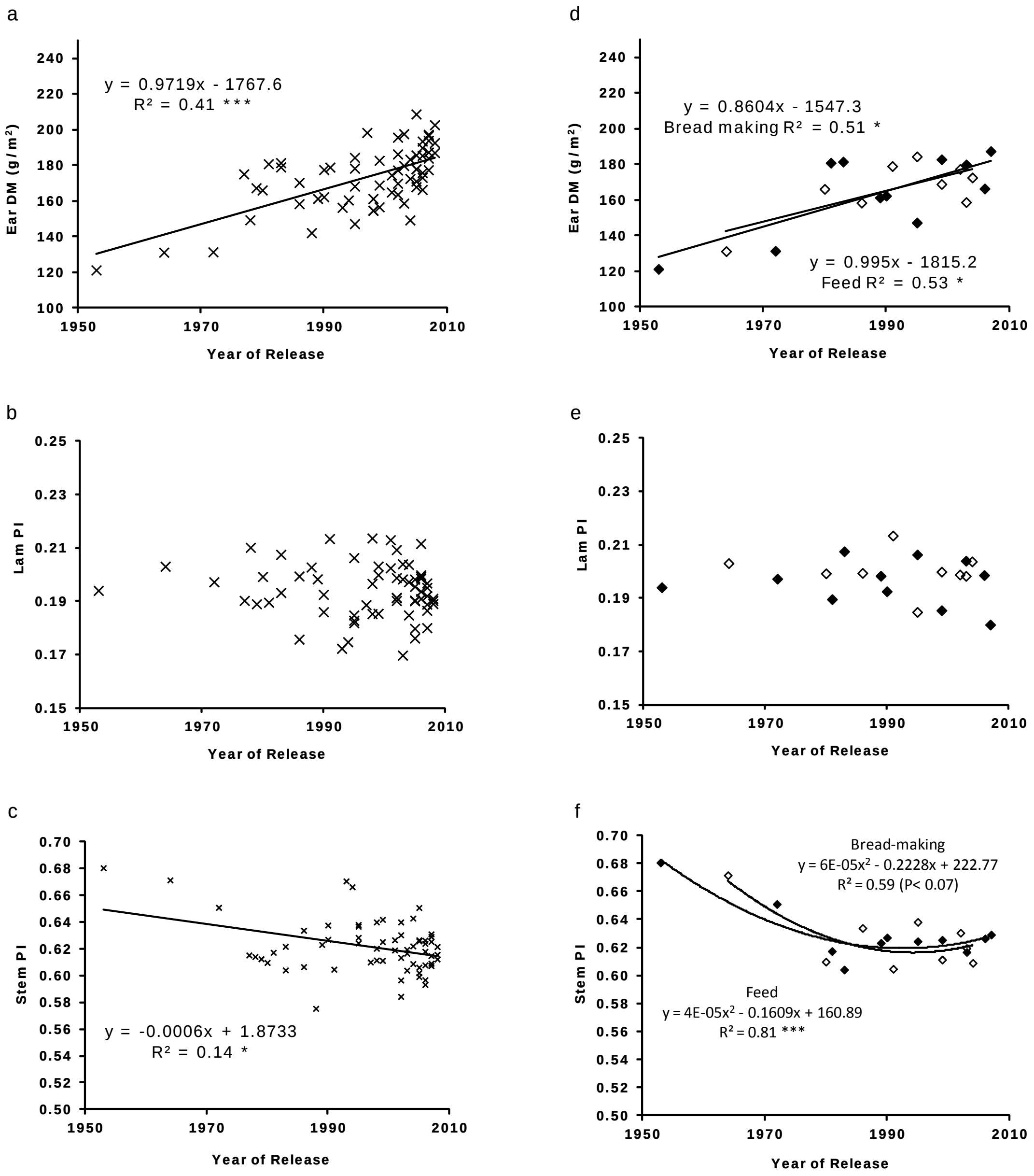


Figure 26. Trends with date of introduction in anthesis (GS61) measurements of ear DM (a), lamina partitioning index (PI) (b), and stem and leaf sheath (PI) (c) for 64 varieties (x); and d, e, and f, respectively, for landmark feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

Trends in pre-anthesis plant development

Amongst the landmark varieties, the bread-making varieties generally exhibited a shorter foundation phase from GS10-GS31 (984-1,012 °Cd) than the feed varieties (1,001-1,059 °Cd; Figure 27). The ranges in construction phase were more similar across the groups in the ranges 565-638 and 588-636 °Cd, respectively, but some feed varieties exhibited shorter construction phases than those in the bread-making group.

The effect of plant breeding has been to increase steadily the duration of the foundation phase in both the feed ($P<0.001$) and bread-making groups ($P<0.05$), although at a slower rate in the bread-making varieties. The duration of the construction phase tended to decrease in landmark varieties over the same period. The regressions were statistically significant for feed landmark varieties, and if data for both groups were pooled the linear decrease with year of introduction was also significant ($P<0.05$).

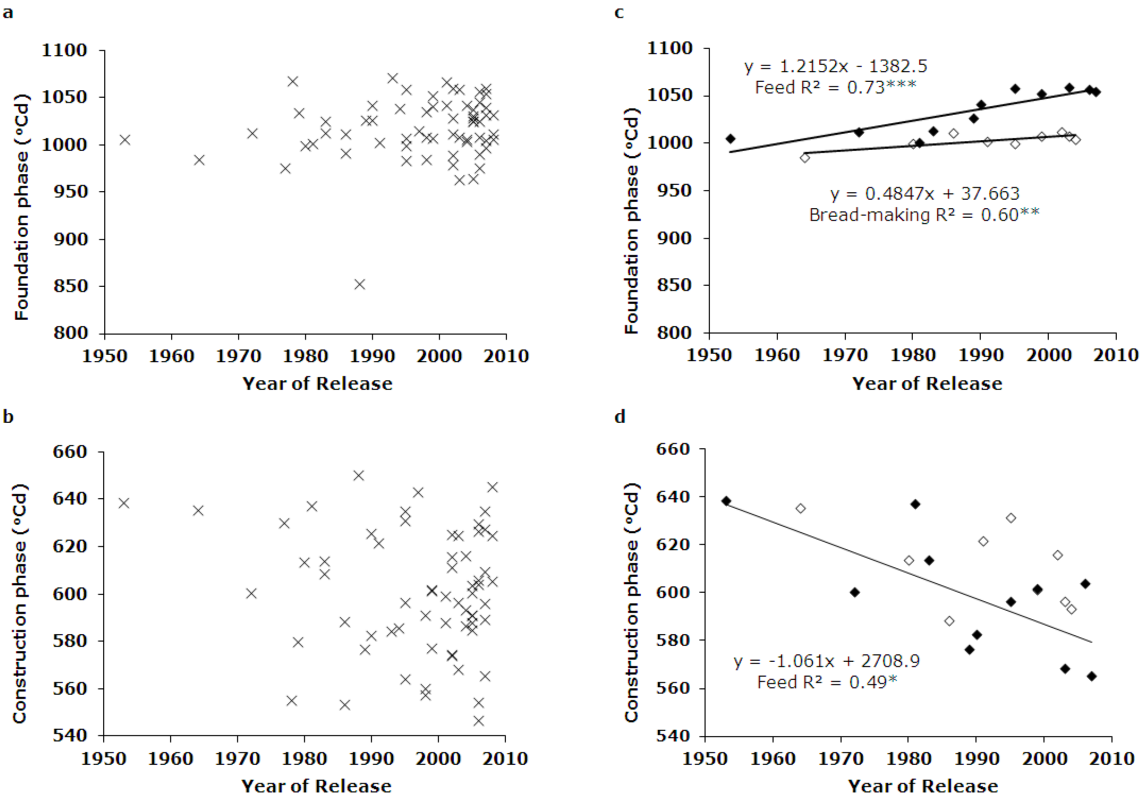


Figure 27. Trends with year of introduction in thermal duration (base temp. 0°C) of (a) the foundation phase (emergence, GS10, to onset of stem elongation, GS31) and of (b) construction phase (from GS31 to anthesis, GS61) for 64 varieties (x); and (c) and (d) respectively, for landmark feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

Relationships between grain per unit area and its determinants

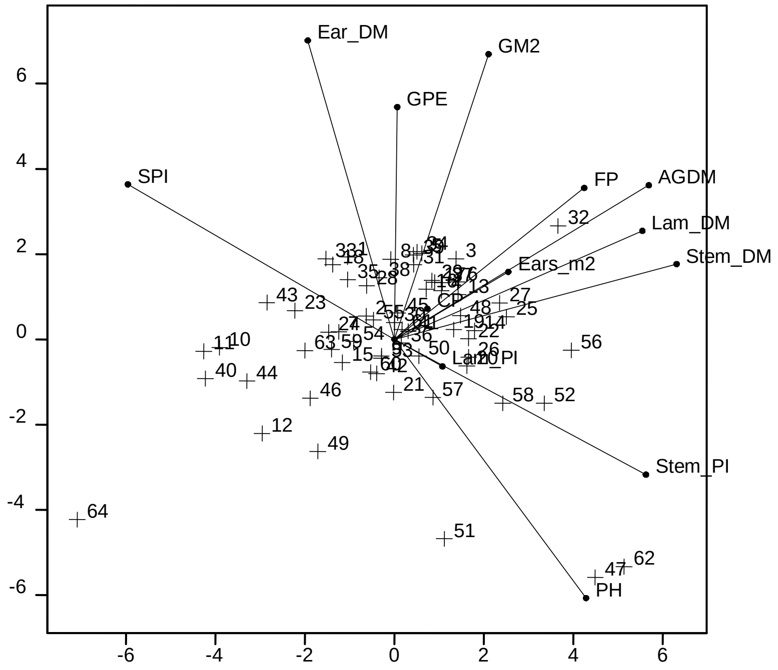
Components of yield, DM production and partitioning

To further analyse how the grains/m^2 of these varieties were determined, biplots were constructed from the variety data using the relevant anthesis and harvest measurements.

Figure 28 presents data from all 64 varieties and Figure 29 presents data from feed and bread-making landmark varieties separately. Amongst all 64 varieties there was a positive association between GN and ears m^{-2} ($P<0.001$), but an even stronger association with grains/ear ($P<0.001$). There was a positive correlation between GN and ears/m^2 amongst the landmark feed varieties ($P<0.05$), but no association amongst the landmark bread-making varieties. There was a positive association between GN and grains/ear for both landmark groups ($P<0.001$ and $P = 0.10$, respectively). The relationship was linear for the feed varieties, but non-linear amongst the bread-making varieties with increases in grains/ear above ca. 45 resulting in no further increase in GN (data not shown).

A positive correlation was found between the duration of the foundation phase (FP) and GN amongst the 64 varieties ($P<0.001$). In both, the feed and bread-making landmark varieties, the FP was very highly correlated with GN ($P<0.001$), and was negatively correlated with the duration of the construction phase (CP; $P<0.05$). In the feed landmark varieties, the FP was positively associated the ears/m^2 and ear dry DM m^2 ($P<0.05$). In the bread-making varieties FP was positively associated with ear partitioning index ($P<0.01$), which in turn was positively correlated with ear DM per m^2 ($P<0.05$).

Associations between physiological determinants of GN as expressed in Eqn 1 are shown as biplots for all 64 varieties in Figure 30 and for the landmark varieties in Figure 31. Amongst all 64 varieties there were significant associations with GN for all four components, but the strongest associations were found for EPI and EFI. For EPI there was a correlation with GN ($R^2 = 0.38$, $P<0.001$). GN increased with EFI up to a value of ca. 0.20, but decreased at higher values (Figure 32). Ear fertility index showed the strongest relationship with GN ($R^2 = 0.42$, $P<001$). For the landmark groups of varieties there was no association between the duration of the pre-anthesis period and GN in either group. CGR was positively associated with GN amongst landmark feed varieties ($R^2 = 0.62$, $P<0.05$) but not amongst bread-making varieties. In both groups there was a non-linear relationship between SPI and GN such that diminishing increases in GN were observed as SPI increased towards values of ca. 0.20 (Figure 32). There was no association between SFI and GN for either group. However, there was a trend for a positive association between EFI and GN for the pooled data from both groups ($P = 0.052$).



No.	Name	No.	Name	No.	Name	No.	Name
1	Equinox	17	Ambrosia	33	Hyperion	49	Cezanne
2	Cordiale	18	Glasgow	34	Gulliver	50	Savannah
3	Robigus	19	Alchemy	35	Timber	51	Maris Huntsman
4	Access	20	Istabraq	36	Consort	52	Paragon
5	Oakley	21	Soissons	37	Battalion	53	Riband
6	Humber	22	Sankara	38	Marksman	54	Norman
7	Malacca	23	Mendel	39	Musketeer	55	Buster
8	Dover	24	Mercato	40	Recital	56	Spark
9	Beaver	25	Deben	41	Hereward	57	Mercia
10	Andalou	26	Xi19	42	Apache	58	Cadenza
11	Royssac	27	Solstice	43	Caphorn	59	Hobbit
12	Exotic	28	Gladiator	44	Alixan	60	Hustler
13	Rialto	29	Brompton	45	Galahad	61	Longbow
14	Exsept	30	Mascot	46	Avalon	62	Maris Widgeon
15	Einstein	31	Zebedee	47	Cappelle Desprez	63	Virtue
16	Claire	32	Gatsby	48	Haven	64	Bacanora

Figure 28. Biplot for 64 varieties (PC1=35.9% and PC2=22.7%) showing anthesis measurements of Spike (ear) DM partitioning index (SPI), stem and leaf sheath DM partitioning index (StemPI) and leaf lamina DM partitioning index (LamPI), above-ground DM (AGDM), ear DM (Ear_DM), lamina DM (Lam_DM) and stem and leaf sheath DM (Stem_DM) /m^2 and at harvest ears per m^2 (Ears_m^2), grains per ear (GPE), grains per m^2 (GM2) and plant height (PH) and thermal durations of the foundation phase (FP) and construction phase (CP). Data represent average values across 8 site-seasons.

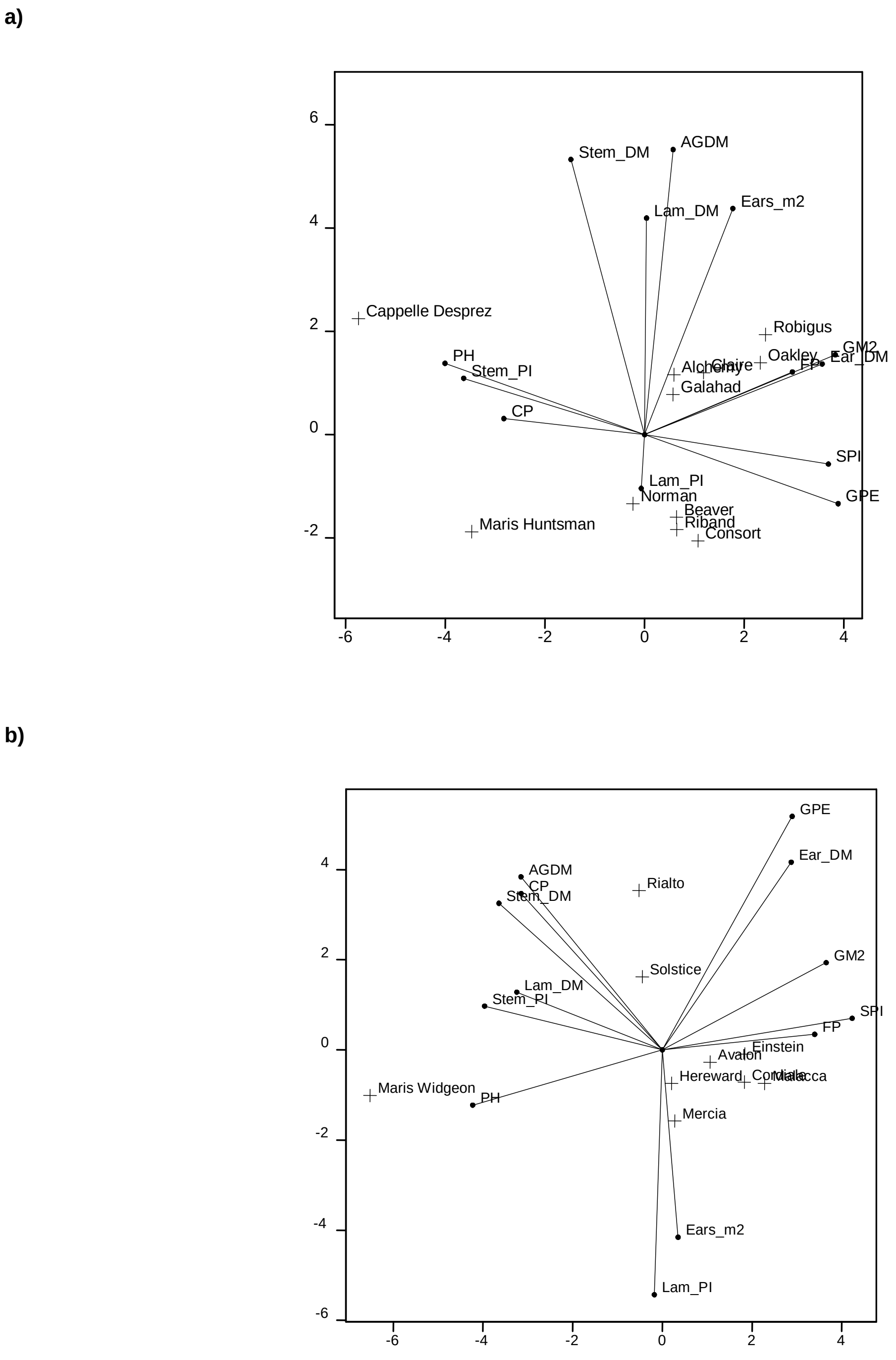
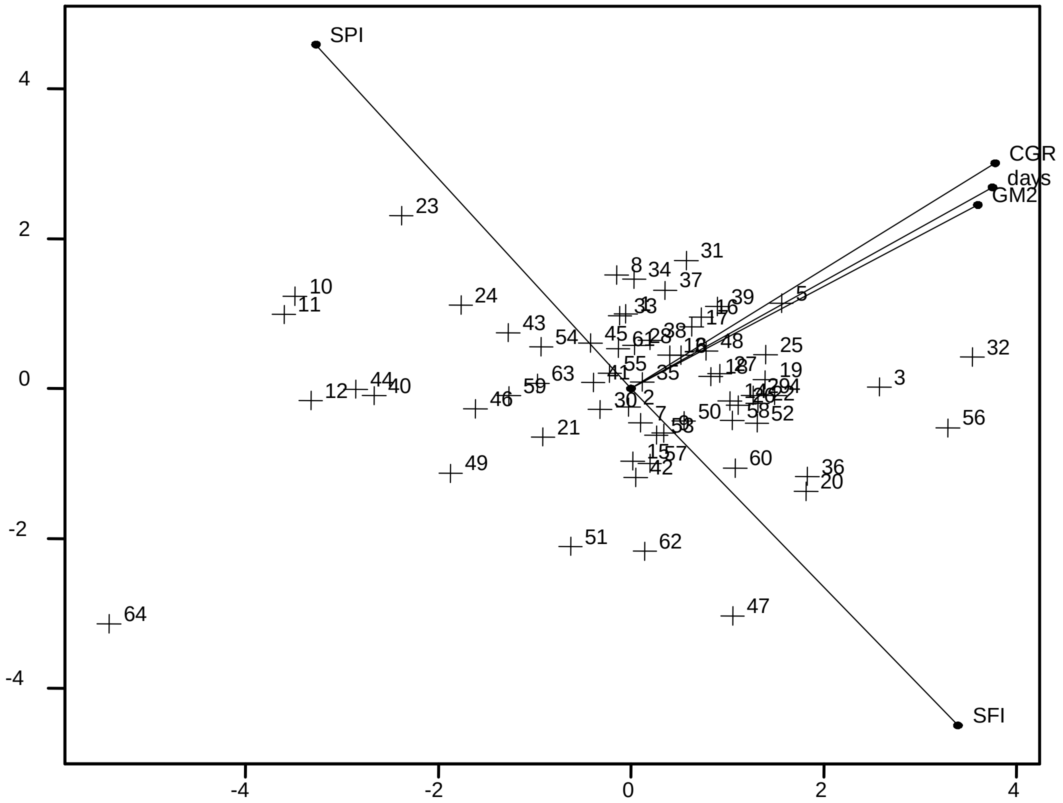


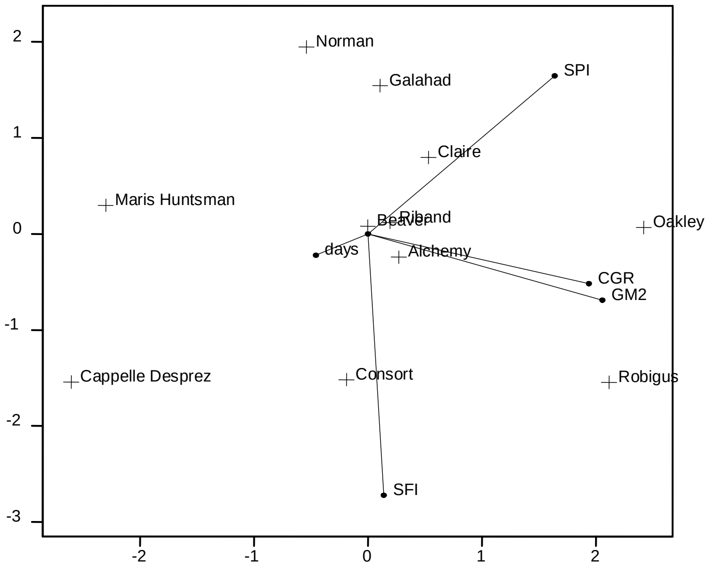
Figure 29. Separate biplots for (a) feed (including soft ‘biscuit’ wheats) (PC1=46.2%, PC2=22.8%) and (b) bread-making landmark varieties (PC1=53.9%, PC2=19.6%) showing anthesis measurements of Spike (ear) DM partitioning index (SPI), stem and leaf sheath DM partitioning index (Stem PI), leaf lamina DM partitioning index (Lam PI) at GS61; above-ground DM (AGDM), ear DM (ear DM), lamina DM (Lam_DM) and stem and sheath DM (stem_DM) /m^2, also ears /m^2 (ears m^{-2}), grains/ear (grains ear^{-1}), grains /m^2 (GM2), and plant height (PH) determined at harvest; also thermal durations of the foundation (FP) and construction phases (CP). Data represent average values across 8 site-seasons.



No.	Name	No.	Name	No.	Name	No.	Name
1	Equinox	17	Ambrosia	33	Hyperion	49	Cezanne
2	Cordiale	18	Glasgow	34	Gulliver	50	Savannah
3	Robigus	19	Alchemy	35	Timber	51	Maris Huntsman
4	Access	20	Istabraq	36	Consort	52	Paragon
5	Oakley	21	Soissons	37	Battalion	53	Riband
6	Humber	22	Sankara	38	Marksman	54	Norman
7	Malacca	23	Mendel	39	Musketeer	55	Buster
8	Dover	24	Mercato	40	Recital	56	Spark
9	Beaver	25	Deben	41	Hereward	57	Mercia
10	Andalou	26	Xi19	42	Apache	58	Cadenza
11	Royssac	27	Solstice	43	Caphorn	59	Hobbit
12	Exotic	28	Gladiator	44	Alixan	60	Hustler
13	Rialto	29	Brompton	45	Galahad	61	Longbow
14	Exsept	30	Mascot	46	Avalon	62	Maris Widgeon
15	Einstein	31	Zebedee	47	Cappelle Desprez	63	Virtue
16	Claire	32	Gatsby	48	Haven	64	Bacanora

Figure 30. Biplot for the 64 varieties (PC1=52.0% and PC2=21.4%) showing time from sowing to GS61 (days), crop growth rate from sowing to GS61 (CGR; g/m^2/d), spike (ear) DM partitioning index (SPI), and spike (ear) fertility index. Data represent average values across 8 site-seasons.

a)



b)

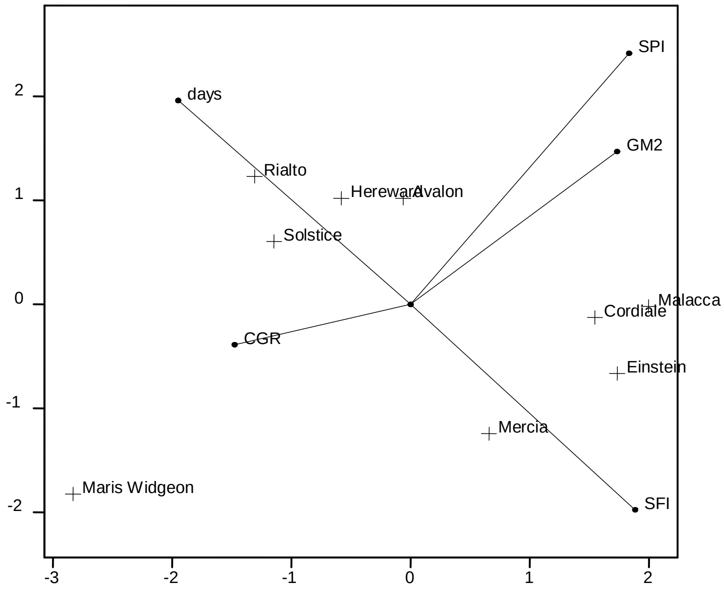


Figure 31. Separate biplots for a) feed (including soft 'biscuit' wheats) (PC1=46.3% and PC2=28.1) and b) bread-making landmark varieties (PC1=53.0% and PC2=23.3%): showing time from sowing to GS61 (days), crop growth rate GS1-GS61 (CGR; g/m^2/d), spike (ear) DM partitioning index (SPI), spike (ear) fertility index. Data points represent average values across 8 site-seasons.

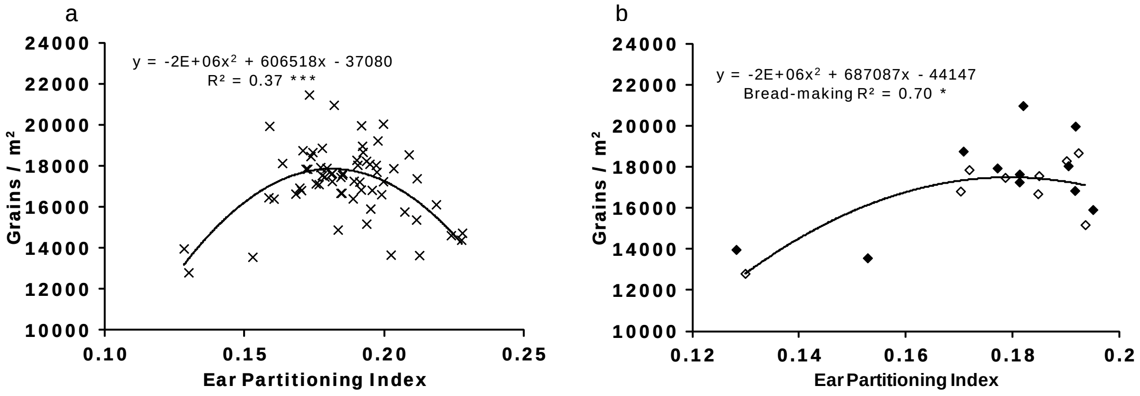


Figure 32. Relationship between grains/m^2 and EPI at GS61 amongst a) 64 varieties (+) and b) landmark feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Points represent means across 8 site-seasons.

No landmark varieties had an EPI exceeding ca. 0.2. Maximisation of GN at EPI ca. 0.2 appeared to be explained by a negative relationship between EPI and EFI. Thus, as EPI and ear DM per m^2 increased, the efficiency or converting unit ear DM into grains decreased (Figure 33). A non-linear relationship was identified between EPI and GN amongst all 64 genotypes and amongst the landmark bread-making varieties, with maximum values of GN occurring at EFI of ca. 0.20. However, since this relationship was non-linear it was not detected by the principal components analysis (see bi-plots in Figs 4.27 and 4.28).

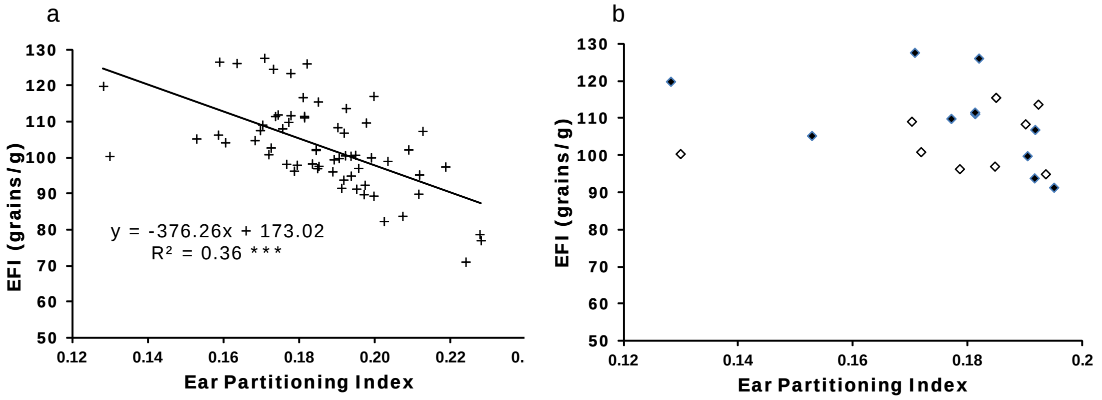


Figure 33. Relationship between ear fertility index and ear DM partitioning index at GS61 amongst (a) 64 varieties and (b) landmark groups of feed (including soft ‘biscuit’ wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

Increased crop growth from sowing to GS61 appeared to be associated with an increase in average incident radiation per day in the construction phase, suggesting that varieties with the CP occurring relatively later in the season coinciding with on average brighter conditions may be been predisposed to have higher CGR (Figure 34)

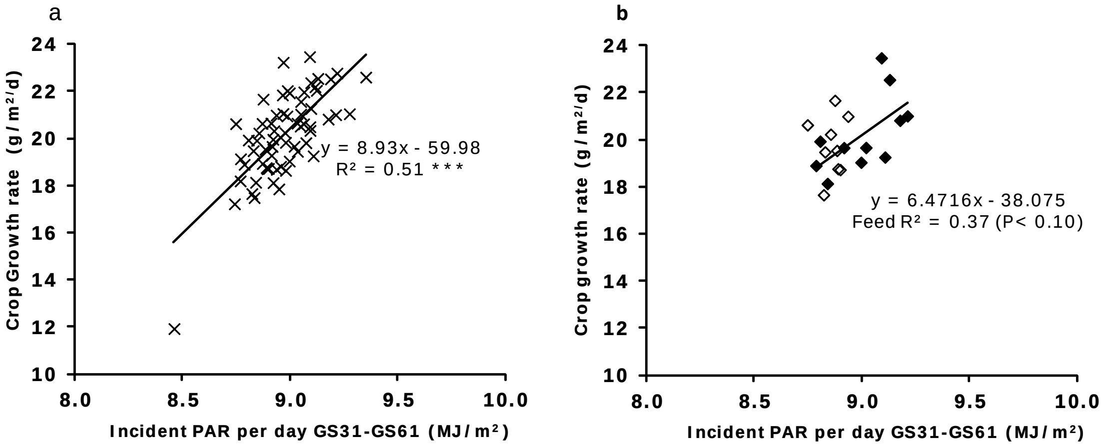


Figure 34. Relationship between crop growth rate GS10-GS61 and incident photosyntheitclly active radiation (PAR) per day during GS31-GS61 amongst (a) 64 varieties and (b) landmark groups of feed (including soft 'biscuit' wheats) (◆) and bread-making (◇) varieties. Data values represent means across 8 site-seasons.

Effect of major genes on grains per m^2 and its physiological determinants

The same caution should be applied to analysis of major gene effects here as in Section 0. The effect of the *Ppd1* allele for photoperiod insensitivity was to shorten the foundation phase by 40^{o}Cd ($P<0.05$; Table 15); the effect of *Ppd1* on the construction phase was not statistically significant. Therefore *Ppd1* advanced flowering through reducing the phase from emergence to the onset of stem extension. Overall, earlier flowering with *Ppd1* reduced grains/m^2 from 17,360 to 15,270 (12%). This was associated with trends ($P<0.10$) for decreases in crop growth rate (-10%) and ear fertility index (-9%), although ear partitioning index was increased with *Ppd1* (10%; $P<0.001$). Biomass at anthesis was reduced by 9% with *Ppd1* ($P<0.05$), although ear DM per m^2 was not decreased by *Ppd1* compared to *ppd* due to the increase in ear DM partitioning.

The effect of the *Rht2* semi-dwarf allele compared to the *rht* tall control was generally consistent with previous reports of the effects of semi-dwarf genes on grain number and DM partitioning (Fischer, 1983). This semi-dwarf allele increased grains/m^2 by 9%, associated with a 24% increase in DM partitioning to the ear at anthesis ($P<0.001$) which led to a 21% increase in ear DM per m^2. There was no effect of *Rht2* on the duration of either the foundation or construction phase. The number of lines containing the semi-dwarf *Rht1* allele was only seven, making comparisons across unbalanced groups of lines less reliable. Nevertheless, similar effects for an increase in grains/m^2 associated with enhanced ear DM partitioning and ear DM per m^2 were observed for *Rht1* lines compared to control group of tall lines.

Table 15. Effects of a) *Ppd1* and *Ppd2* photoperiod genes and b) *Rht1* and *Rht2* semi-dwarf genes on grains m^{-2}, its components and thermal durations of foundation phase (FP) and construction phase (CP). Values represent means across 8 site-seasons.

	No. lines	**Grains** /m^2	**Days** GS31-61	**CGR** g/m^2/d	**EPI**	**EFI** grains/g	**Ear DM** g/m^2	**AGDM** GS61 g/m^2	**FP** ^{o}Cd	**CP** ^{o}Cd
a)										
ppd1/ppd2	53	17,358	48.6	20.4	0.180	105.2	175.8	990	1,020	604.5
Ppd1/ppd2	9	15,269	49.6	18.4	0.199	96.1	175.5	898	980	593.1
ppd1/Ppd2	1	14,515	47.5	20.8	0.221	70.4	212.0	978	1,027	586.7
Ppd1/Ppd2	1	14,864	47.6	18.2	0.216	95.4	177.0	828	991	574.3
LSD (Min rep)		698.0	1.59	0.87	0.0057	5.54	8.96	46.3	9.8	7.9
LSD (Min – Max)		1,785.0	4.04	2.32	0.0155	15.04	23.34	125.7	25.0	20.0
LSD (Max rep)		2,586.1	5.84	3.33	0.0223	21.61	34.98	180.6	36.1	28.9
b)										
Rht	47	15,594	48.2	20.8	0.152	111.2	149.9	1005	1,019	597.7
Rht1	8	18,229	47.1	19.9	0.193	105.1	176.9	934	1,018	583.8
Rht2	8	17,000	49.0	20.0	0.188	101.5	180.8	975.7	1,013	605.9
LSD (Min rep)		666.2	1.507	0.91	0.0058	5.90	9.30	49.2	9.3	7.5
LSD (Min – Max)		801.7	1.827	1.02	0.0064	6.51	10.27	54.3	11.3	9.0
LSD (Max rep)		953.9	2.176	1.21	0.0076	7.72	12.18	64.4	13.4	10.8

3.3.2. Vernalisation experiment

Generally, plants in this experiment resembled plants as commonly grown by breeders in conditions for single seed descent (SSD) i.e. most plants were restricted to one main shoot with few or nil tillers, there were few rosette leaves, stems had four or five internodes, ears were small and the life cycle was short. Transient waterlogging was noted in a few trays early in the experiment, such that plants in two trays became chlorotic on their lower leaves, but these recovered. Minimum temperature data from the glasshouse (Figure 35) showed that even when plants had been removed from vernalisation, they were still experiencing temperatures capable of vernalisation for part of the day (night). This was because, although the glasshouse was heated, heating was inadequate to achieve the target minimum of 14°C during winter and early spring when this experiment was carried out.

Maximum temperatures were generally less than 20°C but exceeded 30°C during the last week or so of the experiment, due to very warm outside conditions. However, plants did not appear stressed, and these temperatures are only likely to perturb grain set, which did not occur during this experiment.

A few plants died during the experiment. These were distributed randomly through the treatments; however, at least one replicate of every variety x vernalisation treatment survived. Five varieties had two plant deaths and 13 varieties had just one plant death.

By the end of the experiment on 7th April plants of 14 varieties which had received little vernalisation showed incomplete or absent reproductive development (Table 16 and Table 17). When internode counts were made (on 16th May; not reported here), only one plant (cv. Haven, variety 48) was noted with no stem or ear development; thus there was always one plant of each vernalisation x variety treatment that did initiate reproductive development.

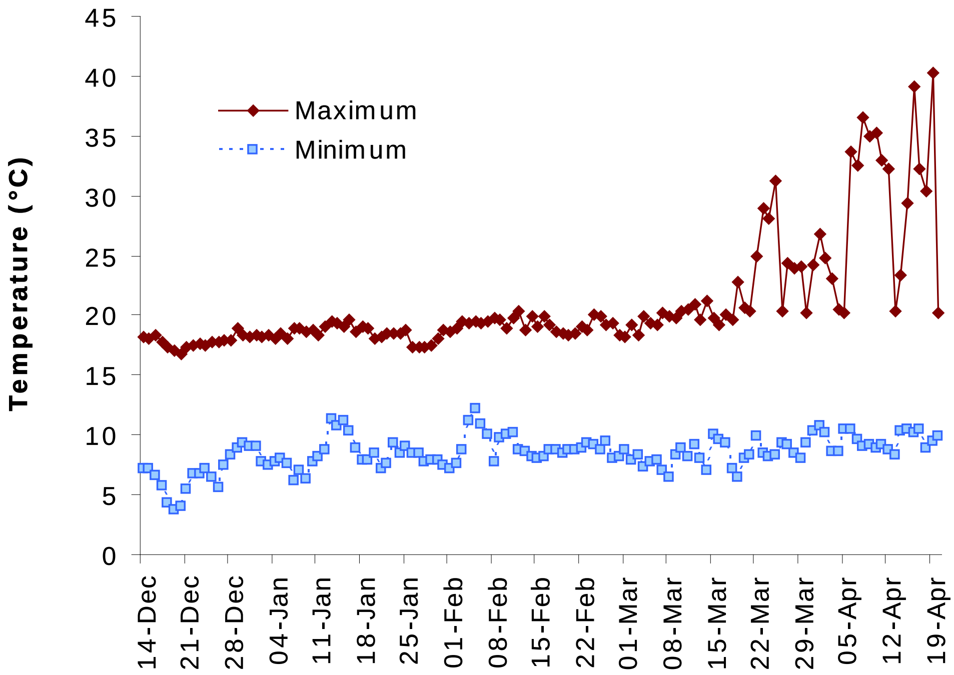


Figure 35. Minimum (blue squares) and maximum (brown diamonds) temperatures (ºC) experienced by plants in the glasshouse after they had been removed from the vernalisation chamber.

Effects of number of weeks in vernalisation on thermal time to growth stages

All of the varieties reached GS39 if they had experienced at least 3 weeks of vernalisation (i.e. excluding the week for dormancy breaking and germination) (Table 16). With 2 weeks of vernalisation, the majority of varieties (50) still reached GS39 in both plants, but with 1 or nil weeks of vernalisation the majority did not reach GS39 by the end of the experiment.

Although only 6 varieties failed to reach GS39 with 2 weeks of vernalisation, 17 did not proceed to GS61 (Table 17). About a third of the varieties needed a further week of vernalisation to proceed to flowering. Most (56) of the varieties reached GS61 after 3 weeks vernalisation and at least one plant of all varieties reached GS61 after at least 4 weeks vernalisation. However, 55 varieties failed to reach GS61 with no vernalisation (Table 17). Both plants reached GS61 in only five varieties when plants had not been exposed to vernalisation (Table 17).

Because data for GS61 were less precise and less complete by the end of the experiment on 7th April, subsequent data analysis focuses on treatment effects on GS39.

Table 16. The number of varieties achieving GS39 by the end of the experiment (7th April) after 0 – 4 weeks in the vernalisation chamber.

Weeks in vernalisation	0	1	2	3	4
Nil plants reached GS39	49	37	6	0	0
One plant reached GS39	5	10	8	1	9
Both plants reach GS39	10	17	50	63	55

Table 17. The number of varieties achieving GS61 by the end of the experiment (7th April) after 0 – 4 weeks in the vernalisation chamber.

Weeks in vernalisation	0	1	2	3	4
Nil plants reached GS61	55	47	17	3	0
One plant reached GS61	4	6	11	5	8
Both plants reached GS61	5	11	36	56	56

Generally, as the number of weeks that varieties spent in vernalisation increased, the thermal time from sowing that it took to reach GS39 reduced, with the thermal time to GS39 minimised at 6-7 weeks vernalisation (Figure 36). The minimum thermal time required to reach GS39 was between 722 and 955°C days (equating to between 22 and 35 days) depending on the variety. However, the rate and timing of decline in days to GS39 differed among varieties, and in this respect varieties fell into three distinct groups. The first group contained four ‘spring’ varieties (26 Xi19, 52 Paragon, 58 Cadenza, 64 Bacanora) which were insensitive to vernalisation and regardless of the number of weeks of vernalisation they took just under 800°C days (around 40 days) to reach GS39 (Figure 36). A second group of ten varieties did reach GS39 with 0 weeks in vernalisation, but it took between 1,350 and 1,700°C days. A third group reached GS39 (before the end of the experiment) only after 1, 2 or 3 weeks in vernalisation (Figure 36).

All varieties, apart from the ‘spring’ varieties showed a rapid decline in the thermal time to reach GS39 due to the initial number of weeks in vernalisation (Figure 36). As the duration of vernalisation increased extra reduction in time to GS39 diminished for each variety; however, an interesting feature of this experiment was the slight increase in time to GS39 which occurred as vernalisation time exceeded 7 weeks. This effect appeared similar for winter and spring types, so is likely to have a cause unrelated to vernalisation, for example, an effect of prolonged cold on subsequent extension growth. Previous workers have observed similar effects of prolonged vernalisation conditions on spring wheat (Brooking & Jamieson, 2002).

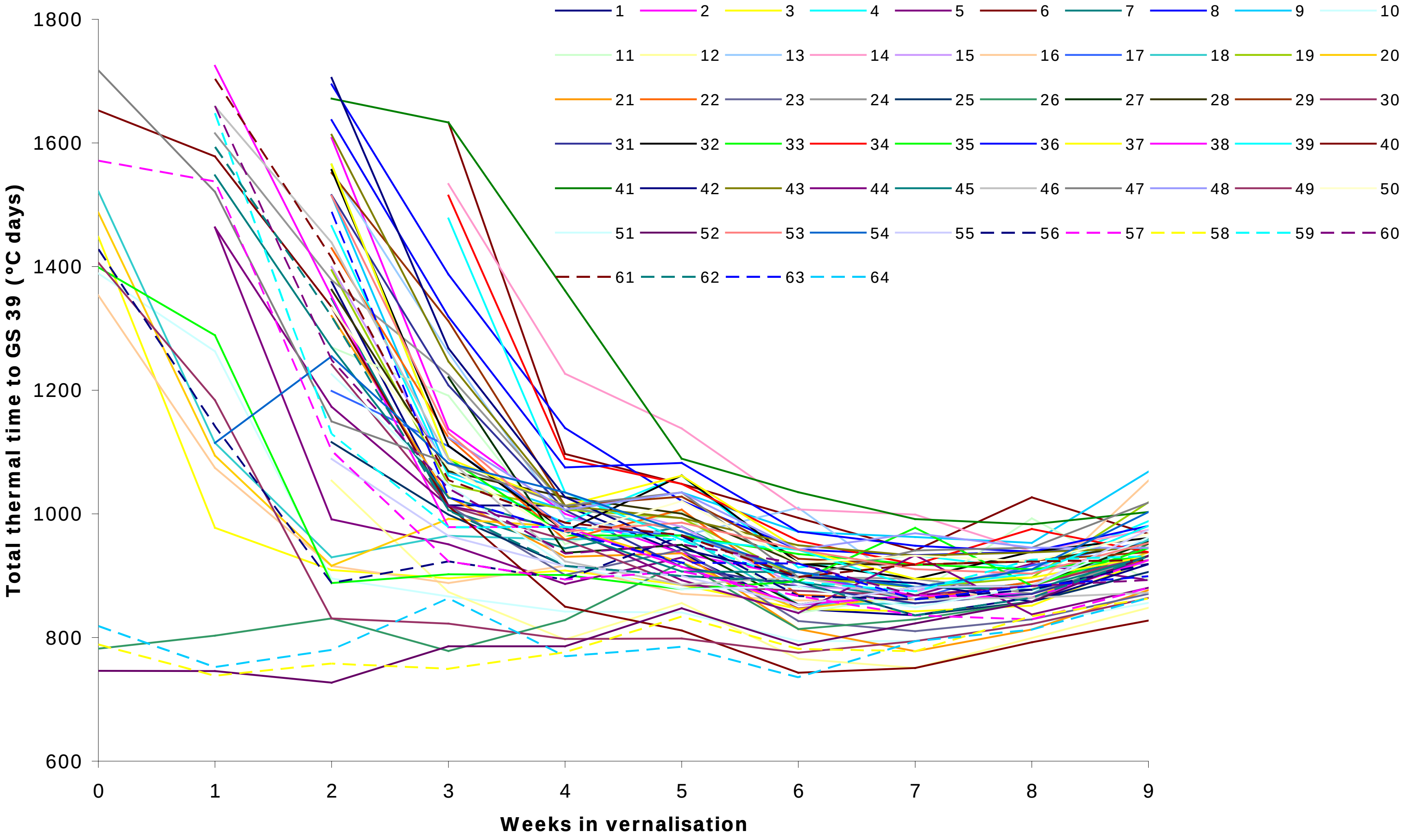


Figure 36. The effect of the number of weeks in a vernalisation chamber on the mean thermal time (^{o}C days) from sowing required to reach full flag leaf emergence (GS39) for each of 64 varieties. For variety codes see Figure 11.

To summarise the treatment effects, parallel exponential curves were fitted of the form:

$$y = a + b \times R^x \qquad \text{Eqn2}$$

where y is the thermal time to GS39, x is the number of weeks in the vernalisation chamber, a gives an estimate of the minimum thermal time needed to complete development to GS39 after reproductive development has been triggered (equivalent to inherent earliness), b is the effect on thermal time to GS39 of nil time in the vernalisation chamber (i.e. the responsiveness to vernalisation), and R is a fitted parameter describing the change in rate of response with increasing vernalisation. This exponential model does not recognise the slight increase in time to GS39 with the longest vernalisation treatments.

Weeks in the vernalisation chamber (V_{Tmin}) (but also with subsequent vernalising temperatures in the glasshouse) required to minimise subsequent thermal time to GS39 were then calculated as

$$V_{T\min} = \log_R\left(\frac{20}{b}\right) \qquad \text{Equ 3}$$

where 20 is a constant set to give values for V_{Tmin} that match y minima. Parallel curve analysis showed that a single value for the parameter R could describe all varieties satisfactorily. The estimate for R was 0.4811 with a standard error of 0.0121. Examples of the fitted curves are illustrated in Figure 37.

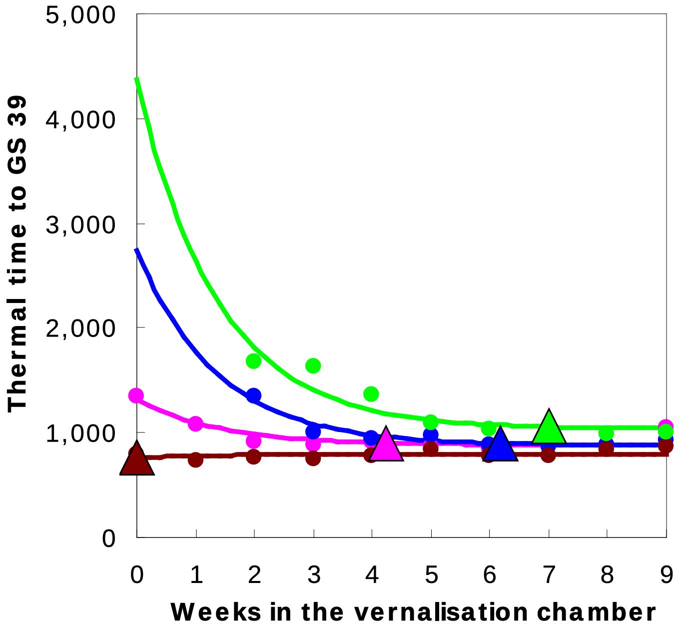


Figure 37. Example exponential curves fitted to thermal times to GS39 (°C days) as they were affected by weeks of vernalisation for Cadenza (brown), Claire (pink), Malacca (blue) and Hereward (green). Circles, experimental means; triangles, vernalisation requirements.

Estimates of parameter *a* and vernalisation requirements and their inter-relationship are shown in Figure 38. Values of *a*, which ranged from 758 to 997°C days, relate to the minimum time that varieties took to reach GS39 after its vernalisation and photoperiod requirements were fully met. As such, they provide assessments of inherent earliness.

Values of *b* were negative for ‘spring’ varieties (26 Xi19, 52 Paragon, 58 Cadenza); the three varieties with large positive *b* values (34 Gulliver, 12 Exsept, 6 Humber) all had three copies of *Vrn1*; however other varieties with three copies had moderate estimates of *b*.

Estimates of *a* and *b* with standard errors are shown for all varieties in (Figure 39 and Figure 40), along with the associated *Vrn1* copy numbers. Varieties with large values of *b* did not reach GS39 in this experiment; hence, if sown in the field late and not vernalised, these are likely to need an excessive time to become reproductive.

One variety (41, Hereward) gave a large value of *a*, and also a large vernalisation requirement (Figure 38), so in addition to needing most thermal time when fully vernalised to reach GS39, it also needed longer periods of vernalisation than most other varieties. However, there is not the same relationship for all varieties although the correlation between the two parameters *a* and *b* was significant overall (Correlation coefficient r=0.4032 p<0.001).

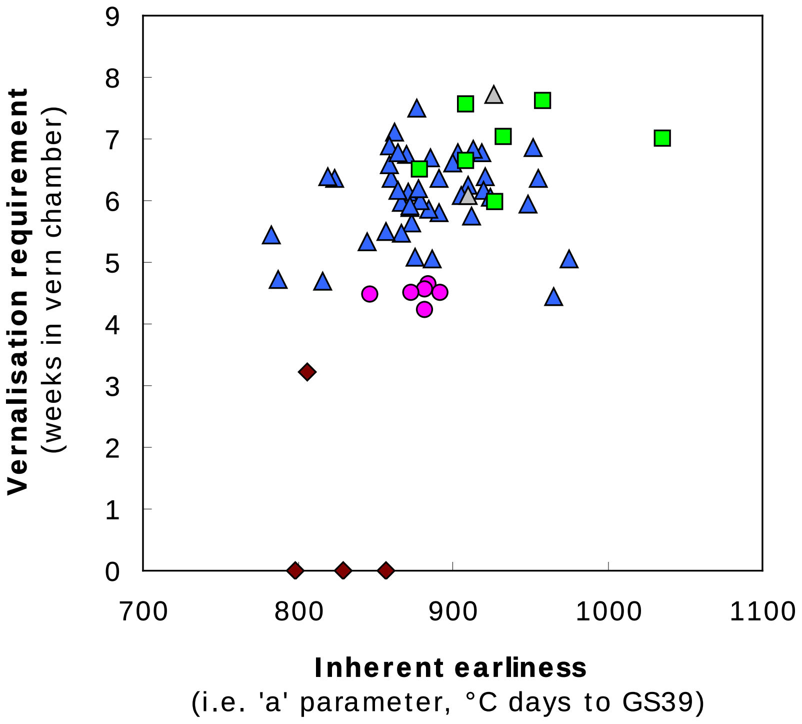


Figure 38. Relationship between vernalisation requirement determined from fitted parameters *R* and *b*, and inherent earliness (parameter *a*) for all 64 varieties, colour-coded by *Vrn1* gene copy number; brown = 1 copy (spring), pink = 1 (winter), blue = 2, green = 3, grey = unknown.

The groups of varieties and patterns of decline in thermal time to GS61 with increased weeks of vernalisation (Figure 41) were similar to those found with thermal time to GS39. The same four ‘spring’ varieties were insensitive to vernalisation and flowered at around 1,050°C days, irrespective of the number of weeks they had spent in vernalisation. However, varieties appeared to show less consistent responses in thermal time to GS61 as number of weeks in vernalisation increased (Figure 41). This was partly because a number of plants died towards the end of the experiment, so some points on the graph are based only one plant rather than two.

Delay from GS39 to GS61

On average, 264°C days (about 18 days) occurred between GS39 and GS61. This means that the probable reason for some varieties not reaching GS61 (Figure 41) was truncation of the experiment. There is no reason to believe that these varieties would not have flowered; non-flowering varieties only had 5 days on average from GS39 until the end of the experiment.

There were significant ($P<0.001$) differences between varieties in the average thermal time from GS39 to GS61, ranging from 227°C days for variety 24 Mercato to 285°C days for variety 19 Alchemy (Figure 42). There also appeared to be a significant ($P<0.001$) increase in thermal time from GS39 to GS61 (of about 2.8°C days for each week of prolonging vernalisation), but this effect was very small and there was no interaction of this with variety.

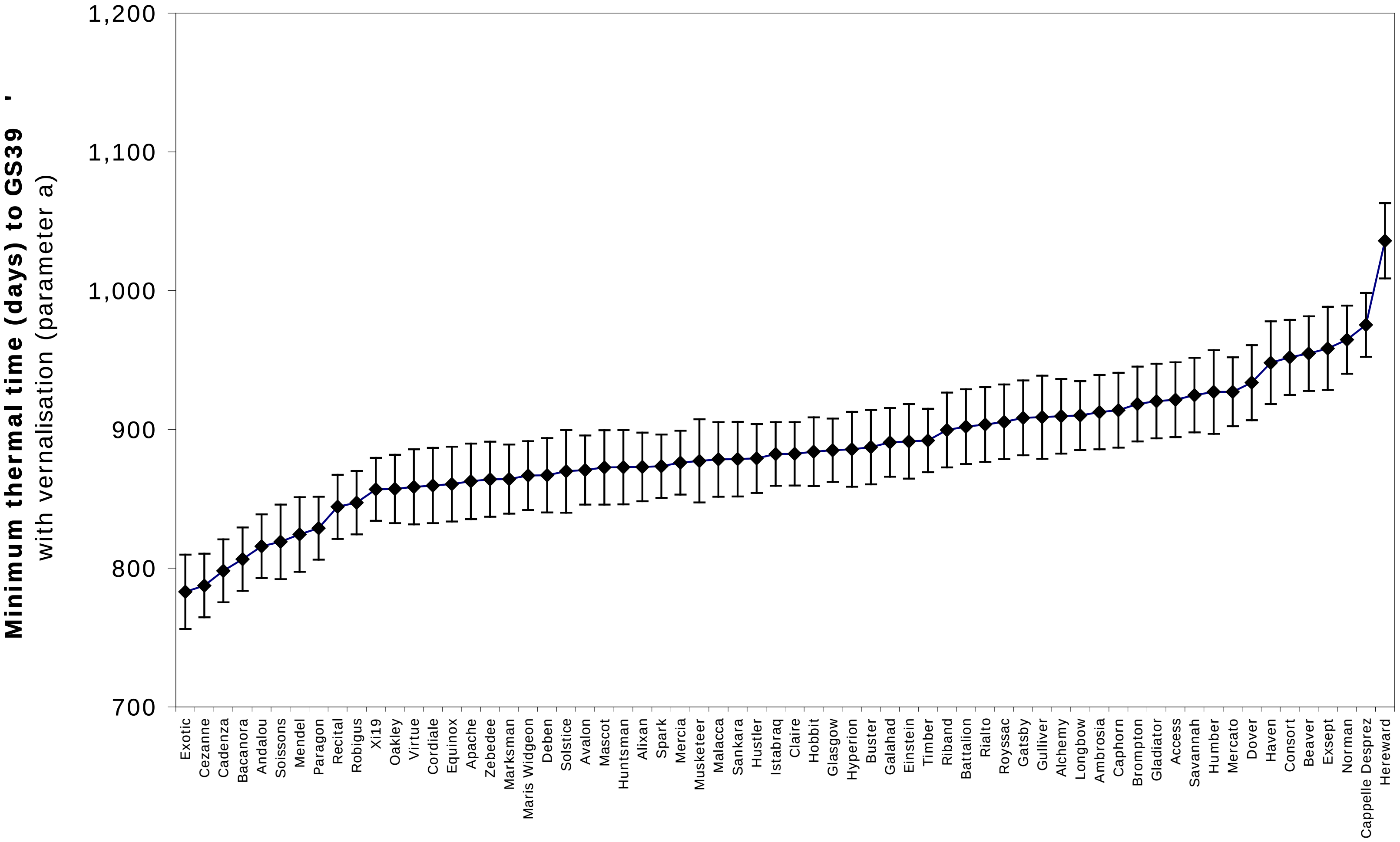


Figure 39. Estimates and standard errors of inherent earliness (parameter *a*) derived from fitting exponential curves to the relationship between thermal time to GS39 and number of weeks in the vernalisation chamber, for all 64 varieties.

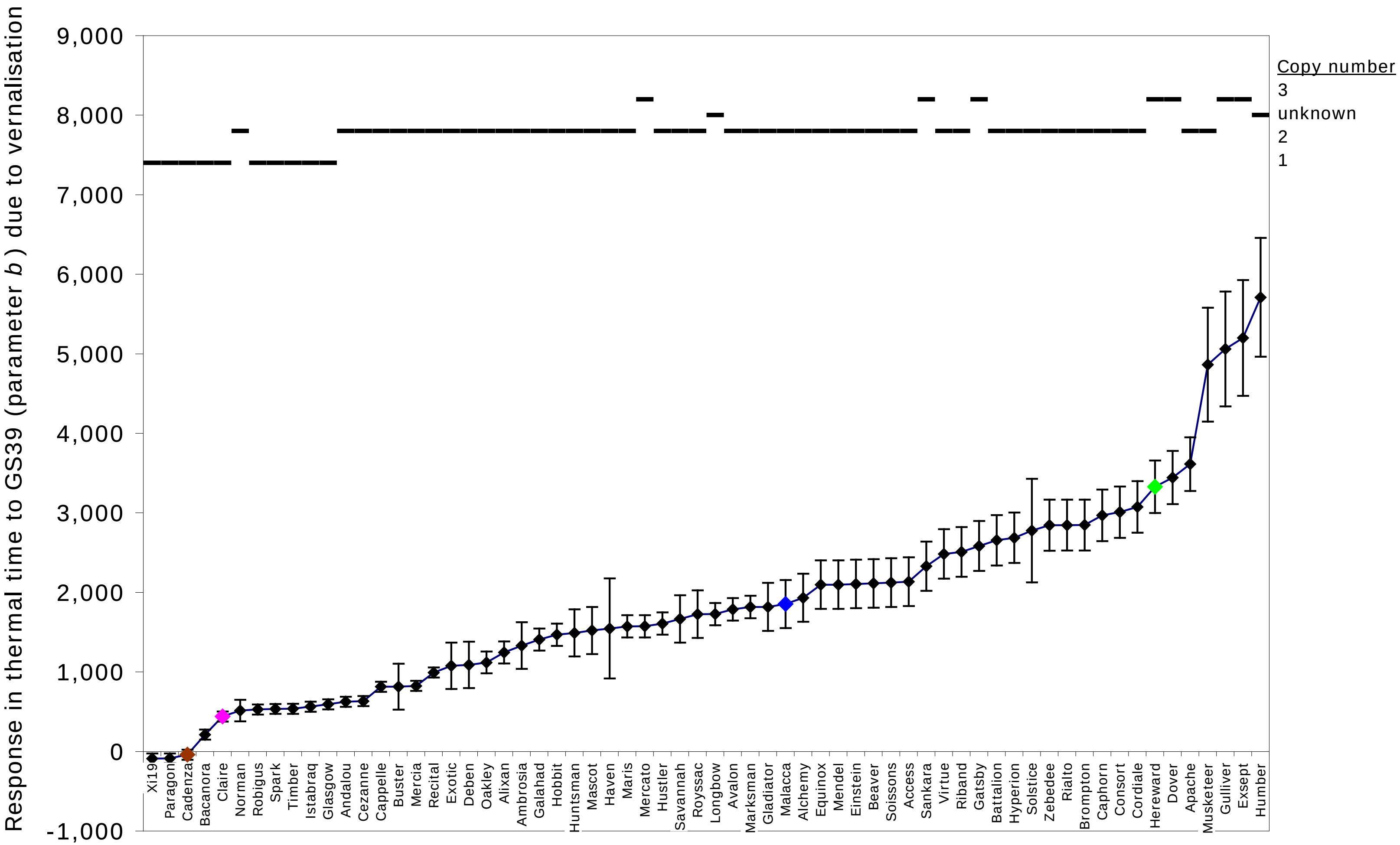


Figure 40. Estimates and standard errors of response in thermal time to GS39 (parameter *b* derived from fitted exponential curves) as affected by number of weeks in the vernalisation chamber for all 64 varieties. The copy number of the *Vrn1* gene (1, 2, or 3) is also displayed for each variety. (Cadenza (brown), Claire (pink), Malacca (blue) and Hereward (green)

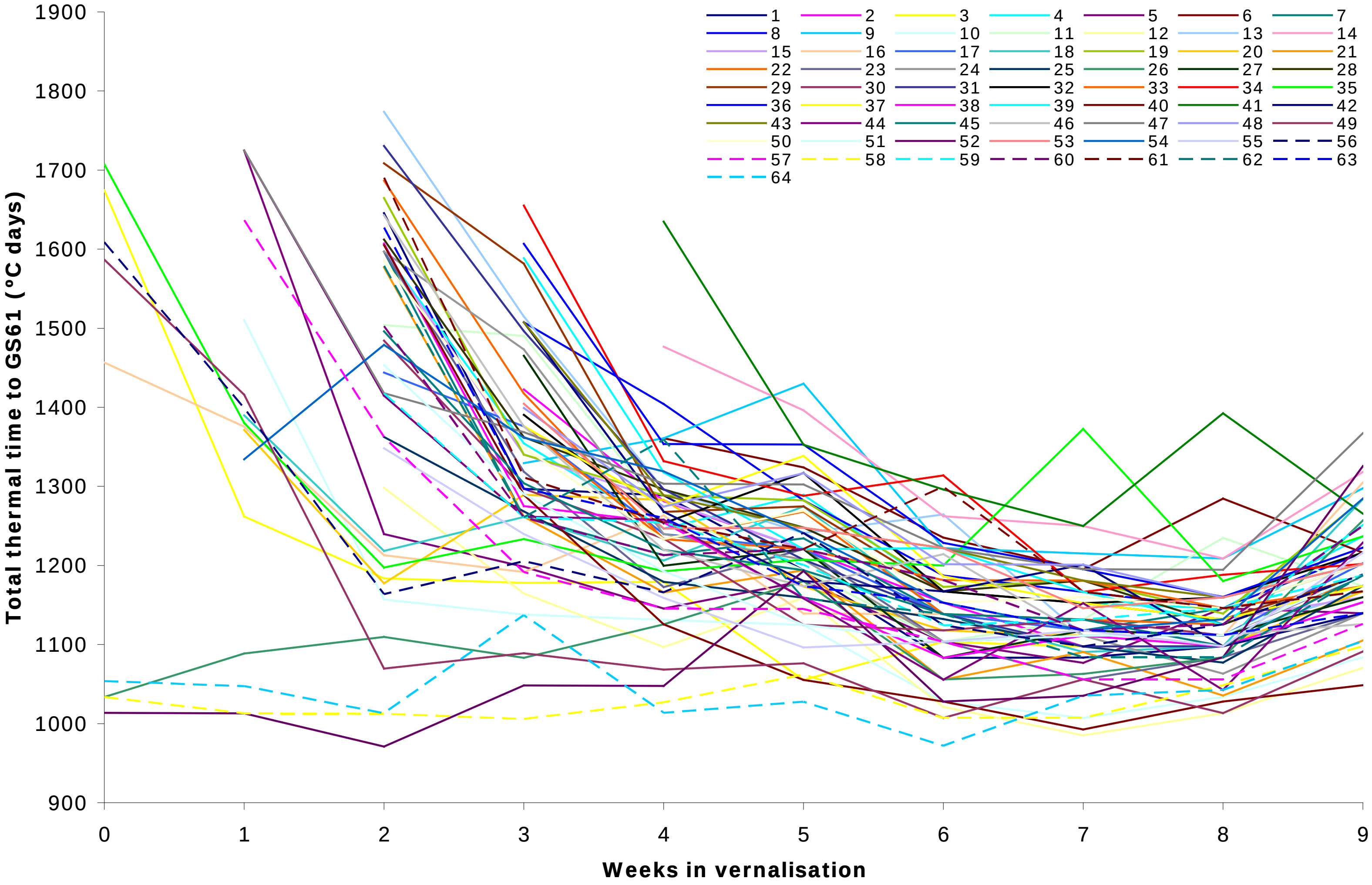


Figure 41. The effect of the number of weeks in vernalisation on the thermal time (^{o}C days) required to reach the start of flowering (GS61) for each of 64 varieties.

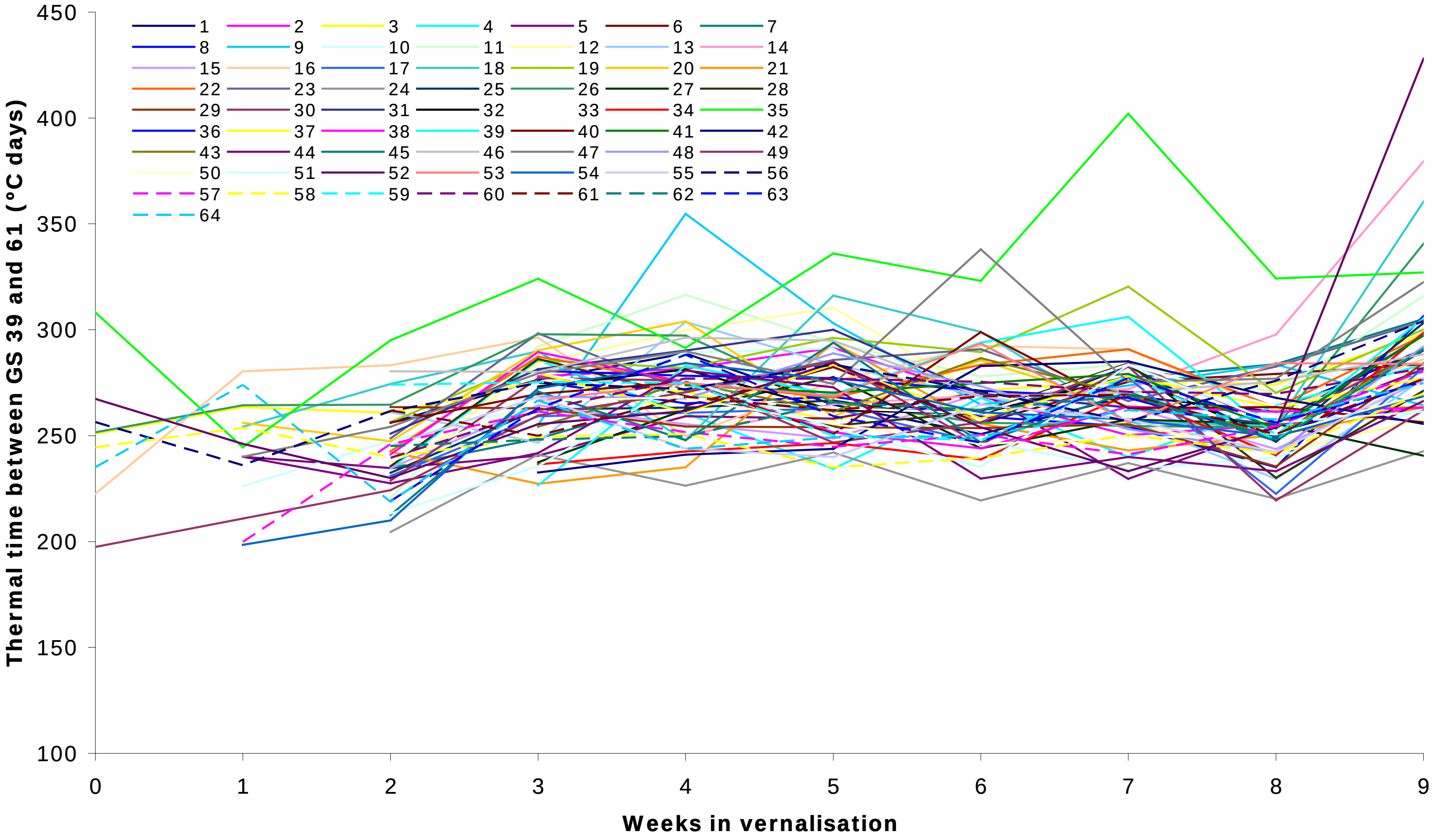


Figure 42. The effect of vernalisation duration on thermal time (^{o}C days) between GS39 and 61 for all varieties.

Number of leaves at GS39.

There was a positive relationship between the thermal time measured in the greenhouse to GS39 and the number of leaves that had developed by this growth stage (Figure 43). Generally, where varieties had experienced less vernalisation, varieties took longer to reach GS39 which allowed more leaves to develop. When a trend line was fitted to the data and constrained so that the origin was zero, the relationship was found to be highly significant ($P<0.01$; $R^2 = 0.66$; Figure 43). The phyllochron, calculated as the reciprocal of the slope, was 111°C days, consistent with the benchmark in the HGCA Wheat Growth Guide.

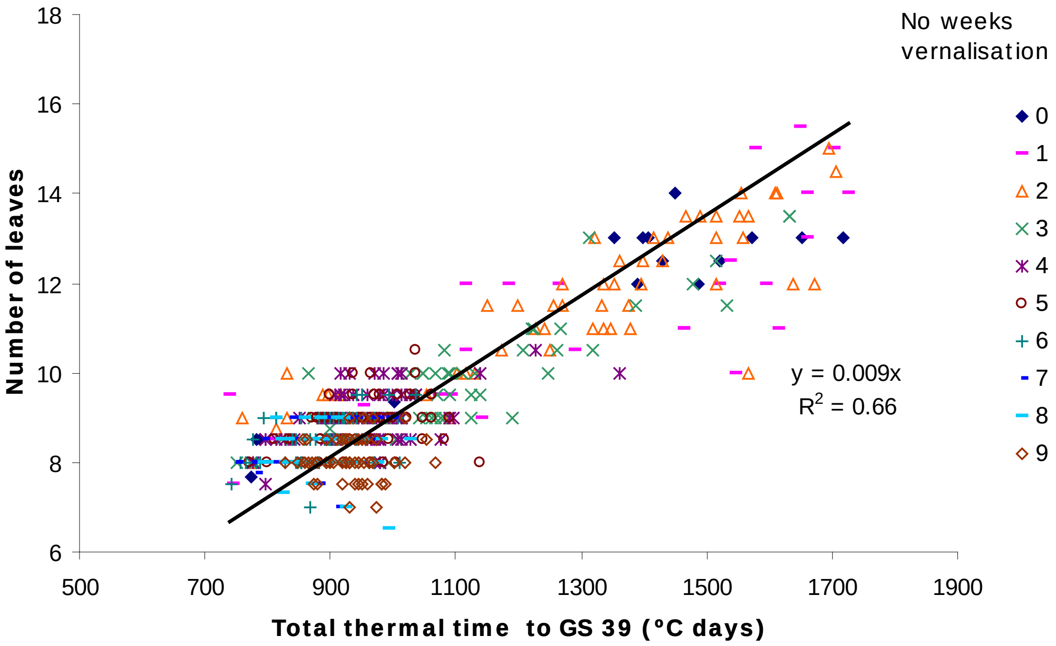


Figure 43. The relationship between the number of leaves at GS39 and the thermal time to GS39 for all varieties and all vernalisation treatments.

Number of nodes on the main shoot.

The average number of culm leaves (leaves associated with nodes) were counted after the end of the experiment for all varieties: There were significant ($P<0.001$) effects of the number of weeks in vernalisation and variety (Figure 44). However, where varieties had experienced 0 or 1 weeks in vernalisation, there was variation associated with the lack of full development to heading. When these data are removed from the analysis, vernalisation time was not a significant effect and only variety significantly ($P<0.001$) affected node number. There were no significant relationships between node numbers and vernalisation parameters. Varieties with least nodes (<3) were 35 Timber and 56 Spark and varieties with most nodes (>3.5) were 48 Haven, 52 Paragon and 53 Riband.

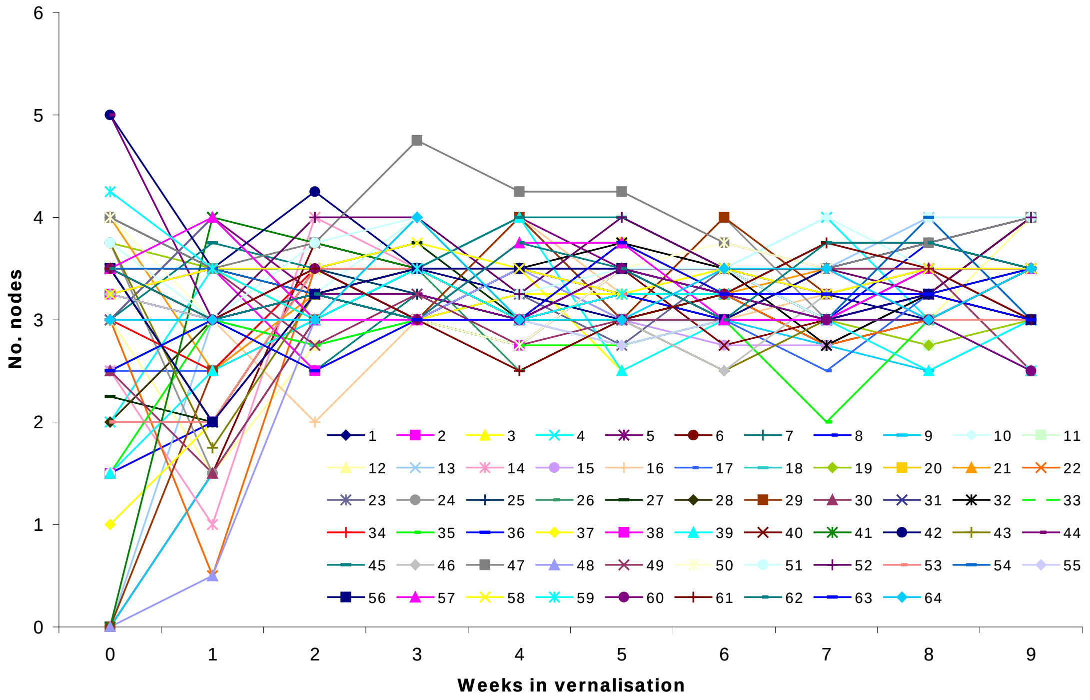


Figure 44. The effect of increasing time in the vernalisation chamber on the number of nodes for each of 64 varieties.

3.3.3. Photoperiod extension experiments

Weather Summary

The 2009 photoperiod experiment experienced the mildest winter months compared to the other two experimental seasons. January 2011 was particularly cold (1.1°C average temperature; Table 18); the cold winter in the 2011 season was then followed by a very dry March (5.5 mm total rainfall) compared to the 2009 and 2010 seasons (28.8 and 20.6 mm total rainfall, respectively; Table 18). There was little rainfall in the April of both 2010 and 2011 (8.3 and 2.7 mm total rainfall, respectively; Table 18). However, dryness is not expected to affect plant development.

Table 18. Average monthly temperature and total quarterly rainfall at Thriplow in each of the three harvest seasons (2009 – 2011).

Month	Average temperature (^{o}C)			Total Rainfall (mm)		
	2009	2010	2011	2009	2010	2011
October	11.1	9.9	11.9	38.8	37.4	51.3
November	7.2	7.1	9.0	60.7	86.4	29.8
December	4.7	3.6	3.0	19.7	54.8	18.1
January	6.7	2.6	1.1	46.3	29.3	52.5
February	4.2	3.9	3.1	44.8	62.1	35.1
March	5.9	7.0	6.8	28.8	20.6	5.5
April	8.1	11.1	10.1	19.8	8.3	2.7
May	12.7	13.9	12.0	21.0	18.6	11.1
June	14.5	16.8	16.7	35.5	22.6	46.9
Total				315.4	340.1	253.0

Effect of photoperiod on growth stages

On average over all treatments, plants reached key growth stages earlier in the 2011 experiment than in the 2009 experiment. GS31 was reached 126^{o}C days earlier and GS39 and GS61 were reached approximately 50^{o}C days earlier in 2011 (Table 19), although part of the GS31 difference may have been due to a slightly different assessment method employed in 2009. The average duration of the construction period (GS31 to 61) over treatments was 75^{o}C days shorter in 2009 than 2011. In 2010, due to grazing of the trial soon after establishment, not all assessments were carried out. However, the date of GS61 was assessed and, although this was on average later than in either 2009 or 2011, when converted to thermal time it was actually the quickest experiment to reach GS61 due to a later sowing date and warmer spring months, and also possibly to the grazing (Table 18).

Extending the photoperiod to 16 hours (EP) significantly ($P<0.001$) brought forward the dates of (or thermal times to) all stages from GS31 onwards in all experiments (Table 19). However, the photoperiod effect differed with growth stage and year. The photoperiod effects on time to GS31 in 2009 and 2011 were 73 and 172^{o}C days, respectively and on time to GS39 were 234 and 166^{o}C days. At GS61, photoperiod effects were more consistent between 2009 and 2011, at 183 and 178^{o}C days, respectively; the photoperiod effect on GS61 in 2010 was 121^{o}C days. There was a significant ($P<0.001$) photoperiod effect on the construction period duration in 2009, but no photoperiod effect in 2011 (Table 19).

There were also significant ($P<0.05$) effects of variety on growth stages, as well as significant interactions between photoperiod and variety treatments in all experiments. However, variety 64 (Bacanora) was always the earliest to reach every growth stage whether with extended or normal photoperiods (Table 19). The duration of the construction period also significantly differed among varieties and effects again differed with photoperiod treatments. However, variety number 44 (Alixan) had the shortest construction period in 2009 under extended photoperiod and in 2011 under normal photoperiod (Table 19).

Table 19. Summary of the dates and thermal times (^{o}C days from sowing) to significant growth stages (GS) and duration of the construction period (GS 31 – 61) for the extended photoperiod (EP) and normal photoperiod (NP) treatments in each experiment carried out at Thriplow. The summary includes standard deviations (SD) of the data and the number codes of varieties.

		2009		**2010**		**2011**	
		EP	**NP**	**EP**	**NP**	**EP**	**NP**
Date of GS31	**Mean**	13/04	19/04			02/04	16/04
	(SD)	(4.3)	(3.8)	-	-	(3.4)	(4.1)
	Max.	19/04	26/04	-	-	9/04	24/04
	(Var. no.)	(3,32,50)	(3,17)			(19,33)	(33)
	Min.	25/03	28/03	-	-	18/03	31/03
	(Var. no.)	(64)	(64)			(64)	(64)
Thermal time to GS 31	**Mean**	1096	1169			920	1092
	(SD)	(48)	(43)	-	-	(39)	(53)
	Max.	1163	1250	-	-	1009	1203
	Min.	912	930	-	-	764	899
Date of GS39	**Mean**	22/04	11/05			23/04	05/05
	(SD)	(2.1)	(5.0)	-	-	(4.6)	(4.3)
	Max.	27/04	19/05	-	-	01/05	10/05
	(Var. no.)	(4,19,27,32)	(32,36,48)			(14)	(14,19)
	Min.	17/04	22/04	-	-	11/04	22/04
	(Var. no.)	(64)	(64)			(64)	(64)
Thermal time to GS 39	**Mean**	1202	1436			1188	1354
	(SD)	(24)	(64)	-	-	(66)	(62)
	Max.	1253	1531	-	-	1303	1427
	Min.	1141	1200	-	-	1032	1171
Date of GS61	**Mean**	18/05	31/05	31/05	08/06	14/05	26/05
	(SD)	(4.8)	(5.4)	(2.4)	(3.3)	(3.3)	(6.6)
	Max.	29/05	07/06	07/06	15/06	22/05	07/06
	(Var. no.)	(14,19)	(45)	(32)	(14)	(45)	(6,43)
	Min.	06/05	10/05	24/05	27/05	07/05	10/05
	(Var. no.)	(64)	(64)	(64)	(64)	(64)	(64)
Thermal time to GS 61	**Mean**	1531	1714	1441	1562	1482	1660
	(SD)	(66)	(83)	(34)	(52)	(45)	(95)
	Max.	1682	1818	1546	1669	1600	1830
	Min.	1371	1417	1343	1376	1388	1433
Days from GS31 to 61	**Mean**	35.4	41.2	-	-	41.9	40.3
	(SD)	(5.3)	(4.8)			(3.2)	(5.4)
	Max.	47.8	51.1	-	-	50.5	51.5
	(Var. no.)	(13)	(45)			(64)	(6,43)
	Min.	25.2	28.4	-	-	36.0	28.0
	(Var. no.)	(44)	(21)			(10)	(44)
Thermal time from GS 31 to 61	**Mean**	435	545	-	-	562	568
	(SD)	(69)	(72)			(40)	(79)
	Max.	609	681	-	-	668	741
	Min.	297	357	-	-	486	399

Despite the apparent differences between 2009 and 2011 growth stage results, there were significant (P<0.001) relationships between the variety results for the two seasons when the thermal times to growth stages 31, 39, 59 and 61 were examined (Figure 45). Relationships were significant when both the extended photoperiod (EP) and normal photoperiod (NP) results were plotted, although the amount of variation accounted for in the relationships was always better for the NP than the EP relationships (Figure 45). The relationships between 2009 and 2011 for GS31 were the weakest of all the growth stages (R^2 = 0.19 and 0.23 for EP and NP, respectively; Figure 5.2.1.a, b), and were controlled by the very early variety, 64. This may have been due to the slightly different method of assessment used in 2009. The variation accounted for was also low in the GS39 EP relationship (R^2 = 0.17; Figure 45.c) due to a very narrow range of thermal times to GS39 in 2009. The growth stage where varieties showed most consistency over the two years was GS59 (Figure 45.e, f).

GS59 was also the only growth stage where there was a significant ($P<0.05$) relationship between the photoperiod effects shown in the 2009 experiment and the photoperiod effects in the 2011 experiment (Figure 46.c.). At the other growth stages (GS 31, 39, 61), there were no relationships between photoperiod effects in 2009 and those in 2011 (Figure 46.a, b, d), indicating a strong interaction between years, photoperiod treatments and varieties. The coefficients of variation for all assessments in each experiment very small (≤3%) so variation between the two years was not due to within-experiment variation or measurement errors; these were genuine interactions between variety, photoperiod and year.

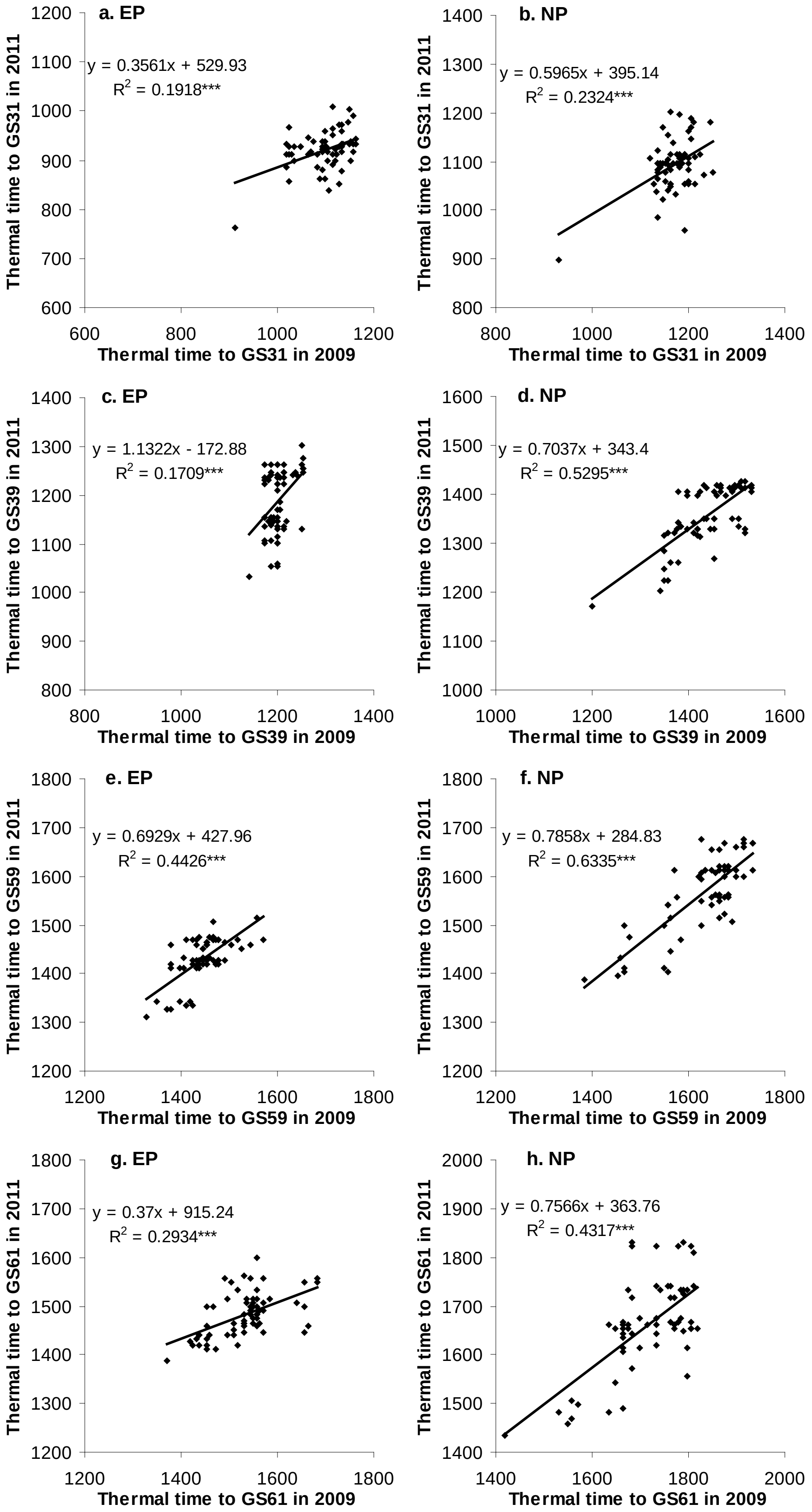


Figure 45. Relationships between thermal time (^{o}C days) to growth stages of varieties grown in 2009 or 2011 grown under extended photoperiod (EP; a, c, e, g) or normal photoperiod (NP; b, d, f, h)

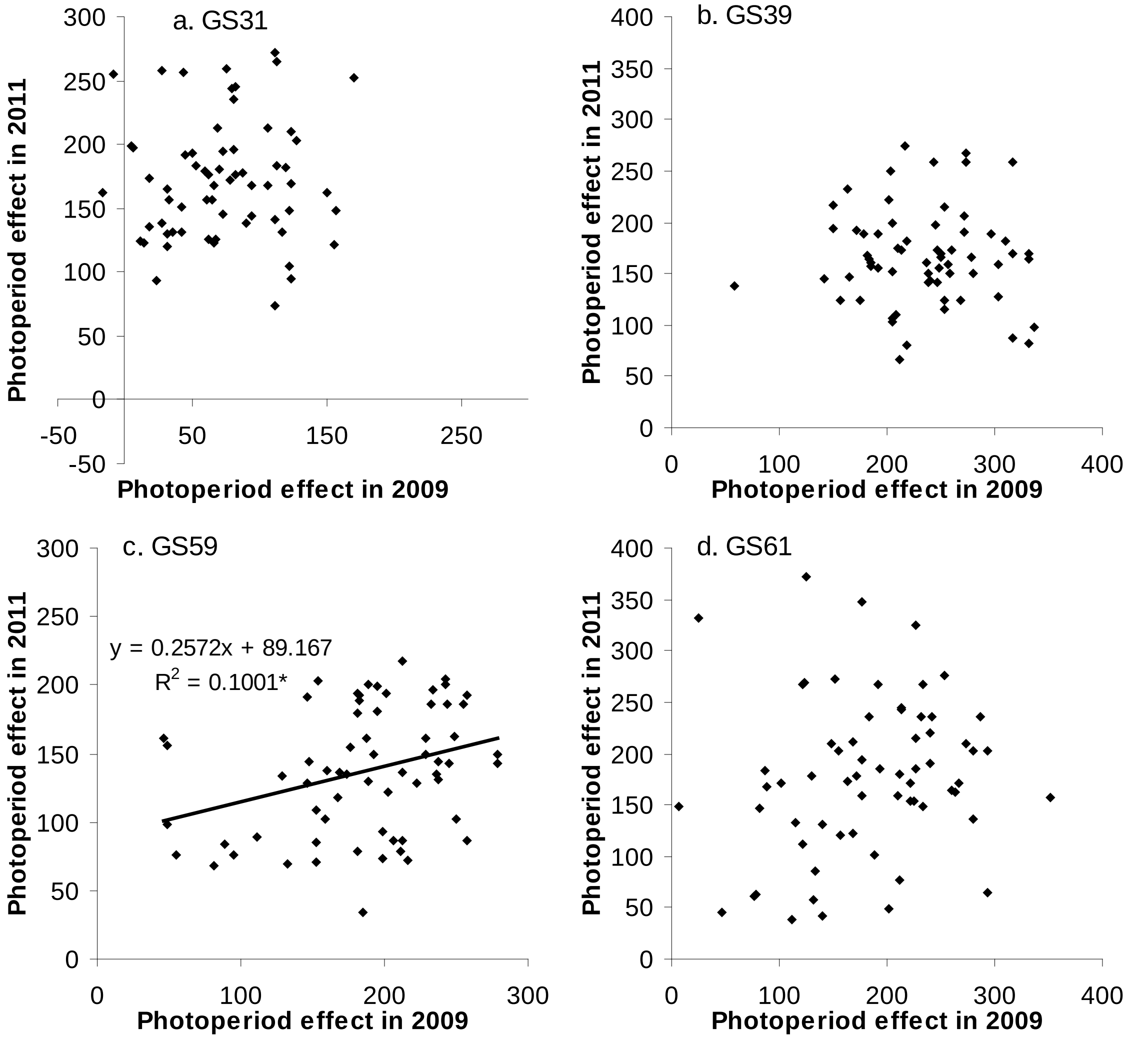


Figure 46. Relationships between effects of extended photoperiod on 64 varieties in 2009 and in 2011 for: a. GS31; b. GS39; c. GS59; d. GS61.

Effect of photoperiod on final leaf number and phyllochron

On average over all treatments, main shoots produced very similar numbers of leaves in 2009 (10.2) and 2011 (10.1). Due to the grazing problems in the 2010 experiment, leaf numbers were not measured. Photoperiods extension significantly reduced the mean number of leaves in 2009 by 1.51 (P = 0.023) and in 2011 by 1.76 (P = 0.037) (Table 20). There were also significant (P<0.01) variety effects in both experiments, but in neither experiment did variety and photoperiod treatments significantly interact.

When the variety means of the two experiments were plotted against each other, significant (P<0.01) relationships were found for the average leaf number over photoperiod treatments and also the extended photoperiod treatments (Figure 47 a and b). There were no relationships between the two years when the normal photoperiod or photoperiod effect data were examined (Figure 47 c and d).

Table 20. Summary of the total leaf number and rate of leaf emergence (Phyllochron; ^{o}C days taken for a leaf to emerge) for the extended photoperiod (EP) and normal photoperiod (NP) treatments in each experiment carried out at Thriplow. The summary includes standard deviations (SD) of the data and the number codes of varieties.

		2009		**2011**	
		EP	**NP**	**EP**	**NP**
Leaf number	**Mean**	9.45	10.96	9.17	10.94
	(SD)	(0.32)	(0.40)	(0.45)	(0.55)
	Max.	10.08	11.58	10.25	11.88
	(Var. no.)	(13,50,60	(3,63)	(51)	(29)
	Min.	8.75	10.00	8.48	9.08
	(Var. no.)	(33)	(9,35,53)	(47)	(40)
Phyllochron Feb-Mar*	**Mean**	119	130	124	122
	(SD)	(6.3)	(8.2)	(8.3)	(7.3)
	Max.	135	152	144	142
	(Var. no.)	(19)	(1)	(34)	(50)
	Min.	106	114	104	106
	(Var. no.)	(49)	(23)	(51)	(31)
Phyllochron post Mar	**Mean**	115	114	198	98
	(SD)	(9.6)	(12.6)	(27.9)	(16.4)
	Max.	134	152	268	174
	(Var. no.)	(16)	(47)	(49)	(40)
	Min.	91	75	146	74
	(Var. no.)	(7)	(64)	(14)	(29)
Mean phyllochron	**Mean**	109	114	161	110
	(SD)	(5.1)	(4.8)	(14.3)	(9.4)
	Max.	126	123	196	148
	(Var. no.)	(15)	(44)	(49)	(40)
	Min.	101	104	134	96
	(Var. no.)	(8)	(16)	(14)	(32)

* In 2009 this phyllochron was measured mid-January to March

Phyllochron (the mean thermal time between emergence of successive leaves) effects differed between seasons. In 2009, the overall average phyllochron was 112^{o}C days, whereas in 2011 it was 136^{o}C days. However, there were also differences within seasons between photoperiod treatments and the periods over which the phyllochrons were measured (Table 20). When phyllochron was determined over the period from February (mid-January in 2009) to the end of March, there was no significant effect of photoperiod treatment in either season, and a significant ($P<0.001$) variety effect in 2009 only. In contrast, there was a significant ($P = 0.044$) effect of photoperiod in 2011 when phyllochron was determined for the period post March to GS39, with the phyllochron of the extended photoperiod treatment 100^{o}C days longer than that of the normal photoperiod treatment (Table 20). This effect was not seen in 2009 (Table 20), but in both seasons there were significant ($P<0.001$) variety effects and significant ($P<0.001$) interactions between variety and photoperiod.

When regression analysis was carried out on the 2009 data, the majority (64%) of the variation in final leaf number could be explained by variation in the thermal time to GS39 (Figure 47). Phyllochron pre- and post-March only explained 5.5% and 4.2% of the variation in final leaf number, respectively, when tested individually. This differed from the 2011 data, where the same analysis showed that the phyllochron measured post-March explained 76% of the variation in final leaf number when tested individually, with the pre-March phyllochron explaining 13% of the variation. The thermal time to GS39 explained slightly less of the variation in final leaf number (57%) than in 2009. Including a combination of these factors in a regression model could explain around 85% of the variation in both seasons. However, given the unexpectedly large interactions in these experiments, such a model cannot be expected to be predictive.

Effects of major Ppd genes under extended and normal photoperiod treatments

An unbalanced analysis of variance revealed significant (P<0.05) effects of major photoperiod genes (*Ppd1* and *Ppd2*) on thermal time to GS31, GS39, GS61 as well as the duration of the construction period (GS31 to 61) and phyllochron (Table 21) in 2009 and 2011. Genotype effects also significantly (P<0.05) varied with photoperiod treatment in the case of GS39, 61 and post-March phyllochron (Table 21) in 2009, and GS31, 61 and pre-and post-March phyllochron in 2011. However, due to the low numbers of varieties with certain genotypes, some of these results should be treated with caution. Generally *Ppd1* reduced the thermal time to key growth stages compared to p*pd*, and the reduction was generally greater under the normal photoperiod treatment compared to the extended photoperiod treatment (Table 21). This meant that the photoperiod effect on the thermal time to key growth stages was generally reduced where *Ppd1* was present, apart from at GS39 in 2011 where there was no difference in the photoperiod effect between the two genotypes (Table 21).

There was a significant (P<0.05) effect of genotype on total leaf number in 2011 only, whereby *Ppd1* and *Ppd2* both reduced the total leaf number under the normal photoperiod treatment only (Table 21), although again results should be treated with caution.

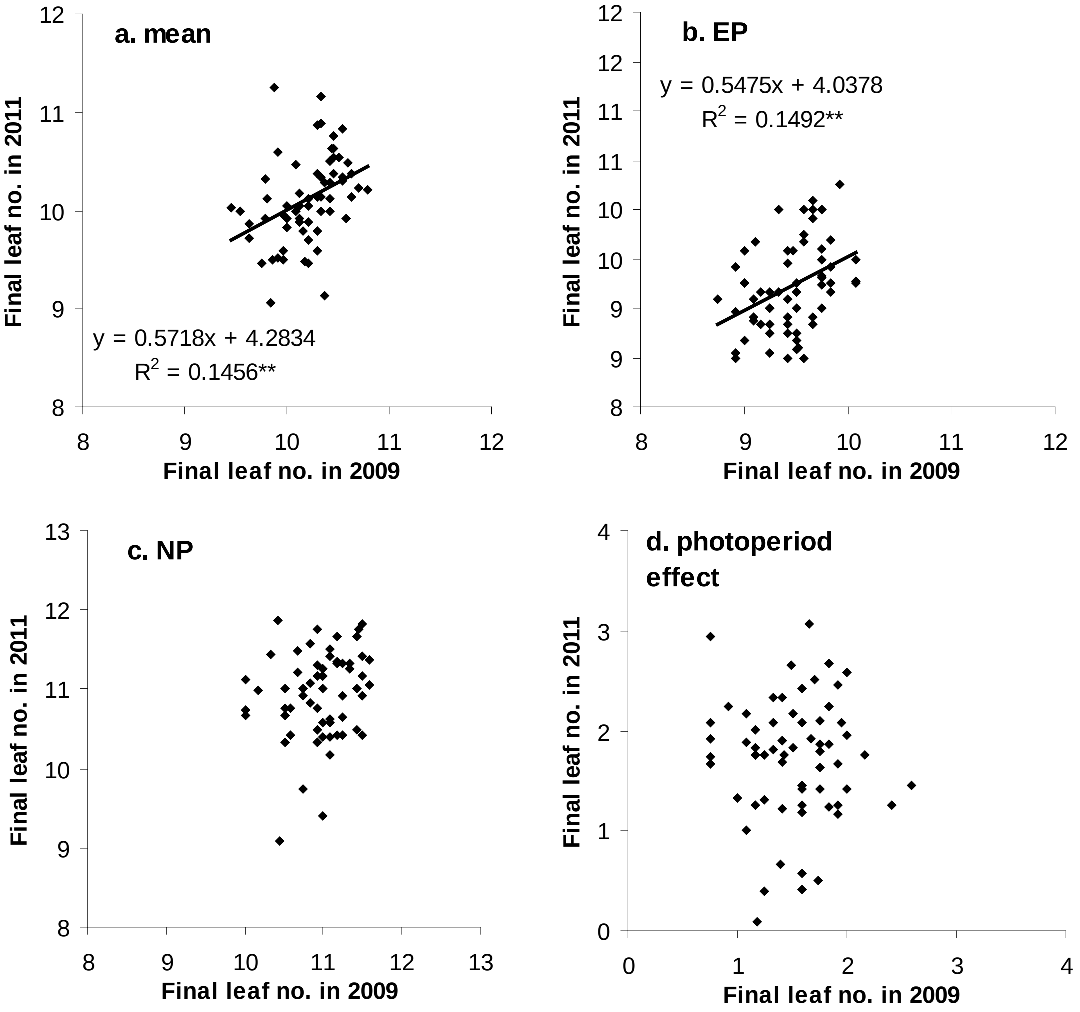


Figure 47. Relationships between total number of leaves per stem of varieties grown in 2009 or 2011. Graphs describe: a. effect averaged over photoperiod treatments; b. extended photoperiod (EP) values; c. normal photoperiod (NP) values; and d. photoperiod effect (NP-EP) values.

Table 21. Effects of *Ppd* genes on thermal times to key growth stages, duration of the construction period (GS31 to 61), total leaf number and phyllochron under extended (EP) and normal photoperiod (NP) treatments in 2009 and 2011 experiments. Different LSDs should be used for comparing genotypes as follows: min. rep. for comparing genotypes with the fewest varieties; Min.-max. for comparing genotypes with the most to those with the fewest varieties; max. rep for comparing genotypes with the most varieties.

Year	**Genotype (former annotation and no. varieties)**	**GS31 (^{o}C day)**		**GS39 (^{o}C day)**		**GS61 (^{o}C day)**		**GS31 to 61 (^{o}C day)**		**Total leaf number**		**Phyllochron Feb–Mar (^{o}C day)**		**Phyllochron Post-Mar (^{o}C day)**	
		EP	**NP**	**EP**	**NP**	**EP**	**NP**	**EP**	**NP**	**EP**	**NP**	**EP**	**NP**	**EP**	**NP**
2009	*ppd* (53)	1099	1174	1205	1453	1545	1737	445	564	9.48	10.97	119	131	114	117
	Ppd1 (9)	1083	1147	1187	1348	1464	1598	380	451	9.36	10.87	117	127	113	100
	Ppd2 (1)	1018	1141	1174	1376	1550	1665	532	524	8.92	11.50	115	114	121	101
	Ppd1+2 (1)	1114	1137	1200	1342	1417	1557	304	420	9.25	10.43	118	136	127	100
	LSD (min. rep.)	89.4		77.7		120.7		61.3		0.938		32.7		25.7	
	LSD (min.-max.)	63.8		55.1		85.5		43.6		0.669		37.9		18.5	
	LSD (max. rep.)	33.1		4.5		6.9		6.4		0.358		106		21.0	
2011	*ppd* (53)	926	1105	1208	1373	1492	1687	566	582	9.20	11.07	124	121	193	94
	Ppd1 (9)	891	1030	1093	1258	1429	1532	538	502	9.03	10.46	125	123	223	113
	Ppd2 (1)	885	1095	1107	1328	1475	1607	591	513	8.97	10.42	119	124	248	106
	Ppd1 + 2 (1)	892	985	1058	1203	1427	1470	535	485	9.00	9.08	130	123	234	174
	LSD (min. rep.)	82.1		90.8		117.6		117.9		1.132		29.0		47.3	
	LSD (min.-max.)	58.4		64.3		83.3		83.7		0.833		28.4		35.2	
	LSD (max. rep.)	14.2		5.3		6.9		16.3		1.430		90.1		69.1	

3.4. Modelling

3.4.1. Aims and Strategies

In the modelling task of this project the intention was to explore the extent to which growth stages of field-grown wheat varieties could be predicted in UK conditions. If successful predictions could be achieved, the resultant understanding could be used to devise phenologies (timings of particular growth stages) to adapt wheat better to global warming, hence the UK's capacity to adapt wheat would be enhanced. Also, on a region, field and year basis, plant development dictates many aspects of crop agronomy, hence a capacity to predict growth stages would enable UK wheat management practices to be scheduled better and improved, e.g. variety choice, and sowing dates, including latest safe sowing dates, timing of agrochemical applications, hence scheduling of agrochemical supplies, fertiliser applications, and harvest scheduling. Thus, the ultimate aim was to develop a growth stage prediction scheme for use by wheat breeders and variety testers, but also that could be used by agrochemical suppliers, agronomists and growers.

There were several extant models of wheat development available at the outset of this project, the most prominent being Sirius, because it was under active development and had a comprehensive literature (Jamieson *et al*., 1998; Lawless, 2005; Richter & Semenov, 2005; Matre *et al*.,2007; Semenov,2009). The original intention was to calibrate Sirius's variety-specific phenology parameters for UK conditions, using UK experimental data, in collaboration with the authors of Sirius at the New Zealand Institute for Plant & Food Research (formerly Crop & Food Research).

However, when tested on UK data, the version of Sirius adopted for this work (Sirius 2000, calibrated in New Zealand for UK varieties) gave GS61 dates that were all significantly later than observed. These discrepancies were attributed largely to the model not representing vernalisation adequately at relatively high vernalising temperatures (11-17°C). However, after considerable effort, the origin of these effects in the model could not be identified or corrected so the Steering Group approved termination of work with Sirius and adoption of a more empirical approach to the description of phenology, similar to that developed by Angus *et al*. (1981) and used by Weir *et al*. (1984). Although this approach depended on fitting parameters to observed data, calibration of Sirius for UK varieties also involved fitting parameters (Jamieson & Munro 2000), thus both approaches were not dissimilar and both would require subsequent independent validation before adoption by the industry.

It was planned that the model would be calibrated using field plot data (available through HGCA) generated in support of the HGCA Recommended List (RL). It would then be validated using the new data generated by ERYCC experiments. It was believed at the outset of the project that varietal differences in vernalisation requirements were sufficiently understood for models to be parameterised for these effects, and that the photoperiod extension trials would allow varietal differences in the less well understood differences in photoperiod responsiveness to be parameterised. However, it proved that field data from RL testing gave inadequate discrimination between the responsiveness of a variety to vernalisation and its responsiveness to photoperiod, and the literature was not found to be sufficiently explicit of the way that responses to vernalisation and photoperiod should be integrated, so attribution of phenological observations to either response tended to be arbitrary.

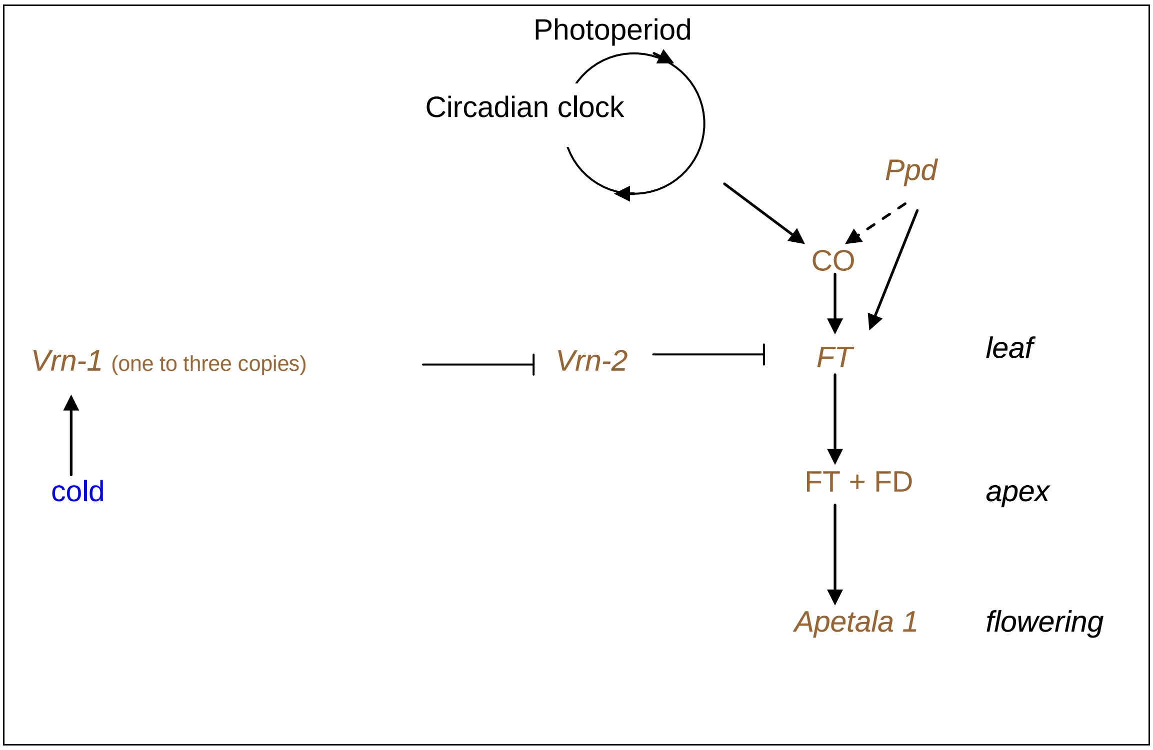


Figure 48. Simplified diagram showing some known interactions between genes controlling flowering of wheat. Genes are shown in brown, positive pathways are arrows (tentative link dotted), repressing pathways are bars.

To assist in this dilemma we turned to the recently developed understanding of the genetic control of vernalisation in wheat as described by Laurie and co-workers (Higgins *et al.*, 2010) and summarised in Figure 48. In this analysis, the *Vrn2* gene represses flowering by reducing the appearance of flowering factors (FT and FD) in the shoot apex. During the vegetative period *Vrn2* is expressed, and then *Vrn1* is expressed in (or after) cold conditions which inhibits *Vrn2* and so allowing FT+FD to accumulate in the shoot apex, prompting the initiation of flowering. Production of FT is also controlled by photoperiod through the *Ppd* genes. Diaz *et al.* (2011) showed that wheat varieties Claire, Malacca and Hereward (also tested in this project) differ in their numbers of copies of *Vrn1* and that this results in varying expression of this gene. It therefore appeared that some of the variation in vernalisation responsiveness of the varieties studied here could be explained by direct genetical characterisation.

Thus subsequent modelling work focussed particularly on vernalisation responsiveness, using data generated under the more controlled conditions described in Sections 0 and 0 to test whether varietal variation could be explained, and to work towards calibrations of vernalisation requirement that might be applied in the field. It was the intention that these calibrations should be validated using field data from both within and outside this project (see below), but this work remains incomplete at the time of reporting.

3.4.2. Sources of UK Data for modelling wheat phenology

Data from Recommended List experiments

Data for Latest Safe Sowing Dates

Data were obtained from HGCA relating to the assessment of latest safe sowing dates as reported in the RL. Data were generated from experiments at NIAB, Cambridge from 2002 to 2007. In each year there were three sowings: in mid March, late March and mid April and plants were scored (1-9) in late July for the extent to which all shoots had 'headed', i.e. come to ear and flowered. The proportion of shoots of each variety which had headed was estimated from these heading scores. The data represented 76 varieties, but not all varieties in all years. Only varieties with data from three or more years were used. Associated local weather data were obtained from ADAS Boxworth.

Data for Rate of Development to GS31

The RL also reports rates of development to GS31 from early, normal and late sowings. These are derived from three autumn sowings of all candidate varieties made at both Throws Farm, Essex, and Headley Hall, Yorkshire. Data were provided by HGCA and Masstock from 2003 to 2009 relating to about 40 varieties in each year, but with some varieties differing between years. Associated local weather data were obtained from the Met Office.

Data from this project

The data already described in Sections 0 and 0 were used for modelling. Weather data were normally obtained from automated weather stations or loggers installed within the experimental area. Where weather data were not available, a temperature dataset was either interpolated from the nearest recording site, or interpolated using the Met Make module of the Irriguide programme (Bailey & Spackman, 1996) for the Ordnance Survey grid reference and altitude of the site. Met Make interpolates temperature using a least squares model from 5 surrounding weather stations run by the UK Meteorological office, and gives good correlations of estimated vs. actual mean temperature (Silgram *et al.*, 2007). To achieve consistency, although hourly temperature had been measured for all the measured sites, the dataset was reduced to maximum and minimum daily temperatures.

Hours of daylight were calculated using the equation published in Weir *et al*. (1984). This takes into account the twilight period as well as when the sun is above the horizon. Daylengths for extended photoperiod treatments at Thriplow in 2009 and 2010 (2011 data were not included) were set at 16.5 hours from 21st December, until the ambient daylength exceeded this.

Thermal time (°C days) was accumulated from daily temperatures: for each day the difference between the mean of the minimum and maximum temperatures (t_i) and a base temperature (t_b) was calculated. If both the minimum and maximum were below the base temperature the daily temperature was set to zero; if only the minimum was below the base temperature then the daily temperature was set at half the difference between the base and the maximum.

3.4.3. Modelling Results

Using Sirius and the Angus approaches

Attempts were made to calibrate the phenology parameters of Sirius and to derive and fit a simpler expression to describe wheat development, using the approach of Angus *et al.* (1981). The outcome of this work was to conclude that (a) breeders' knowledge of varietal differences in vernalisation sensitivity was insufficiently quantitative to parameterise models of plant development in wheat, (b) confounding between vernalising temperatures and daylength changes in spring prevented discrimination between varietal vernalisation and photoperiod responses using field data with different sowings, hence (c) further experimentation was necessary to separate the vernalisation and photoperiod responses (or 'requirements') of UK wheat varieties.

Modelling vernalisation

The vernalisation requirements determined in the vernalisation experiment (Section 3.3.2) were expressed in terms of weeks in a vernalisation chamber, but these plants all experienced some additional vernalisation after they had been transferred to the glasshouse. The results are thus experiment-specific; they could not be used to interpret other field observations, or indeed other similar experiments involving glasshouse cultivation because the extent of vernalisation caused in the vernalisation chamber, the glasshouse or the field could not be inter-related. Modelling work was therefore undertaken to explore whether the different times to GS39 for all the (10) vernalisation treatments applied to one variety could be reconciled by translating these into one common vernalisation requirement, expressed in terms of vernal time, V where

$$V = (t_i - t_b)_+ \times (t_v - t_i)_+ \qquad \text{Eqn 4}$$

Vernal time, the extent (arbitrary units) to which any day affected progress towards the fully vernalised state, was accumulated from hourly temperatures interpolated using a linear function between the minimum and the maximum. For each hour the difference between the maximum vernalising temperature (t_v) and the observed temperature (t_i) was multiplied by the difference between t_i and the base temperature (t_b, taken as 0°C). If hourly t_i exceeded t_v or if t_b exceeded t_i, the result was taken as zero (Figure 49). The sum of the 24 hourly products was divided by 24 to give daily vernal time, V.

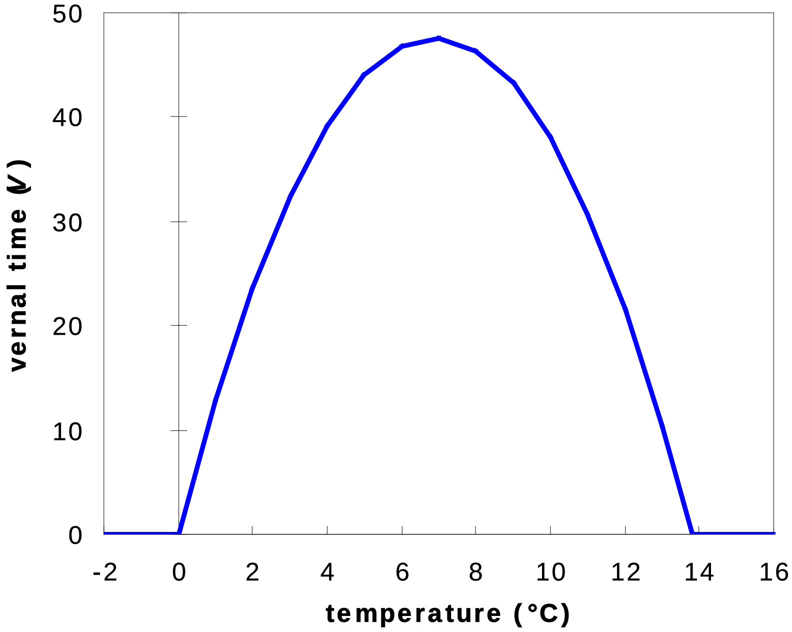


Figure 49. The relationship assumed between vernal time and observed temperature, with t_b and t_v set at 0°C and 13.8°C respectively.

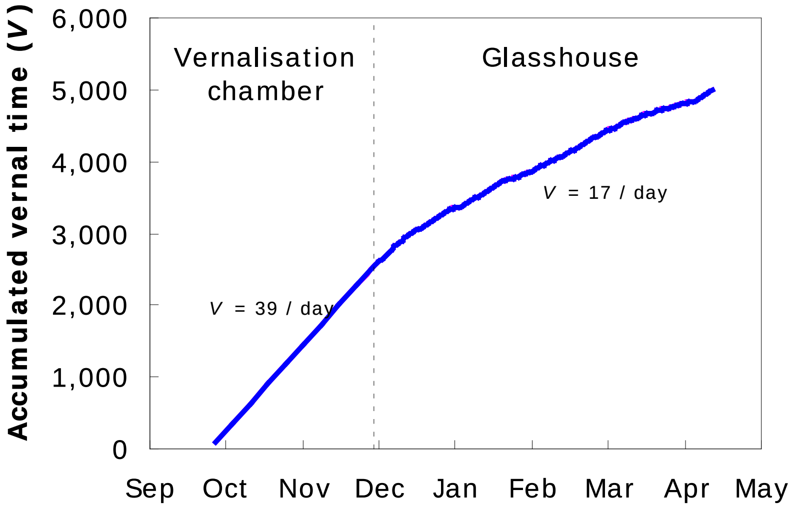


Figure 50. The pattern of vernal time (V) accumulation through the vernalisation experiment, calculated by the method illustrated in Figure 49. The mean rate was 39 day^{-1} in the chamber and 17 day^{-1} in the glasshouse.

Optimisation of t_v showed that a value of 13.8°C minimised the standard deviation of V for all treatments. If t_v was allowed to vary between varieties, no additional variation was accounted for. Thus, t_v was set at 13.8°C for all varieties. With t_b set at 0°C, the mean rates of accumulation of vernal time were 39 day^{-1} in the chamber and 17 day^{-1} in the glasshouse (Figure 50).

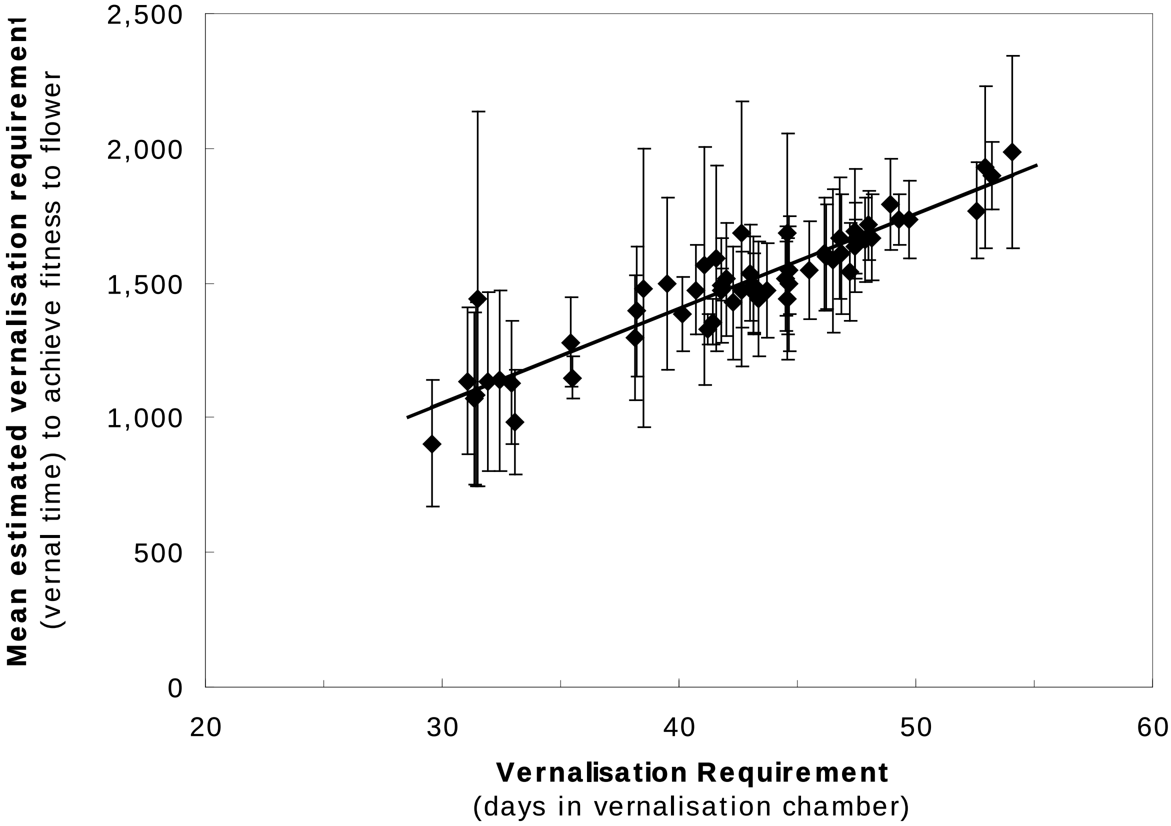


Figure 51. Relationship between vernalisation requirements modelled in vernal time and determined from differentiating a fitted exponential curve. The slope is 35.1 per extra day in the vernalisation chamber; r^2 = 0.863.

There was a close relationship between vernalisation requirements determined in this way and vernalisation requirements determined by curve fitting of thermal time to GS39 to weeks in the vernalisation chamber (Section 0), the slope being 35 per day (Figure 51). Thus, it seems feasible that vernalisation requirements specific to the experiment conducted here might be extrapolated to other conditions, such as those in the photoperiod extension experiment described in Section 3.3.3. It might also be possible to interpret growth stages in the field trials described in Section 3.3.1.

3.5. Discussion

3.5.1. How varieties have changed over time

Many previous studies have estimated rates of increase in grain yield of wheat (Table 22). These either used experiments to make direct comparisons (as here) between varieties introduced over a range of years, or they made indirect comparisons (e.g. Silvey, 1981) via series of variety experiments conducted over a number of years, with varieties common over years providing a means of assessing and eliminating environmental effects. Rates of genetic gain inferred from both types of study have then been compared with national reports of on-farm yields to infer the contribution of breeding to overall yield improvement. Note that national rates of yield change will include interactions between genetic changes and environmental changes, including changes in husbandry. It is generally unclear in indirect comparisons whether rates of genetic gain include or exclude these interactions. Also, responsibility for these interactions is a matter of debate; breeders may or may not have been responsible, either intentionally or unwittingly. Thus it would appear that direct comparisons provide the most objective test of the contribution of breeders to yield improvement. However, even here, ‘old’ varieties are generally grown with current husbandry, so direct comparisons cannot assess any contribution of plant breeding to interactions with husbandry or with other environmental changes.

None of the direct comparisons known to us have included as many varieties (64) or as many experiments (15) as in this project. This has allowed rates of improvement to be assessed separately for bread and feed types and for just those varieties which were widely grown (‘landmark’ varieties). Other studies have sometimes confounded quality and age of varieties.

Table 22. Summary of previous studies analysing yield progress with year of introduction.

Source	**Variety introduction dates** *(range)*	**Data description and Method**	**Genetic gain** *(t/ha/decade)*
Direct comparisons – UK			
Austin *et al.*(1980)	1953 - 1978	2 sites, 1 season, 6 varieties	0.42
Austin *et al.* (1989)	1953 - 1986	1 site, 3 seasons, 7 varieties	0.62
Shearman *et al.* (2005)	1972 - 1995	1 site, 3 seasons, 8 varieties	1.19
Jones *et al.* (2010)	1936 - 2000	2 sites, 3 seasons, 13 varieties	0.63
Indirect comparisons – UK			
Silvey (1981)	1947 - 1978	NIAB/RL data and MAFF/Defra national yields.	0.80
Silvey (1986)	1947 - 1983		0.51
Philpott *et al.* (2008)	1982 - 2007		~0.70
Example international studies			
Waddington *et al.* (1986)	1950 - 1982	Mexico – Direct	0.59
Bell & Fischer (1994)	1968 - 1990	Mexico – Indirect	1.03
Rodrigues *et al.* (2007)	1940 - 1992	Brazil – Direct, 7 varieties	0.45
De Vita *et al.* (2007)	1900 - 1990	Italy – Direct, 14 vars. of *T. durum*	0.20
Anon. (2008)	1980 - 2008	Denmark – Indirect	0.82-1.00

A crucial element of variety improvement has been increased resistance to lodging. Austin in his studies used netting to prevent lodging of older varieties. The paper of Shearman *et al*. excluded two varieties that lodged from their published analysis (10 varieties were included in their experiments). Differential lodging was a feature of some of the experiments reported here, despite use of plant growth regulators, but it only accounted for a small proportion of the genetic improvement in yield and its effects were retained within the rates reported. The rates of 0.52 and 0.62 t/ha/decade for feed and bread varieties, respectively, are in keeping with the range of previous reports (Table 22). The difference between bread and feed types is probably not significant. The lack of improvement from a quadratic over a linear fit indicates that there is no evidence of a slowing in the rate of genetic improvement.

It is very clear from data on average farm yields (Figure 52) that there has been a slowing of farm yield improvement in the last decade. However, there have been previous pauses, most notably in the 1960s, that were followed by increased rates. The mean rate of improvement in farm yields over a similar period to the cultivation of the varieties tested here shows a similar rate of improvement (0.7 t/ha/decade). However, it cannot be deduced that agronomy or climate have not affected yield progress because there has been a decrease in the rate of farm yield improvement (R^2 for linear fit = 0.66; R^2 for quadratic fit = 0.70) over the last 3 decades, whereas there is no evidence for a change in rate of genetic improvement.

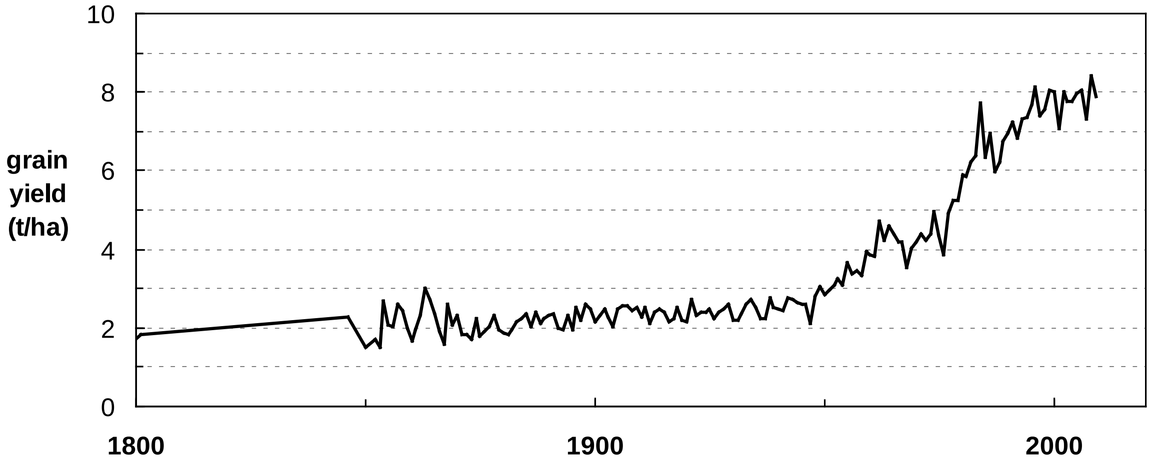


Figure 52. Annual average farm yields of winter wheat from 1800 to 2009. Data from national statistics, augmented by data from Percival (1948). Rates of increase in each successive decade between 1950 and 2009 were: 0.9, -0.2, 1.0, 0.6, 1.1, and 0.3 t/ha/decade. The rate since 1980 was 0.70 t/ha/decade.

Further analysis of which elements led to the yield increases seen in this study showed significant linear increases in the number of grains per m^2, through increases in the number of grains per ear and ears per m^2 (all 64 and landmark feed varieties only). There was no effect of year of introduction on TGW, consistent with the study of Shearman *et al.* (2005). The increases seen in the number of grains per m^2 in this project (1,231 and 1,323 grains/m^2/decade for landmark feed and bread-making varieties, respectively) were less than the 2,166 grains/m^2/decade increase found by Shearman *et al.* (2005). The estimate by Shearman *et al.* (2005) of the increase in the number of ears per m^2 with year of introduction (37 ears/m^2/decade) was also higher than that found in the landmark feed varieties (13 ears/m^2/decade), and there was no relationship in the landmark bread-making varieties. The differences may be due to the method used to determine the number of ears per m^2 in this study compared to the direct counting method used by Shearman *et al.* (2005). Although the number of ears in a quadrat was counted for each plot, these counts were found to be unreliable and instead calculations from combine yield, TGW and grains per ear were used to calculate the number of ears per m^2. This has resulted in a number of ears per m^2 generally lower than the benchmark of 400 ears/m^2 quoted in the HGCA wheat growth guide. Austin *et al.* (1989) also found that the number of ears per m^2 increased with year of introduction, and the average of their counts was 412 ears/m^2, determined by the counting method which, in their case, was carried out in late June.

Total crop biomass and harvest index were also found to be increasing with year of introduction in the full set of 64 varieties and landmark feed varieties. There was no effect of year of introduction on crop biomass in landmark bread-making varieties. The slowing of the increase in harvest index found here is consistent with the trend found by Shearman *et al.* (2005), although there harvest index appeared to start declining after around 1990, whereas here it appeared to have reached a plateau but had not started declining. The plateau is at around 55%, 7% less than the theoretical maximum proposed by Austin *et al.* (1980). Shearman *et al.* (2005) also found an accelerating increase in crop biomass after 1983, whereas here there was no statistical justification for fitting a quadratic over a linear function, where there was a significant relationship (no relationship for bread-making varieties). There were also significant relationships between year of introduction and stem carbohydrate reserves (WSC), consistent with the effect found by Shearman *et al.* (2005).

A reduction in grain N concentration was seen in both the bread-making and feed subsets with year of introduction, associated with higher yields consistent with results of Jones *et al.* (2010) and Sylvester-Bradley & Kindred (2009). However, the decline found by Sylvester-Bradley & Kindred (2009) with 200 kg/ha N applied was less (-0.034 N%/decade) than found in this study (-0.071 and -0.063 N%/decade for landmark feed and bread-making varieties, respectively). Nevertheless, it is concerning that bread-making varieties are continuing to see a decline in grain N concentrations, albeit a slower one than that found in the feed varieties. A reduction in the natural level of grain protein in bread-making varieties will result in more fertiliser having to be applied to meet the UK milling requirement of 13% protein, unless changes are made to protein quality and / or to the baking process.

From this physiological analysis it appears that the general trend in wheat breeding have been to increase the total sink for assimilate (indicated by grains/m^2). If this had taken place in the absence of an equivalent increase in the supply of assimilate ('source': photosynthetic capacity during grain-filling plus redistributable assimilate) it would be expected that yields would be less stable because any variation in source would not be constrained so much by sink. Assimilate source (indicated by total DM) has apparently increased to some extent, as indicated by total biomass, but Figure 4-8 appears to show some evidence that higher yielding varieties in the ERYCC panel do indeed have marginally reduced yield stability (expressed as CV%), since yield and CV were positively related across sites and seasons. It is worth considering whether yield progress might be enhanced if plant breeders placed less emphasis on yield stability. However, it is also worth considering the relative economic advantages of high yields and stable yields.

3.5.2. The importance of the construction phase

In keeping with widely made physiological argument (Slafer *et al*., 1999; Slafer *et al*., 2005; Sylvester-Bradley *et al.,* 2005; Miralles & Slafer 2007; Foulkes *et al.,* 2009) it was hypothesised at the beginning of this project that maintenance of the construction phase (CP) is important for yield and yield stability in a changing climate, because of a number of beneficial traits developing during this period, including the accumulation of redistributable carbohydrate in stem material, sink capacity, and total assimilate source.

From biplot and regression analyses, it was found that the duration of the CP did not relate to yield. This was surprising as a number of other studies have found the duration of the CP to be important (e.g. Miralles and Slafer, 2007), Slafer *et al*., 2009). However, other traits that are developed during the period between GS31 and 61 do appear to be important in determining yield. There was a significant, but not strong, relationship between stem water soluble carbohydrates and yield. There was also a very strong relationship between the number of grains per m^2 and yield.

The key physiological traits underlying grains/m^2 in feed varieties included an extended foundation phase (FP) promoting high ears/m^2 combined with a high crop growth rate. High ear partitioning index associated with a reduced stem and leaf sheath partitioning was associated with increase ear partitioning and ear DM, but only up to values of EPI of ca. 0.20. At higher values of EPI, there was a negative trade-off with EFI. Therefore, for future gains in grains/m^2 a part of the ideotype may be an ability to maintain SFI at high values of EPI. A summary of the traits for an ideotype for improved grains/m^2 is provided in Table 2.

In bread-making varieties the same traits were generally associated with improvements in grains/m^2. However, the association with the extended duration of the FP and ears/m^2 was weaker. This may reflect that maintaining the duration of the CP is relatively more important in the bread-making varieties. Since this is the main phase of N accumulation in the crop, it could be that reduced N accumulation would result from a longer FP (and shorter CP); and therefore if the FP is to be extended further in bread-making wheats a longer FP must be combined with traits which can compensate by favouring a high rate of N uptake per day during the CP, e.g. a larger root system. The crop growth rate was not associated with genetic progress in bread-making wheats; which may again imply that C accumulation must be balanced with high N accumulation in bread-making wheats to favour high N remobilization post-anthesis and high stability of grain protein percentage.

Results showed that EPI was negatively correlated with grains/m^2 above a value of ca. 0.20. Many previous studies in wheat (e.g. Slafer & Savin, 1994; Gonzalez *et al*., 2003) showed increased partitioning of assimilate to the ear amongst genotypes led to an increased grains /m^2. Ear partitioning index was positively correlated with ear biomass per m^2 amongst the 64 varieties and the landmark varieties ($P<0.05$). The extra ear biomass at flowering with increased EPI > ca. 0.20 didn't translate into higher grains/m^2. This was because there was a negative relationship between EPI and EFI, i.e. lines which partitioned more assimilate to ears were less efficient at converting that assimilate into grains at anthesis. In order to exploit large ear phenotypes in breeding it will be essential to break this negative linkage.

Table 23. Values of traits for improving grains/m^2 in high yielding feed wheat lines

Variety character	How it might work	Value
Long foundation phase phase (GS1- GS31 ^{o}Cd)	Favours tiller/production survival	High
High crop growth rate (g DM /m2/d)	Maximises light capture/light conversion efficiency during construction phase Light	High
High ear fertility index (grains / g ear DM)	Reduces chaff DM costs per grain, increase grains /ear	High
High ear partitioning index (ear DM / AGDM)	Reduced partitioning to stem and leaf sheath, increase ear DM per m2 at GS61	Moderate
Positive residual from SPI vs SFI trade-off	Exploit extra ear DM due to ear partitioning > 0.20; increase grains/spikelet	High

Table 24. Values of traits for improving grains/m^2 in high yielding feed wheat

Variety character	How it might work	Value
Longer foundation phase phase (GS1- GS31 ^{o}Cd)	Favours tiller/production survival; but optimum duration shorter than in feeds	Moderate
High ear fertility index (ear DM /AGDM)	Reduces chaff DM costs per grain, increase grain /ear	High
High ear partitioning index	Reduced partitioning to stem and leaf sheath, increase ear DM per m^2 at GS61	Moderate
Positive residual from SPI vs SFI trade-off	Exploit extra ear DM due to ear partitioning > 0.20; increase grains/spikelet	High

Abbate *et al*. (1998) found among historic Argentinean wheat varieties differences in EFI in the range of 61 to 106 grains per g, and that grains/m^2 was more closely related to this ratio than to dry weight of ears at anthesis. In the UK, Shearman *et al*. (2005) reported a range of 73 to 129 grains per g but observed that this ratio was not associated with breeding progress in grains/m^2, and Reynolds *et al*. (2007) found no association of the trait with yield in three populations of random sister lines grown in the same environment as the current study. In the present study, values for EFI in the range 66 - 126 grains per g ear DM (at anthesis) was generally similar to the range reported by Shearman *et al.* (2005). The potential mechanisms underlying the negative association between EPI and EFI cannot be certain from the present results. It can be speculated that in phenotypes with high EPI floret fertility may be partly limited by pathway resistance in the phloem in addition to sink size and strength (see Bancal & Soltani, 2002; Minchin *et al*., 1993 for an extended discussion of potential effects of pathway resistance on floret fertility). Resistance is dependent on floret vascularization and could theoretically vary according to position, but Hanif & Langer (1972) indicated that the lower three florets in every spikelet are always supplied directly by the principal vascular bundles of the rachilla, regardless of the growth treatments applied to the plant. Therefore, extra assimilate supply may potentially increase floret fertility only in the most proximal 3 florets in the spikelet, with more distal florets still limited by resistance according to the vascular connections within the rachilla. If so, additional assimilate allocated to the ear may contribute to additional chaff DM (rachis, glumes, paleas and lemmas) rather than increased floret fertility.

3.5.3. Vernalisation and photoperiod effects

The vernalisation experiment was successful in distinguishing different vernalisation requirements of different varieties. Limagrain had carried out a basic screen of the varieties in 2009 to identify ‘spring’ types and had identified the same four ‘spring’ varieties as in the above experiment (26

Xi19, 52 Paragon, 58 Cadenza, 64 Bacanora), but had also identified 35 Timber and 63 Virtue as ‘spring’ varieties. In the above experiment, although 35 Timber did reach GS39 with no vernalisation, its thermal time to this growth stage was actually minimised at 5 weeks of vernalisation. Variety 63 Virtue behaved rather differently in the above experiment compared to the Limagrain screen; it did not reach GS39 until it had been exposed to 2 weeks of vernalisation.

One effect of vernalising temperatures continuing in the glasshouse was to generate response curves to vernalisation treatments, rather than the ‘all or nothing’ effects that were expected. The b and R parameters of the exponential curves fitted to these responses proved useful in allowing vernalisation requirements to be estimated quite precisely. Although these were expressed in days or weeks of vernalisation treatment, these requirements appeared to be a good single descriptor of the overall responsiveness of a variety to vernalisation and it correlated well with *Vrn1* gene copy number. If the experiment had been extended so that GS61 date could have been identified in more varieties, it is likely that similar curves could have been fitted to thermal time to GS61 and *Vrn1* copy number would again be related to vernalisation requirement.

Although successful, the vernalisation experiment did have the limitation that, when in vernalisation, varieties were only exposed to short days (8h). This may mean that vernalisation of some varieties was confounded by photoperiod effects. Also, the different *Vrn1* copy numbers appeared to be associated with inherent earliness, as well as with vernalisation requirements. The reasons for this are not yet clear, although it may be that selection for earliness has favoured several plant development genes together, not just *Vrn1* copy number.

If the vernalisation had been carried out in long days it might have been possible to consider inherent earliness with greater confidence. In future, modelling of vernal time (i.e. accounting for the effectiveness of different temperatures in driving vernalisation) may allow estimation of dates in the photoperiod experiment when varieties would have been expected to vernalise. This might then allow the strong year x photoperiod x variety interaction found in the photoperiod experiments to be resolved. Of course, some of the interaction would have come from seasonal differences; the 2010-2011 winter was particularly cold with a period of snow cover and it was then followed by a very dry spring, which contrasted with the milder 2008-09 winter followed by a wetter spring. However, the interactions were highly significant and relationships of thermal times to growth stages between years, despite being significant, were very variable and the relationships at the earlier growth stages (GS31 and 39) controlled by the early variety 64 (Bacanora).

The lack of consistency between years in photoperiod effects on all growth stage dates underlines the difficulties that the industry faces in predicting the behaviour of any variety in any particular region in any particular year. And attempts to model plant development, either with Sirius, an established model, or with simpler statistical approaches, only confirmed that significant progress has yet to be made. It would seem that empirical observations of growth stages are still the best way of informing the industry about plant development of varieties, even though the inconsistency in empirical observations noted here is evident in the growth stage data that have been collected to inform the RL. Perhaps the most encouraging observation here is that dates to growth stages were more consistent over seasons when the effects of major photoperiod genes were examined; *Ppd1* reduced the thermal time to key growth stages compared to *ppd1*.

In terms of leaf appearance, it should be noted that there was no significant relationship between 2009 and 2011 when final leaf numbers of the NP treatment and the photoperiod effect were examined, and that phyllochron was 24^{o}C days longer in 2011 than 2009. Hence it would seem that leaf appearance forecasts must continue to be short term, and based on in-field observations of the crop in question, rather than being based on remote calculations from variety information and weather data such as were the aspiration at the outset of this work.

3.5.4. Opportunities to enhance yields and respond to a change in climate

The varieties tested in this project have displayed a relatively wide variation in phenotype, which provides encouragement that there are opportunities to exploit this variation in future breeding programmes so to develop enhanced yields and varieties better suited to a changing climate. Whilst it is apparent that there was a large measure of mutual compensation between yield components, the wide variation in each yield component and the relatively high heritability of some traits indicates scope for more targeted crossing and selection to search for positive recombinations. At the extreme, if the best average yield component traits found in this project were combined in one variety, without compensation - the highest average TGW from variety 12 Exotic (56.3g), the highest average number of ears per m^2 from variety 56 Spark (521) and the highest average number of grains per ear from variety 35 Timber (51.9) – a grain yield of 17.9 t/ha @ 85% DM would be the result. This is quite close to the theoretical maximum of 19.2 t/ha @ 85% DM proposed by Sylvester-Bradley *et al.* (2005). This theoretical maximum was associated with a total above ground biomass of 27 t/ha @ 100% DM, a level not achieved in this project, the closest being 22.2 t/ha by variety 6 Humber at Newton in 2008. To achieve 17.9 t/ha grain yield total above ground biomass would have to increase to 24.5 t/ha, assuming a maximum harvest index of 0.62 (Austin, 1980).

In order to further analyse, and possibly exploit, the diversity in wheat yields and yield determinants, three mapping populations were developed during the project. The aim was to create new populations using varieties that contrasted in different traits, but that also used moderate- to high-yielding varieties so that any useful lines could be exploited commercially. Discussions among stakeholders in the project decided on varieties to cross, based on the data collected up to and including the grain yields from harvest 2009, and taking account of populations that already existed. It was decided that there should be a common variety in all populations for easier comparison of lines. The three populations generally show good representation for the ranges of key traits are representative of the highest values identified in the panel of 64 varieties (Table 25). Variety 5 Oakley was chosen as the common parent because of its high yields, resulting from a high number of grains per ear and a long production phase (Table 25). Of the other parents, variety 32 Gatsby was chosen for its contrast with 5 Oakley in yield components; Gatsby had the highest number of grains per m^2 of all varieties from a high number of ears per m^2, but had a below average number of grains per ear (Table 25). Variety 14 Exsept shows large contrasts with 5 Oakley in ear PI and ear DM per m^2 at GS61 (Table 25). Variety 37 Battalion contrasted with 5 Oakley on construction and production phase durations, with Battalion having much longer construction and much shorter production durations than Oakley and also has a low CGR.

Populations were created by Limagrain and lines are now being multiplied up by RAGT seeds in the 2011-12 growing season for analysis in the 2012-13 season.

Table 25. Mean values of the key determinants of yield for the parents of the three DH mapping populations developed in the project (Oakley x Gatsby; Oakley x Exsept and Oakley x Battalion), with the ranges and mean values for the 64 varieties

	Grains /m2	TGW (g)	Ears /m^2	Grains/ ear	FP ^{o}Cd	CP ^{o}Cd	PP ^{o}Cd	CGR ^{o}Cd	Ear PI	Stem PI	Ear DM g/m^2	EFI grains/g	EPI vs EFI resid.
Oakley	19982	45.5	389.2	50.0	1054	565	820	22.6	0.200	0.624	201.3	100.1	6.2
Gatsby	21479	39.0	484.7	44.4	1045	626	726	21.8	0.177	0.614	191.2	118.1	16.3
Exsept	16650	46.9	338.2	49.5	1067	588	756	21.4	0.175	0.614	168.8	99.6	-2.8
Battalion	17234	45.6	418.0	42.2	1032	635	747	20.4	0.194	0.622	195.1	92.6	-3.3
Max	21479	56.3	500.1	52.6	1070.7	650.0	827	22.6	0.270	0.675	229.0	124.6	19.2
Min	12815	38.8	316.6	34.9	852.8	546.5	710	10.8	0.133	0.544	131.0	66.2	-24.0
Mean	17198	45.6	371.2	46.3	1016.7	600.6	763	19.8	0.196	0.615	186.7	95.4	0
LSD 5%	1031.2	0.866	26.34	1.98	59.85	72.62	30.74	1.93	0.01	0.03	19.11	10.68	*

3.6. Conclusions and recommendations

3.6.1. Conclusions

1. The yield potential of varieties continues to be increased by breeders through increases in the number of grains/m2 (grains per ear and ears per m2). However, these increases are not being translated into increased farm yields.
2. High yields were not associated with the duration of the construction period (GS31-61), but were associated with traits developed during this period e.g. grains per ear, stem WSC.
3. Genetic gains in grains/m2 in the sets of landmark varieties were associated in slightly different combinations of traits for different variety types:

   Feed (including soft 'biscuit' wheats) varieties:

   - Extended foundation phase associated with increased ears /m^2
   - Increased crop growth rate pre-anthesis associated with increased ear DM per m^2 and grains per ear
   - Increased SPI up to about 1990 associated with an increase in ear DM per m^2 and grains per ear during this phase

   Bread-making varieties:

   - Extended Foundation phase
   - Increase SPI up to about and SFI (post 1990) linked to increase in ear DM per m^2 and grains per ear

   It appeared that the delay in ear development due to a prolonged foundation phase caused ear development to occur under brighter conditions, possibly explaining the association between foundation phase and grain yield.
4. The grain N concentration of landmark bread-making varieties showed a linear decline, so bread-making quality must be achieved through higher fertiliser N applications by farmers. Alternatives would be breeding for better quality protein at the same N%, and / or changing industry requirements.
5. The 64 varieties tested in this project showed significant variation in traits which may be used for breeding for a future climate where shortening of wheat development to avoid both winter frosts and summer drought and high temperatures. These could be further understood through analysis of the Oakley x Gatsby, Oakley x Battalion and Oakley x Exsept mapping populations developed here.
6. The vernalisation requirement of varieties is now understood better and can be explained by *Vrn1* gene copy number.
7. There is significant variation in response to photoperiod among varieties which can partly be explained by major photoperiod genes, but which appears to significantly interact with season.

3.6.2. Recommendations for further research

1. The mapping populations resulting from this project should be analysed for yield determining traits and genetic determinants of these traits. Promising lines might also be exploited by breeders.
2. The vernalisation experiment delivered very useful information from a moderate investment and should be repeated, to include vernalisation in long days and glasshouse temperatures that would not allow further vernalisation. This promises a significantly better understanding of vernalisation, and even if it does not, this technique could provide better predictions of latest safe sowing dates for varieties.
3. The photoperiod extension experiment should be repeated, once vernalisation requirements have been quantified better, to further understand photoperiod effects and seasonal interactions.
4. Further modelling should be carried out so that the dates of emergence of the final 3 leaves can be predicted to allow better prediction of spray application dates.

3.7. Knowledge transfer

The results from this project have been presented to farmers and agronomists at: HGCA/ADAS Open days in Herefordshire, Cambridgeshire and North Yorkshire in June 2009, 2010 and 2011; at an ADAS High Mowthorpe Farming Association meeting in 2011; and at BASF and breeders' events. Conference papers have been presented to: CIMMYT Wheat Symposium, CIMMYT, Mexico, November 2009; Wheat Genetic Improvement Network (WGIN) stakeholder meetings, November 2010 and November 2011; and an Ideotypes AAB meeting, University of Reading, December 2010.

3.8. Acknowledgements

Sincerest thanks go to the breeders from KWS UK Ltd., RAGT Seeds and Limagrain for their significant practical and intellectual contribution to, and continued interest and enthusiasm in, this project. Thanks must also go to BASF for managing and assessing the Clopton trials, to HGCA and Masstock for providing growth stage data, and to David Laurie (John Innes Centre) for his contribution on genetic control of vernalisation. We thank Pete Jamieson and Rob Zyskowski of the New Zealand Institute of Crop & Food Research for work on the Sirius model. In addition to members of the organisations above, thanks go to Peter Shewry, Robbie Waugh, and Dhan Bhandari for their work on the Project Steering Group. Funding from HGCA is gratefully acknowledged. This Project was sponsored by Defra through the Sustainable Arable LINK Programme.

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Appendix A: Experimental site details

Site	Harvest year	No. varieties tested	Location	Field name	Soil type	Previous crop	Sowing date	Harvest date	N applied (kg/ha)
Phenotyping									
Framlingham	2007	49	52 º16’ N,1º17’ E	2007148	Clay loam	Oilseed rape	10/10/06	11/08/07	~240
Grantchester	2007	49	52^{o} 11’ N, 0^{o}4’ E	Cantelupe 11	Clay loam over gravel	Oilseed rape	18/10/06	09/08/07	210
Woolpit	2007	49	52º12’N,0º 54’E	Park East	Sandy	Mustard	03/11/06	23/08/07	?
Clopton	2008	64	52º 13’N,0º 19’E	Clopton	Clay loam	Mustard	13/10/07	20/08/08	200
Langton	2008	64	54^{o} 6’N 0^{o} 46’W	Whitegate Way	Clay loam	Oilseed rape	01/09/07	29/08/08	185
Newton	2008	64	52^{o} 7’ N, 0^{o} 5’ E	Hurrels, Garden Field	Sandy, gravel over chalk	Non-cereal	19/10/07	14/08/08	~240
Terrington	2008	64	52^{o} 46’ N, 0^{o} 18’E	Highland 21	Silty clay loam	Vining peas	12/10/07	21/08/08	190
Clopton	2009	64	52 ^{o} 12’N,0 ^{o} 55’E	Piebush	Sandy	Beans	17/10/08	13/08/09	221
Langton	2009	64	54 ^{o} 6’N,0 ^{o} 46’W	Slant road field	Clay loam	Potatoes	29/10/08	29/08/09	?
Newton	2009	64	52^{o} 8’N, 0^{o} 6’E	Hurrels	Sandy, gravel over chalk	?	04/10/08	20/08/09	~240
Terrington	2009	64	52^{o} 46’N, 0^{o} 17’E	Brickyard	Silty clay loam	Oilseed rape	03/10/08	15/08/09	220
Clopton	2010	64	52^{o} 12’ N, 0^{0} 51’E	Drinkstone green	Medium	Oilseed rape	08/10/09	21/08/10	190
Langton	2010	64	53^{o} 52’ N, 0^{o} 38’W	Sanction Road	Clay loam	Oilseed rape	08/10/09	03/09/10	210
Newton	2010	64	52^{o} 8’ N, 0^{o} 8’E	Hurrels, Newton	Light chalky loam	Non-cereal	16/10/09	22/08/10	~240
Terrington	2010	64	52^{o} 47’N, 0^{o} 13’ E	Brickyard	Silty clay loam	Oilseed rape	28/09/09	01/09/10	190
Photoperiod									
Thriplow	2009	64	52^{o} 6’N, 0^{o} 6’E	Play pen	Light gravel loam	Fallow	15/10/08	N/A	120
Thriplow	2010	64	52^{o} 6’N, 0^{o} 6’E	Play pen	Light gravel loam	Wheat	04/11/09	N/A	120
Thriplow	2011	64	52^{o} 6’N, 0^{o} 6’E	Play pen	Light gravel loam	Wheat	22/10/10	N/A	120

Appendix B: Genotype results for the ERYCC panel of 64 varieties

Table B1. The ERYCC panel of 64 cultivars used throughout the project with associated year of introduction, cultivar code, and allocation to ‘Historical’ (H), ‘Phenology’ (P) or ‘Modern/control’ (M) groups. ‘Landmark’ Feed (F) and Bread-making (B) varieties are highlighted in bold text. Further columns indicate presence (1) or absence (0) of major genes, as defined in Table 3.4.

NOTE: Any future reference to or use of genotype data provided here should acknowledge the ERYCC project using the following words: “These data were generated within the ERYCC LINK project (‘Adapting wheat to global warming’) sponsored by Defra and HGCA through the Sustainable Arable LINK Programme (Project LK0992), and involving ADAS, University of Nottingham, KWS, RAGT, Limagrain, BASF and Agrii. For information on genotyping, please contact Peter Jack (RAGT) or Peter Werner (KWS).”

Cultivar	Year	Code	Gp.	Ppd1	Ppd2	Rht1	Rht2	Rht8 (wms261)			Lr37	Pch1	Sm1 (WM1)		1RS
								196/192 bp	174 bp	165 bp			1	2 (null)	
Access	2002	4	M	0	0	0	1	0	1	0	1	0	0	1	1
Alchemy (F)	**2006**	**19**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**
Alixan	2005	44	P	0	0	0	1	0	0	1	0	0	0	1	0
Ambrosia	2005	17	M	0	0	0	1	0	1	0	1	0	0	1	1
Andalou	2002	10	P	1	0	0	1	0	0	1	0	0	1	0	0
Apache	1998	42	P	1	0	0	0	0	1	0	1	0	1	0	0
Avalon (B)	**1980**	**46**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
Bacanora	1988	64	P	1	0	1	0	1	0	0	0	0	1	0	1
Battalion	2007	37	M	0	0	0	1	0	0	1	1	1	0	1	0
Beaver (F)	**1990**	**9**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**
Brompton	2005	29	M	0	0	0	1	0	1	0	0	0	1	0	1
Buster	1995	55	P	0	0	0	1	0	1	0	0	0	1	0	0
Cadenza	1994	58	P	0	0	0	0	1	0	0	0	0	0	1	0
Caphorn	2002	43	P	1	0	0	1	0	0	1	1	0	1	0	0
Cappelle Desprez (F)	**1953**	**47**	**H**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**
Cezanne	1998	49	P	1	0	1	0	0	1	0	0	0	0	1	0
Claire (F)	**1999**	**16**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**
Consort (F)	**1995**	**36**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**
Cordiale (B)	**2004**	**2**	**P**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**
Deben	2001	25	M	0	0	0	1	0	0	1	0	0	1	0	0
Dover	2007	8	M	0	0	0	1	0	1	0	1	0	0	1	0
Einstein (B)	**2003**	**15**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**
Equinox	1997	1	H	0	0	0	1	0	1	0	1	0	0	1	1
Exotic	2006	12	P	1	0	0	1	0	1	0	1	0	0	1	0
Exsept	2001	14	P	0	0	0	1	0	0	1	0	0	1	0	0
Galahad (F)	**1983**	**45**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**
Gatsby	2006	32	P	0	0	1	0	0	1	0	0	0	1	0	1
Gladiator	2004	28	M	0	0	0	1	0	1	0	1	0	1	0	1

Cultivar	Year	Code	Gp.	Ppd1	Ppd2	Rht1	Rht2	Rht8 (wms261)			Lr37	Pch1	Sm1 (WM1)		1RS
								196/192 bp	174 bp	165 bp			1	2 (null)	
Glasgow	2005	18	M	0	0	0	1	0	0	1	0	0	1	0	0
Gulliver	2008	34	M	0	0	0	1	0	0	1	1	0	0	1	0
Haven	1990	48	H	0	0	0	1	0	1	0	0	0	1	0	1
Hereward(B)	**1991**	**41**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**
Hobbit	1977	59	H	0	0	0	1	0	1	0	0	0	1	0	0
Humber	2007	6	M	0	0	0	1	0	1	0	1	0	0	1	1
Hustler	1978	60	H	0	0	0	1	0	1	0	0	0	1	0	0
Hyperion	2006	33	P	0	0	0	1	0	0	1	1	1	0	1	0
Istabraq	2004	20	M	0	0	0	1	0	0	1	0	0	1	0	0
Longbow	1983	61	H	0	0	0	1	0	1	0	0	0	1	0	0
Malacca (B)	**1999**	**7**	**M**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**
M. Huntsman (F)	**1972**	**51**	**H**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
M. Widgeon(B)	**1964**	**62**	**H**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**
Marksman	2008	38	M	0	0	0	1	1	0	0	1	1	1	0	0
Mascot	2006	30	M	0	0	0	1	0	1	0	1	0	0	1	0
Mendel	2005	23	P	0	1	0	1	0	0	1	0	0	0	1	0
Mercato	2006	24	P	1	0	1	0	0	1	0	1	0	1	0	0
Mercia (B)	**1986**	**57**	**H**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
Musketeer	2008	39	M	0	0	0	1	1	0	0	1	1	0	1	0
Norman (F)	**1981**	**54**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
Oakley (F)	**2007**	**5**	**M**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**
Paragon	1999	52	P	0	0	0	0	1	0	0	0	0	1	0	0
Recital	1986	40	P	1	1	1	0	0	1	0	0	0	1	0	0
Rialto (B)	**1995**	**13**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**1**
Riband (F)	**1989**	**53**	**H**	**0**	**0**	**0**	**1**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
Robigus(F)	**2003**	**3**	**M**	**0**	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0**
Royssac	2003	11	P	1	0	0	1	0	1	0	0	0	1	0	0
Sankara	2005	22	P	0	0	0	1	0	1	0	1	1	1	0	0
Savannah	1998	50	H	0	0	0	1	0	1	0	1	0	0	1	1
Soissons	1995	21	P	1	0	1	0	0	1	0	0	0	0	1	0
Solstice (B)	**2002**	**27**	**M**	**-**	**-**	**0**	**1**	**-**	**-**	**-**	**0**	**0**	**0**	**1**	**0**
Spark	1993	56	P	0	0	0	0	1	0	0	0	0	1	0	0
Timber	2007	35	P	0	0	0	1	0	1	0	0	0	1	0	0
Virtue	1979	63	H	0	0	0	1	0	1	0	0	0	0	1	0
Xi19	2002	26	M	0	0	0	1	1	0	0	0	0	0	1	0
Zebedee	2007	31	M	0	0	0	1	0	0	1	0	0	1	0	0