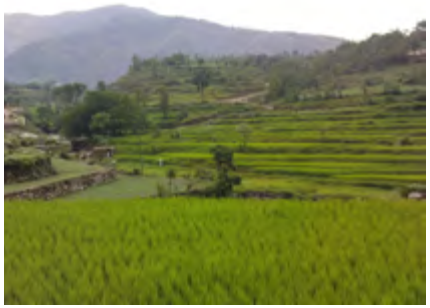
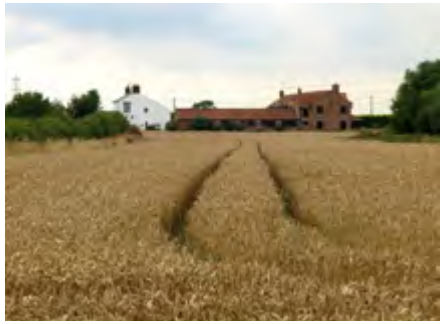
Wheat genetics research in the UK

A case study describing the history and impact of five areas of UK wheat genetics research



Whear ear; rice fields near Martung, Pakistan; wheat infected by yellow rust; wheat field near Preston, UK. Credits: Graham Moore/JIC; Serajulhaque (public domain); US ARS; Andy Beecroft/Wikimedia Commons

A history of wheat genetics research in the UK

Wheat was first domesticated around 10,000 years ago in the Fertile Crescent in the Near East. From there it spread around the world, reaching the UK around 3000BC[1]. Wheat now makes up 20% of the calories consumed by people around the world[2], and new higher-yielding wheat varieties play a vital role in ensuring food security as demand for food grows.

In 1940, wheat yields in the UK were around 2.5 tonnes per hectare[3]. Since then, new varieties and better farming practices mean that wheat yields have been rising[4]. Today farmers regularly harvest more than eight tonnes per hectare[3].

Wheat makes up 20% of the calories consumed by people globally

These wheat yield increases are due in part to advances in our understanding of the complex genetics of wheat, enabled by investments in agriculture and plant science research from BBSRC and its predecessors the Agriculture and Food Research Council (AFRC) and the Agriculture Research Council (ARC).

New varieties that harness the genetic discoveries made by BBSRC-funded researchers and others have had a measurable impact on wheat yields. Genetic improvements to wheat have added around 0.05 tonnes per hectare per year to average UK wheat yields since the early 1990s[5]. In 2012, these improvements added around £16.9M to the value of UK wheat production[6].

AFRC and BBSRC investments have provided long-term support for research into the genetic basis of specific wheat traits and the genetic tools needed to fully understand and exploit such traits in breeding programmes. Much of the research into wheat also depended on continued support for fundamental bioscience research into plant genetics.

This case study tells five stories where BBSRC investments are making significant contributions to the development of new wheat varieties, and where the UK is internationally recognised as leading the way in wheat genetics research.

Wheat was grown on two million hectares of land (from a total of 17.2 million hectares of farmland)[7] in the UK in 2012, and wheat production was worth £2Bn to the UK economy[8]

Impact Summary

UK wheat research, which has received long-term support from BBSRC and its predecessors the ARC and AFRC, has contributed to UK and global increases in wheat yields by enabling the creation of new wheat varieties. These added around £16.9M to the value of UK wheat production in 2012 alone.

An ear of wheat. Credit: Professor Graham Moore/JIC

1. Unifying cereal genetics

To investigate the immensely complex wheat genome, researchers now turn to the smaller genomes of related cereals such as rice and a grass called *Brachypodium*.

This is possible thanks to synteny between the cereal genomes, which means the order of genes in regions of the wheat genome is the same as in certain regions of rice and other cereal genomes. As a result, researchers can identify genes in rice, which has a much smaller genome than wheat, and use them to quickly find the same genes in wheat. The concept of synteny, developed in the UK, now underpins wheat research and breeding in academia and industry around the world.

Another benefit of synteny is that it is allowing plant breeders to use genetic markers identified in rice and other cereals for wheat breeding, greatly increasing the number of markers available and making it easier to track desirable traits.

Wheat growing near Elswell, Suffolk. Credit: Keith Evans

1970s

1979: Working at the AFRC-funded Plant Breeding Institute (PBI), Dick Flavell is the first researcher anywhere in the world to successfully clone plant DNA.

The former PBI building in Trumpington, Cambridge. Credit: James Yardley/Wikimedia

1980s

1989: Graham Moore receives funding from AFRC and the Department for Trade and Industry (DTI) to demonstrate synteny between rice and wheat using the early genetic maps of wheat developed by Mike Gale at the John Innes Centre (JIC) and the work on rice genetics led by Moore's Japanese collaborators.

1989: Mike Gale produces the first RFLP (restriction fragment length polymorphism) maps of wheat. RFLP mapping is an early form of genome mapping (assigning DNA fragments to chromosomes).

1990s

1992: At a conference in San Diego, Moore describes the first comparative mapping of rice and wheat.

1993: Between 1993 and 1996, Moore receives funding from BBSRC to carry out comparative analysis of the rice and wheat genomes.

1994: In a paper published in Nature Biotechnology, Moore and colleagues demonstrate that the comparatively small rice genome and the larger and more complex wheat genome are structured similarly, with genes in the same order.

1995: Moore unifies cereal genetics through the synteny concept. Using mapping data for rice (from Japan), maize and sorghum (USA), sugar-cane (France), and rye, wheat and millets (Mike Gale, UK), Moore and colleagues show they can reconstruct all of the cereal genomes from a conserved set of genetic building blocks. When they look at the order of these blocks, they are also able to construct a hypothetical ancestral genome for all of the cereals, and by cleaving this they can derive all other cereal genomes.

1995: The landmark 'crop circles' paper is published, in which Moore presents a diagram-matic representation of the synteny concept that allows comparisons to be made between the genomes of all the major cereals. The diagram is subsequently used in teaching material, government strategies and reports around the world.

1990s

2004: Moore uses his newly-created library of genetic resources in *Brachypodium* to confirm synteny with the other cereals.

Putting synteny to use

Since 1995, synteny has been at the heart of wheat breeding and genetics research around the world. Researchers have identified numerous genes, and large agriculture companies such as Syngenta and Limagrain have exploited synteny within their research and breeding programmes. For instance:

2002: Syngenta sequence the rice genome, partly in order to exploit synteny with other crops of interest.

2003: Powdery mildew resistance gene cloned by researchers at the University of Zurich using synteny, protecting wheat from a common fungal pathogen.

2003-2006: Jorge Dubcovsky's group in the USA use the synteny concept to identi-fy wheat genes for vernalisation (a plant's ability to flower in spring after exposure to the cold of winter).

2006: Dubcovsky's group use synteny to identify wheat genes for high grain protein.

2009: Dubcovsky and colleagues identify gene for stripe rust resistance, another fun-gal pathogen of wheat, using synteny.

2008: Tillering (production of side shoots) gene mapped using synteny by Kansas State University researchers.

Yellow Rust. Credit: US ARS

2000s

2. Harnessing the diversity of wild wheat

Historians have argued that western civilisation was built on the domestication of wheat, and wheat as we know it would not exist without a gene known as Ph1. Ph1 controls how wheat chromosomes pair up during meiosis, the process which produces the plant's reproductive cells. It stabilises the wheat genome by ensuring pairing between similar or 'homologous' chromosomes i.e. from the same ancestral genome (see 'The wheat genome', below). Without it, wheat would be sterile.

However, Ph1 also prevents chromosomes from wild varieties pairing and exchanging genetic material with those from elite wheat varieties created by plant breeders. This makes it difficult for breeders to introduce valuable new traits such as disease resistance to elite lines.

Sixty years of sustained funding from BBSRC and its predecessors has allowed researchers to dissect the Ph1 locus, enabling breeders to create new and improved wheat varieties.

Wild wheat. Credit: Eeliuth/Wikimedia Commons

1950s

1952: Ralph Riley joins the PBI in Cambridge, which is funded by AFRC, where he begins to investigate how to introduce traits from wild wheat into elite wheat varieties.

1958: Riley recognises that the Ph1 locus on wheat chromosome 5B stabilises chromosome pairing in wheat by preventing chromosomes from different ancestral wheat genomes (see 'The wheat genome', below) from associating during meiosis. This makes it difficult to introduce new useful traits such as disease resistance from wild wheat.

1960s & 1970s

1968: Riley demonstrates experimental interventions during wheat meiosis to encourage chromosome pairing between chromosomes from different ancestral genomes. He uses this to introduce resistance to Yellow Rust, a major fungal pathogen of wheat.

1980s & 1990s

1987: Graham Moore is recruited by the John Innes Institute (now JIC) to clone the Ph1 locus. However, the large size of the wheat genome makes it difficult to identify specific genes, so Moore proposes using rice, which has a much smaller genome, to develop genetic tools which can be used in wheat.

1996: Having demonstrated synteny in the cereals, Moore (working in collaboration with the University of Cambridge Genetics Department) receives funding from BBSRC to create the rice genetic resources he proposed in 1987.

2000: Funding from BBSRC enables Moore to create wheat and *Brachypodium* genomic libraries to help characterise Ph1, in collaboration with Institut national de la recherche agronomique (INRA), France. (*Brachypodium* is also a grass and a now model plant for geneticists due to its amenability to experimental manipulation and compact genome).

2003: The libraries of genetic resources for wheat and *Brachypodium* are completed.

2006: Moore and colleagues use synteny to characterise the Ph1 locus. The research gives breeders perfect DNA 'markers' – stretches of DNA that identify a particular location in the genome – that can be used to trace the movement of particular genes, in this case a cluster of genes or loci, through breeding programmes.

2000s

2010: Exploiting this information, Moore and colleagues show that okadaic acid can be used to mimic the effect of deleting Ph1, by inducing pairing between the ancestral genomes.

2012: BBSRC funds a wheat pre-breeding programme to bring together researchers and plant breeders to exploit the latest advances in wheat genetics using Moore's work on Ph1.

Winter wheat. Credit: Professor Graham Moore/JIC

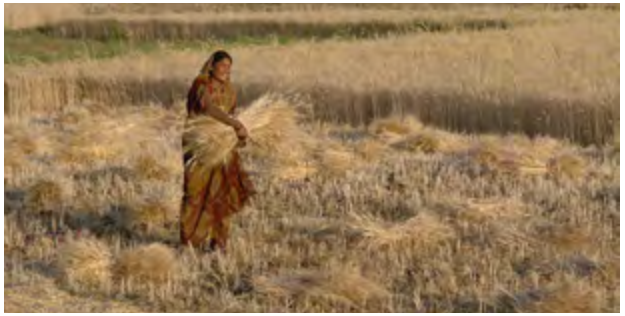
2010s

3. Exploiting the Green Revolution gene

The Green Revolution, which took place from the 1940s to the 1970s, significantly increased grain yields from major cereals such as wheat and rice. This was particularly important in India and Pakistan, where new high-yield crop varieties saved millions of people from starvation. Driving the yield increases in wheat was the reduced height (or Rht) characteristic, which reduced the length of the wheat's stalk but increased the size of the edible grain.

The Rht1 gene responsible for the Green Revolution was identified thanks to support from AFRC for fundamental research into Arabidopsis genetics at PBI and, later, BBSRC funding for the JIC. By identifying the equivalent gene in Arabidopsis, an important model organism for plant science research, researchers could look for a similar gene in wheat.

The Rht1 trait is now ubiquitous in crop breeding programmes around the world.



Woman harvesting wheat, Raisen district, Madhya Pradesh, India. Credit: Yann/Wikimedia Commons

1960s & 1970s

1960s: The height of the Green Revolution. New crop varieties and better management practices and use of fertilisers greatly increase crop yields around the world. Many of these crops use the Rht trait, which results in much shorter plants that put more of their energy into grain production, increasing yields.

1960s and 1970s: PBI breeders develop several successful wheat lines, harnessing the Rht characteristic, which dominate UK wheat production and are worth around £75M to the UK economy each year.

1980s

1980s: PBI drives the adoption of Arabidopsis as a model organism for plant scientists in Europe. Arabidopsis is now the model organism for plant science, underpinning research around the world.

Arabidopsis thaliana. *Credit: AJC1/Wikimedia Commons*

1990s

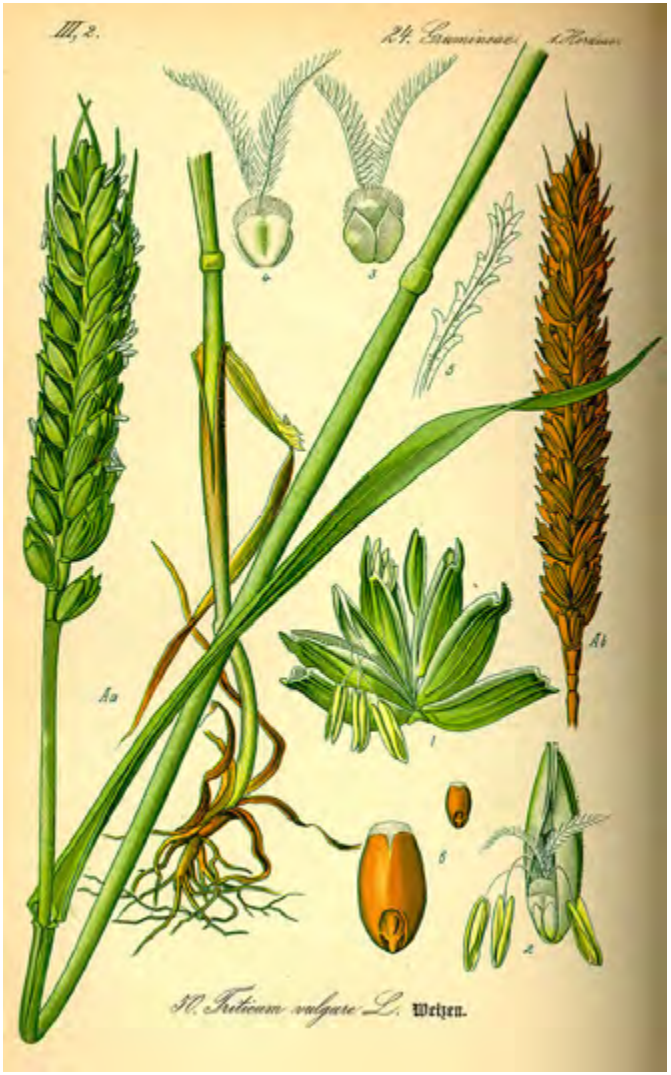
1990: Nick Harberd joins JIC. He aims to clone the GAI gene in Arabidopsis as a route to cloning the Rht1 gene in wheat and the equivalent maize gene, D8. Although Arabidopsis and wheat are not closely related, mutations in GAI and Rht-1 genes produce similar results – such mutants are insensitive to the plant hormone gibberellin (so they have short stems) and accumulate large quantities of gibberellin in their tissues.

1997: Harberd and colleagues successfully clone GAI in Arabidopsis.

1999: Harberd and colleagues identify the Rht-1 gene in wheat, based on their work on GAI in Arabidopsis. The discovery gives breeders a perfect genetic marker for the trait, allowing them fine control over the height of their wheat plants by introducing different variants, or 'alleles', of the Rht-1 gene.

2011: Researchers from JIC and Rothamsted, which receive strategic funding from BBSRC, characterise the Rht-1 genes, adding to our understanding of the Rht trait in wheat.

1990s & 2000s



The wheat genome

The wheat genome was published in 2012 (following an initital draft, published in 2010) by a consortium of researchers from the UK, Germany and the USA. They identified around 96,000 genes; four times as many as in the human genome.

Modern domesticated wheat is also hexaploid i.e. it has six copies of each chromosome, as its genome consists of three different 'ancestral' genomes. This great size and complexity makes the wheat genome much more difficult to work with than smaller cereal genomes such as rice.

Wheat genome	Human genome
42 chromosomes, comprising three ancestral genomes (A, B and D) of fourteen chromosomes each.	46 chromosomes
17 billion base pairs	3 billion base pairs
94-96,000 genes	20-25,000 genes
'Shotgun' sequence in 2012	Sequenced in 2001

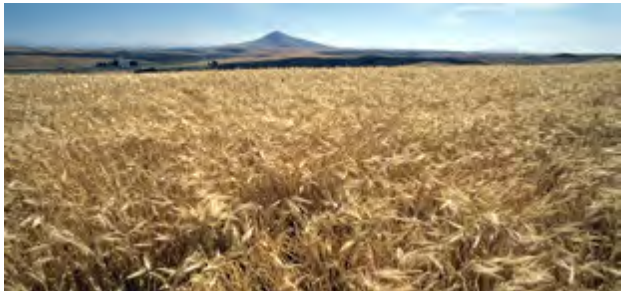
(Left) Illustration of common wheat, Triticum aestivum, from Prof. Dr. Otto Wilhelm Thomé Flora von Deutschland, Österreich und der Schweiz 1885, Gera, Germany (public domain).

4. Developing wheat for changing climates

To maximise yield, farmers need to grow crops that flower at the right time for the environment they are growing in. Flowering too early could expose the plants to frost damage, and flowering too late, particularly in regions with short growing seasons, could also expose the plant to unfavourable conditions for grain production.

One of the environmental cues plants use to determine when to flower is day length, or 'photoperiod'. Many wheat varieties need a period of longer days before they will flower. However, some plants carry a mutation which means they are not sensitive to day length.

By understanding the genetics of flowering time, breeders can precisely control when wheat will flower, allowing them to develop varieties adapted to new environments, which will be particularly important as global climates change.



A field of barley. Credit: USDA

1970s

1978: Building on earlier studies of flowering time in wheat, Colin Law and others at PBI identify three loci involved in control of flowering time based on day length, Ppd-1, Ppd-2 and Ppd-3, each located on one of the three group 2 chromosomes (one from each ancestral genome).

1980s & 1990s

1983: Work at PBI identifies the location of the major photoperiod gene, Ppd-2, on wheat chromosome 2B.

1986: PBI researchers identify the location of the gene Ppd-1 on chromosome 2D in wheat.

1995: David Laurie and colleagues at BBSRC-funded JIC identify two flowering time genes in barley, using RFLP mapping.

2000s

2004: Researchers from JIC, Germany and Mexico produce a physical and genetic map of gene Ppd-2 (now known as PPD-B1).

2005: Laurie clones the Ppd-H1 gene in barley using synteny with rice and *Brachypodium*, building on earlier research into photoperiod response in Arabidopsis.

2007: Using their knowledge of the location of Ppd-H1 in barley, researchers at JIC are able to precisely identify the Ppd-D1 gene in wheat.

5. Better UK wheat for bread-making

Historically, the UK imported much of its wheat for bread-making from the USA and Canada, as the flour it produced was rich in gluten proteins. However, after the Second World War, researchers at PBI began to study the bread-making qualities of wheat to allow them to breed UK varieties suitable for making bread.

Now, 4.5M tonnes of wheat grown in the UK each year is used to make bread.

Good bread-making quality in wheat depends on the gluten in the dough. Gluten is made of two proteins, gliadins and glutenins, and the presence of different gliadin and glutenin sub-units affects the properties of dough made from the wheat flour.

Breads. Credit Scott Bauer/US Department of Agriculture

1970s

1979: At PBI, Peter Payne establishes the link between high molecular weight sub-units of glutenin and the strength of dough made from wheat flour – an important component of bread-making quality.

1980s

1981: Payne continues to demonstrate the link between high molecular weight glutenin and bread-making quality.

1983: At PBI, Dick Flavell identifies and partially sequences a cluster of genes which produce the high molecular weight glutenin sub-units.

1984: Payne, Law and others at PBI identify the gene loci for three high molecular weight glutenin sub-units on chromosomes 1A, 1B and 1D, as well as other loci for gliadins and low molecular weight glutenins.

1989: Flavell and colleagues determine the DNA sequence of one of the genes for a low molecular weight glutenin sub-unit.

1990s & 2000s

1990s-2000s: The molecular characterisation of the glutenin sub-units by Peter Shewry and colleagues at Rothamsted Research advances our understanding of dough strength and elasticity.

1997: Shewry shows that disulphide bridges (chemical bonds between two sulphur molecules) play an important role in determining the properties of the gluten responsible for bread-making quality.

2010: Shewry and colleagues characterise one of the low molecular weight sub-units of glutenin, which are difficult to study due to their complex mix of components.

Notes and references

With thanks to Professor Graham Moore and Professor Nick Harberd for their input to this case study

1. Shewry, P.R. (2009). Wheat. Journal of Experimental Biology. 60 (6): 1537-1553. doi: 10.1093/jxb/erp058

2. FAO Briefing Paper (2012). Second Global Conference on Agriculture for Development. Available online at: http://www.fao.org/docs/eims/upload//306175/Briefing%20Paper%20(3)-Wheat%20Initative%20-%20H%C3%A9l%C3%A8ne%20Lucas.pdf

3. UK National Ecosystem Assessment Synthesis Report (2010).

4. See www.nabim.org.uk for data from 1976 – 2010, see: Defra Obser-vatory Programme Indicators, Indicator B11: Crop and milk yields. [webpage no longer available – February 2017]

5. According to the results of a Defra/HGCA project: Knight. S., Kightley, S., Bingham, I., Hoad, S., Lang, B., Philpott, H., Stobart, R., Thomas, J., Barnes, A. and Ball, B. (2012). Project Report No. 502. Desk study to evaluate contributory causes of the current 'yield plateau' in wheat and oilseed rape. Available online at: http://www.campaignforrealfarming.org/wp-content/uploads/2013/01/desk-study-re-yield-plateau-in-wheat-etc.pdf [Accessed 31/05/2013]

6. In 2012, an increase of 0.05 tonnes per hectare on 1.992M hectares, multiplied by 2012 wheat prices of roughly £170 per tonne, suggests genetic improvements resulted in an additional £16.9M of UK wheat production in 2012 alone. Values taken from Agriculture in the United Kingdom 2012, Defra.

7. Farming Statistics. Final Crop Areas, Yields, Livestock Populations and Agricultural Workforce at 1 June 2012, United Kingdom. Defra.

8. Agriculture in the United Kingdom 2012. Defra.

Unifying cereal genetics

1979: Bedbrook, J., Gerlach, W., Thompson, R., Flavell, R.B. (1980) in Emergent Techniques. eds Rubenstein I, Gengenbach B, Phillips R, Green CE (University of Minnestoa Press, Minneapolis), pp 93–113.

1989: Gale, M.D., P. J. Sharp, P.J., S. Chao, S., Law, C.N.. (1989) Applications of genetic markers in cytogenetic manipulation of the wheat genomes. Genome. 31: 137-142. Doi:10.1139/g89-025

1993: Moore, G., Gale, M.D., Kurata. N., Flavell. R.B. (1993) Molecular analysis of small grain cereal genomes. Nature Biotech. 11: 584-589.

1994: Kurata, N., Moore, G., Nagamura, Y., Foote, T., Yano, M., Minobe. Y., Gale, M. (1994) Conservation of genome structure between rice and wheat. Nature Biotech. 12: 276-278.

1995: Moore, G., Foote, T., Helentjaris, T., Devos, K., Kurata, N., Gale, M. (1995) Was there a single ancestral cereal chromosome? Trends In Genetics. 11, 81-82.

1995: Moore, G., Devos, K., Wang, Z., Gale, M. (1995) Cereal Genome Evolution: Grasses, line up and form a circle. Current Biology. 5, 737-739.

2004: Foote, T.N., Griffiths, S., Allouis., S, Moore, G. (2004) Construction and analysis of a BAC library in the grass Brachypodium sylvaticum: its use as a tool to bridge the gap between rice and wheat in elucidating gene content. Functional & Integrative Genomics. 4, p26-33. doi:10.1007/s10142-003-0101-y
Examples of the uses of synteny:

2002: Goff SA, Ricke D, Lan TH, Presting G, Wang R, Dunn M, Glazebrook J, Sessions A, Oeller P, Varma H, Hadley D, Hutchison D, Martin C, Katagiri F, Lange BM, Moughamer T, Xia Y, Budworth P, Zhong J, Miguel T, Paszkowski U, Zhang S, Colbert M, Sun WL, Chen L, Cooper B, Park S, Wood TC,

Mao L, Quail P, Wing R, Dean R, Yu Y, Zharkikh A, Shen R, Sahasrabudhe S, Thomas A, Cannings R, Gutin A, Pruss D, Reid J, Tavtigian S, Mitchell J, Eldredge G, Scholl T, Miller RM, Bhatnagar S, Adey N, Rubano T, Tusneem N, Robinson R, Feldhaus J, Macalma T, Oliphant A, Briggs S. (2002). A draft sequence of the rice genome (Oryza sativa L. ssp. japonica). Science. 296(5565): 92-100.

2003: Yahiaoui, N., Srichumpa, P., Dudler, R. , Keller, B. (2004) Genome analysis at different ploidy levels allows cloning of the powdery mildew resistance gene Pm3b from hexaploid wheat. Plant Journal. 37: 528–538. doi: 10.1046/j.1365-313X.2003.01977.x

2003 – 2006: For example, see:
Yan, L., D. Fu, D., Li, C., Blechl, A., Tranquilli, G., Bonafede, M., Sanchez, A., Valarik, M., Dubcovsky, J. (2006) The wheat and barley vernalization gene VRN3 is an orthologue of FT. Proc. Natl. Acad. Sci. U.S.A. 103: 19581-19586.

Yan, L., Loukoianov, A., Tranquilli, G.,Helguera, M., Fahima, T., Dubcovsky, J. (2003) Positional cloning of wheat vernalization gene VRN1. Proc. Natl. Acad. Sci. USA. 100: 6263-6268.

2006: Distelfeld A., C. Uauy, T. Fahima, J. Dubcovsky, J. (2006) Physical map of the wheat high-grain protein content gene Gpc-B1 and development of a high-throughput marker. New Phytologist 169: 753-763.

2008: Kuraparthy, V., Sood, S., Gill, B. (2008) Genomic targeting and mapping of tiller inhibition gene (tin3) of wheat using ESTs and synteny with rice. Functional & Integrative Genomics. 8:,33-42.

Harnessing the diversity of wild wheat

1958: Riley, R., Chapman, V. (1958) Genetic Control of the Cytologically Diploid Behaviour of Hexaploid Wheat. Nature.182:713-715. doi:10.1038/182713a0.

1968: Riley, R., Chapman, V., Johnson, R. (1968) Introduction of Yellow Rust Resistance of Aegilops comosa into Wheat by Genetically Induced Homoeologous Recombination. Nature. 217: 383 – 384. doi:10.1038/217383a0

2006: Griffiths, S., Sharp, R., Foote, T.N., Bertin, I., Wanous, M., Reader, S., Colas I, Moore, G. (2006) Molecular characterization of Ph1 as a major chromosome pairing locus in polyploid wheat. Nature. 439: 749-752. doi:10.1038/nature04434

2010: Knight, E, Greer, E., Draeger, T., Thole, .V, Reader, S., Shaw, P., Moore, G. (2010) Inducing chromosome pairing through premature condensation: Analysis of wheat interspecific hybrids. Funct. Integr. Genomics. 10: 603–608.

Exploiting the Green Revolution gene

1960s and 1970s: “Breeders at the PBI were among the first to use the Rht character to develop a stunningly successful set of wheat lines that dominated UK wheat production.” From ~Economic Impact, JIC (2010).

1997: Peng, J., Carol, P., Richards, D.E., King, K.E., Cowling, R.J., Murphy, G.P. and Harberd, N.P. (1997) The Arabidopsis GAI gene defines a signaling pathway that negatively regulates gibberellin responses. Genes and Development. 11: 3194-3205.

1999: Peng, J., Richards, D.E., Hartley, N., Murphy, G.P., Devos, K.M., Flintham, J.E., Beales, J., Fish, L.J., Worland, A.J., Pelica, F., Sudhakar, D., Christou, P. Snape, J.W., Gale. M.D.,Harberd, N.P. (1999) “Green Revolution” genes encode mutant gibberellin response modulators. Nature. 400: 256-261. doi:10.1038/22307

2011: Pearce S, Saville R, Vaughan SP, Chandler PM, Wilhelm EP, Sparks CA, Al-Kaff N, Korolev A, Boulton MI, Phillips AL, Hedden P, Nicholson P, Thomas SG. (2011) Molecular characterization of Rht-1 dwarfing genes in hexaploid wheat. Plant Physiology. 157: 1820-31. doi: 10.1104/pp.111.183657.

Developing wheat for changing climates

1978: Law, C.N., Sutka, J., Worland, A. J. (1978) A genetic study of day-length response in wheat. Heredity. 41: 185-191.

1983 Scarth, R. Law, C.N. (1983) The location of the photoperiod gene, Ppd2 and an additional genetic factor for ear-emergence time on chromosome 2B of wheat. Heredity. 51: 607–619. doi:10.1038/hdy.1983.73

1986: Worland AJ, Law, C.N. (1986) Genetic analysis of chromosome 2D of wheat 1. The location of genes affecting height, day-length insensitivity, hybrid dwarfism and yellow-rust resistance. Zeit Pflanzenzucht 96. p331–345

1995: Laurie, D.A., Pratchett, N., Snape, J.W., Bezant , J.H. (1995) RFLP mapping of five major genes and eight quantitative trait loci controlling flowering time in a winter x spring barley (Hordeum vulgare L.) cross. Genome. 38: 575-85.

2004: Mohler, V., Lukman, R., Ortiz-Islas, S., William, M., Worland, A.J., van Beem, J., Wenzel, G. (2004) Genetic and physical mapping of photoperiod insensitive gene Ppd-B1 in common wheat. Euphytica. 138: 33-40.

2005: Turner, A., Beales, J., Faure, S., Dunford, R.P., Laurie, D.A. (2005) The Pseudo-Response Regulator Ppd-H1 Provides Adaptation to Photoperiod in Barley. Science. 310: 1031-1034. DOI: 10.1126/science.1117619

2007: Beales, J., Turner, A., Griffiths, S., Snape, J.W., Laurie, D.A. (2007) A pseudo-response regulator is misexpressed in the photoperiod insensitive Ppd-D1a mutant of wheat (Triticum aestivum L.). Theor Appl Genet. 115:721-33.

Better UK wheat for bread-making

1979: Payne, P.I., Corfield, K.G., Blackman, J.A. (1979) Identification of a high molecular weight subunit of glutenin whose presence correlates with breadmaking quality in wheats of related pedigree. Theoretical and Applied Genetics. 55: 153-159.

1981: Payne, P. I., Corfield, K. G., Holt, L. M. Blackman, J. A. (1981) Correlations between the inheritance of certain high-molecular weight subunits of glutenin and bread-making quality in progenies of six crosses of bread wheat. J. Sci. Food Agric., 32: 51–60. doi: 10.1002/jsfa.2740320109

1983: Thompson, R. D., Bartels, D., Harberd, N. P., Flavell, R. B. (1983) Characterization of the multigene family coding for HMW glutenin subunits in wheat using cDNA clones. Theoretical and Applied Genetics. 67: 87-96.

1984: Payne, P. I. Holt, L.M., Jackson, E.A., Law, C. N., Damania, A. B. (1984) Wheat storage proteins: Their genetics and their potential for manipulation by plant breeding. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences. 304: 359-371

1989: Colot, V., Bartels, D., Thompson, R., Flavell, R. (1989) Molecular characterization of an active wheat LMW glutenin gene and its relation to other wheat and barley prolamin genes. Mol. Gen Genet. 216: 81-90.

1990s – 2000s: For example:
Shewry, P.R., Popineau, Y., Lafiandrax, D., Belton, P. (2001) Wheat glutenin subunits and dough elasticity: findings of the EUROWHEAT project. Trends in Food Science & Technology. 11: 433–441.

Shewry PR, Halford NG, Belton PS, Tatham AS. (2002) The structure and properties of gluten: an elastic protein from wheat grain. Philos.T. R. Soc. B 357:133-142.

Wellner N, Marsh JT, Savage AWJ, Halford NG, Shewry PR, Mills ENC, Belton PS (2006). Comparison of repetitive sequences derived from high molecular weight subunits of wheat glutenin, an elastomeric plant protein. Biomacromolecules 7:1096-1103.

1997: Shewry P.R.,Tatham, A.S. (1997) Disulphide Bonds in Wheat Gluten Proteins. Journal of Cereal Science. 25: 207–227.

2010: Lambourne, J., Tosi, P., Marsh, J., Bhandari, D., Green R., Frazier, R, Shewry, P.R. (2010) Characterisation of an s-type low molecular weight glutenin subunit of wheat and its proline and glutamine-rich repetitive domain. Journal of. Cereal Science. 51: 96-104.