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**REVIEW**

# Balancing quality with quantity: A case study of UK bread wheat

**Nick S. Fradgley**[1] | **Keith A. Gardner**[2] | **Matt Kerton**[3] | **Stéphanie M. Swarbreck**[1] | **Alison R. Bentley**[2]

[1]NIAB, Cambridge, UK
[2]International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico
[3]DSVUK Top Dawkins Barn, Banbury, UK

**Correspondence**
Nick S. Fradgley, NIAB, 93 Lawrence Weaver Road, Cambridge, CB3 0LE, UK.
Email: nick.fradgley@csiro.au

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**Societal Impact Statement**

Increasing crop productivity is often proposed as a key goal for meeting the food security demands of a growing global population. However, achieving high crop yields alone without meeting end-use quality requirements is counter to this objective and can lead to negative environmental and sustainability issues. High yielding feed wheat crops in the United Kingdom are a typical example of this. The historical context of UK agricultural industrialisation, developments in plant breeding and wheat end-use processing are examined. We then outline how employing innovations in plant breeding methods offer the potential to redress the balance between wheat quantity and quality.

**Summary**

Bread wheat (*Triticum aestivum* L.) has historically been an important crop for many human civilisations. Today, variability in wheat supply and trade has a large influence on global economies and food security. The United Kingdom is an example of an industrialised country that achieves high wheat yields through intensive cropping systems and a favourable climate. However, only a minority of the wheat grain produced is of suitable end-use quality for modern bread baking methods and most wheat produced is fed to livestock. A large agricultural land area and input use dedicated to producing grain for animal rather than human food has wide-ranging negative impacts for environmental sustainability and domestic food production. Here we present an historical perspective of agricultural and economic changes that have resulted in UK production primarily focussing on wheat quantity over quality. Agricultural intensification, liberalisation of free trade in agricultural commodities, innovations in the milling and baking sector, developments in scientific understanding of genetics and plant breeding, and geopolitical changes have all played a role. We propose that wheat breeding plays a crucial role in influencing these issues and although wheat breeders in the United Kingdom have historically applied the most-up-to-date scientific advances, recent advances in genomics tools and quantitative genetics present a unique opportunity for breeders to redress the balance between quantity and quality.

**KEYWORDS**
grain protein content, history, quality, United Kingdom, wheat, yield

## 1 | THE ROLE OF UK WHEAT IN THE GLOBAL FOOD SYSTEM

Domestication of wheat (*Triticum aestivum* L.) from its ancestors played a major role in the formation of early agrarian civilisations in the fertile crescent (Bhargava et al., 2019; Faris 2013), which for better or for worse, involved sedentarism and the first centralised states (Scott, 2017). Over the last century, agricultural industrialisation and progress in plant breeding has sustained substantial increases in wheat yields (Mackay et al., 2011; Mondal et al., 2020; Tadesse, 2019), broadly meeting the food demands of the rapidly growing global population. However, recent volatility in the global wheat trade (Bentley, 2022), projected increases in population growth and demand beyond supply (Godfray et al., 2010), as well as climate change impacts (Ray et al., 2019) underline the vulnerability of wheat production and distribution. Use of agricultural inputs, including inorganic nitrogen and phosphorus fertilisers as well as pesticides, will also become increasingly limited due to scarcity of their component resources and requirements to reduce environmental impacts (Basosi et al., 2014; Dawson & Hilton, 2011; Skowrońska & Filipek, 2014; van der Werf, 1996).

Wheat grains contain mostly starch (80%), while total proteins (e.g., glutenins) typically constitute between 9% and 15%. Fibre, mainly derived from non-starch cell walls, and minerals important for human dietary health (Fradgley et al., 2022), are present in much smaller proportions (Shewry et al., 2013). The suitability of grain for human consumption, as defined by quality end-use classes (e.g., bread baking and biscuit making), is determined by variations in both the overall quantity and the specific properties of different proteins that affect the ease of grain milling, processing and baking characteristics, defined by the prevalent bread baking industries. Grain that falls below threshold quality criteria is generally used as feed for livestock. These quality criteria for processing and human nutrition have historically evolved along with developments in industrial processing methods and consumer product preferences.

Temperate wheat growing regions, such as north-western Europe, have favourable climates for achieving high yields. In comparison to other major wheat producing regions, the United Kingdom has relatively mild winters and cool summers with long day lengths, conducive to optimising the reproductive and grain filling phase (Worland, 1996). Reflecting this, several recent world record breaking wheat yields have been achieved in the United Kingdom (Jones, 2023; Senapati et al., 2019). However, this highly productive system providing large quantities of feed grain for livestock consumption underpins an unsustainable food system and intensifies the environmental impacts of industrial farming land use. The lack of focus in the United Kingdom on producing high quality wheat grain for human consumption has been an outcome of many factors including agricultural intensification, developments in milling and baking industry requirements as well as difficulties in plant breeders' simultaneous selection for multiple quality traits, some of which are negatively correlated with yield.

Here we give an historical perspective of changes and developments in quality wheat production and breeding in the United Kingdom. We highlight the important role that plant breeding can play to redress the current imbalance between quantity and quality and shape a more sustainable food system in future.

## 2 | THE HISTORICAL CONTEXT FOR CHANGES IN UK WHEAT QUALITY

### 2.1 | Industrialisation and globalisation drove highly productive wheat farming in the United Kingdom

Wheat was not the dominant cereal crop grown and consumed by the majority of Britons as the 'the staff of life' until the industrial revolution of the mid-19th century (Collins, 1975). The enclosure of common land (McCloskey, 1972) and the agricultural revolution towards the end of the 18th century was the first major step change in increasing the productivity of British agriculture and the dominance of wheat (Allen, 1999). Consolidation of small holdings of less than an acre (~0.4 ha) and adoption of crop rotations as well as integration of livestock to fertilise cropland led to greater farm system efficiency (Thompson, 1968). The beginnings of mechanisation saw horse-drawn seed drills enabling greater productivity with reduced manual labour. The enclosures also paved the way for private ownership of farmland and the urbanisation of labour that fuelled the industrial revolution (Fairlie, 2009).

Agriculture in Victorian Britain, particularly between 1830 and 1880, has been considered to have been a golden age of 'High Farming' where mechanisation and mixed farming, integrating livestock into crop rotations, ensured steady increases in output and competitiveness of British farmers with European contemporaries (Harley, 2018; Perry, 1981; Walton, 1999). Mixed farmers already valued both yield of straw for forage and grain for bread making but the value of grain for livestock feed was also becoming increasingly important so that high yielding and soft, low-quality varieties that responded well to manure fertilisation were generally preferred. With the lack of a coordinated wheat quality grading system, there was already little incentive for farmers to produce lower yielding, but high-quality wheat crops for bread making.

Pressure from the increasing urban population to reduce food prices led to the 1846 repeal of the Corn Laws to allow free trade in lower cost imported wheat, which was a major first step towards a globalised food system (Fay, 2017). Wheat imports to the United Kingdom came mainly from the United States, Canada and Russia, where wheat could be grown much more cheaply over larger areas. These shorter season growing environments with reduced summer rainfall meant that the hard milling red spring wheat types were grown at lower yields and higher protein content, producing stronger and higher-quality flour than the softer United Kingdom produced wheat. With farmers' higher production costs and reduced grain prices Britain entered a period known as the great agricultural depression which saw increased reliance on grain imports, decreased agricultural productivity, and a shift towards extensive permanent pasture-based livestock systems over grain production (Figure 1; Turner, 1992; Walton, 1999). Facing the financial challenges of lower domestic grain prices due to cheaper imports and increased labour costs in competition with the booming urban industries, British wheat farmers were obliged to prioritise yield over quality. Another consequence of this was the development of the market for British soft wheat flour for biscuit making as an international trade exchange for higher quality bread wheat imports, but no formal quality grading system existed for domestically produced grain (Walton, 1999).

The second industrial revolution (from the second half of the nineteenth century) saw the decoupling of the inverse relationship between workers' wages and population size so that both increased sharply (Harley, 2018). This was also a significant turning point for the milling industry with the invention of roller mills which rapidly replaced traditional stone mills throughout the 1870s and facilitated a more centralised processing system (Figure 1a). Roller mills operate a series of incrementally narrowly spaced steel rolls that separate much more efficiently the white endosperm as fine white flour from the larger sized bran and germ components of the grain as different fractions (Belderok et al., 2000). A higher extraction rate of sifted white flour can therefore be achieved from roller milled flour compared to stone milling. This new industrial milling method redefined the wheat quality criteria with greater value placed on high extraction rates from hard milling imported grain that could not be matched by domestic wheat growers. The increased prevalence of wheat in the diets of the urban population was therefore also accompanied by a shift to more efficiently refined white flour across societal classes, and was endorsed by food chemists for perceived health benefits (Tann & Jones, 1996). Beginning in the south-east with increased demand from the population in London, pulses and other grains including barley, oats and rye were replaced by wheat as the dominant cereal consumed in the United Kingdom (Collins, 1975).

The agricultural depression in Britain lasted from 1876 to the end of the 19th century (Figure 1a). Despite the beginnings of systematic plant breeding in the United Kingdom in the early 20th century, the United Kingdom continued to import more than three quarters of wheat for domestic use throughout the agricultural depression and up until World War II (Figure 1b; Belderok et al., 2000; Mitchell, 1988). However, the constraints on imports due to the war abruptly necessitated the United Kingdom to ‘dig for victory’ and become more self-sufficient. Large areas of permanent pasture were again cultivated for cereal grain production (Figure 1d; Angus et al., 2009). In addition, implementation of the Haber Bosch process (Kissel, 2014) saw nitrogen fertiliser availability and application (together with wheat yields) rapidly increase up until the end of the 20th century (Figure 1c; Muhammed et al., 2018). Increases in grain yield from the 1960s onwards were partly achieved through increased fertiliser rates (Hawkesford & Riche, 2020), but genetic advances made through intensive selection and breeding have also become increasingly important (Figure 1c; Mackay et al., 2011).

## 2.2 | Progress and challenges faced by UK wheat breeding to combine yield and quality

Although breeding high quality and highly productive varieties has long been an endeavour of UK wheat breeders, the context of industrialisation of wheat production and market forces favouring quantity over quality has historically presented many challenges. At least as far back as the 18th century, arable farmers were encouraged to follow the common practice of livestock farmers managing the best stock for breeding and select seed from the most vigorous plants in the heterogenous landraces (a plant variety that is heterogeneous and has evolved in particular location) grown at the time (Walton, 1999). However, more formal plant breeding was not undertaken until towards the end of the 19th century. Following the 18th century age of enlightenment when rapid advances in scientific thinking and discoveries were made across Europe (Hankins & Hankins, 1985), Gregor Mendel's work in the 1850s on inheritance of genes in plants laid the foundations for the science of genetics and plant breeding (Gliboff, 1999). Nevertheless, the implications of Mendel's work were only considered by a few contemporaries in the scientific community before the end of the century (Olby & Gautrey, 1968). From the mid-19th century, heterogeneous landrace varieties were replaced by higher yielding pure-line selections from them, and then through deliberate crossing of individual lines and selection of high performing pure-line varieties (Belderok et al., 2000; Bradshaw, 2017). For example, the newly identified Squarehead wheat types were adopted and used for crossing by plant breeders across northern Europe, bringing steady increases in yield (Figure 1c), but were generally of poor quality for milling and bread making (Pujol Andreu, 2011). The National Association of British and Irish Millers (NABIM) had raised concerns over the deterioration of the quality of United Kingdom produced wheats from as far back as 1890 (Walton, 1999). For example, Squareheads Master (Figure 2) was one of the early varieties developed by crossing distinct parental varieties and was mainly used as a biscuit wheat (Percival, 1934).

The Cambridge Plant Breeding Institute (PBI) was established in 1912 to lift Britain out of financial depression and apply the accepted Mendelian understanding of genetics and heredity to plant breeding (Palladino, 1996; Radick, 2023). Although the classical population geneticists and statisticians of the time advocated a more quantitative biometric model of evolutionary processes, Mendelism prevailed as the accepted concept, assuming that discreet qualitative traits were more simply inherited (Harwood, 2015; Provine, 2001). Much in the

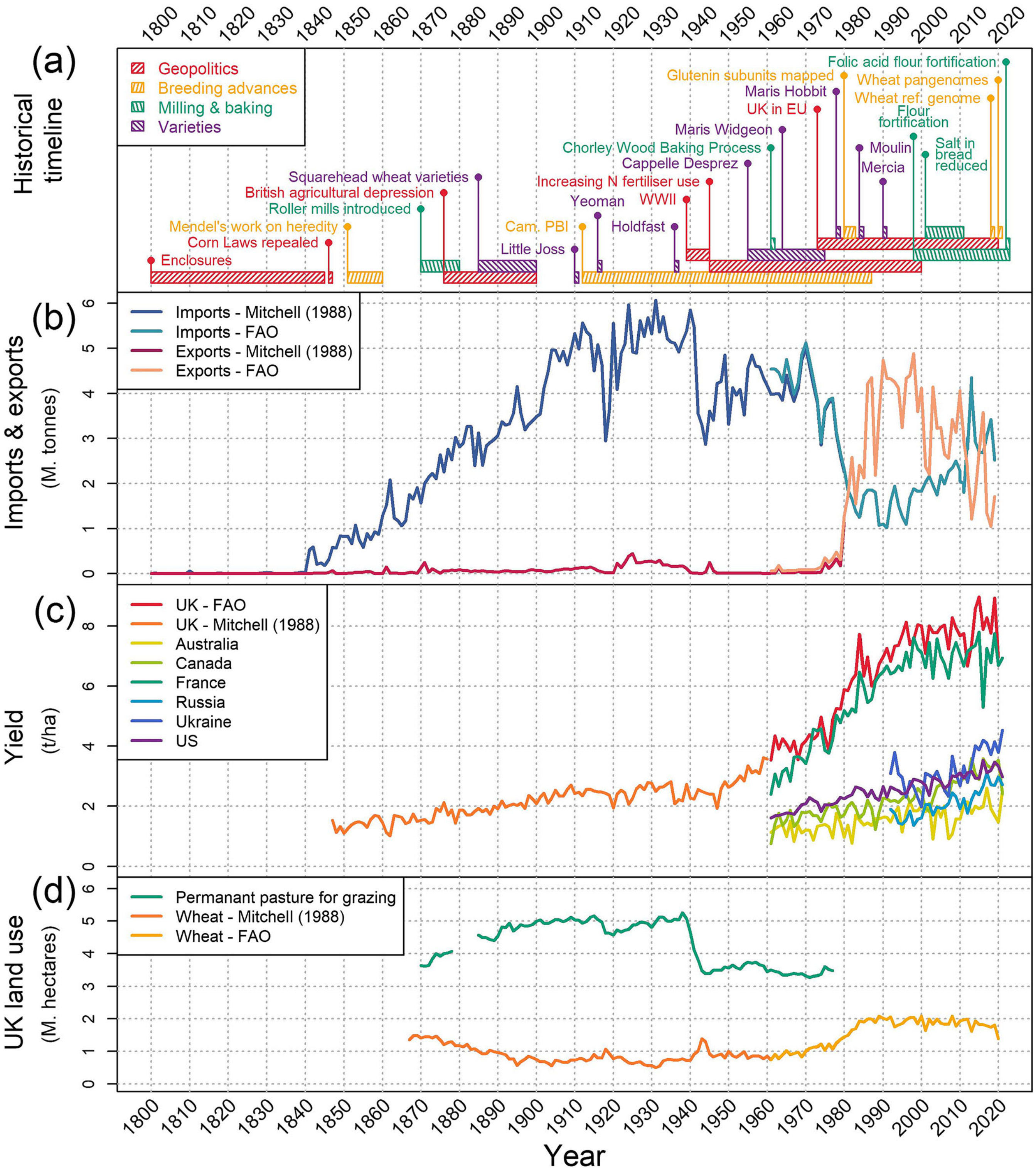

**FIGURE 1** A historical overview of trends in wheat production in the United Kingdom from 1800 to 2022. (a) Historical timeline for UK wheat production including geopolitical events, advances in the science of crop genetics and breeding, key innovations in the milling and baking industry and significant wheat varieties released. (b) Trends in imports and exports of wheat in the United Kingdom. (c) Trends in grain yield of wheat in the United Kingdom and the six countries with the largest wheat exports. (d) Trends in land area use for wheat and permanent pasture for livestock grazing in the United Kingdom. Data sourced from Mitchell (1988) and FAO (2022).

same way as Mendel had demonstrated with pea flower colour and seed shape, Biffen considered directed crosses of inbred parent lines to be an effective approach to combine and fix simply inherited traits for yield and quality. Despite contentious correspondence with the Canadian wheat breeder Charles Saunders, who argued the contrary, Biffen assumed 'strength' (of dough viscoelastic properties) in wheat behaved as a purely Mendelian trait (Saunders & Biffen, 1909). Although components of gluten protein quantity and quality were not clearly understood at the time, Biffen aimed to combine the high yield of the Squarehead type varieties with gluten strength from other sources (Humphries & Biffen, 1907). Rather than using the traditional high quality UK landraces that had been displaced, he looked further afield and used the spring wheats that were being imported to the United Kingdom. Biffen achieved early success with the first few released varieties each being grown over large proportions of the UK wheat area (Lupton, 2005; Srinivasan et al., 2003). These included Little Joss, which was bred from Squareheads Master and Ghirka (a Russian spring wheat), as well as Yeoman which was bred from another English Squarehead type wheat (White-chaffed Browick) and Red Fife; a Canadian spring wheat. Despite Biffen's early successes and close collaborations with the established milling and baking industry (Humphries & Biffen, 1907), there was still a disconnect with the market forces and requirements influencing farmers' decision making. Although the minority of quality wheat growers supported Biffen's work, the growing poultry feed industry was still able to offer comparable premiums to those of bread baking quality wheat (Halnan, 1928), thus shifting production incentives towards lower quality. As work at PBI progressed, white grained varieties such as Steadfast (released: 1942) and Holdfast (released: 1936) were released but achieved only limited acceptance due to susceptibility to pre-harvest sprouting (leading to reduced grain quality), despite Holdfast's otherwise good quality profile (Belderok et al., 2000; Palladino, 1996).

The shortcomings of PBI extended after World War II as varieties from foreign private breeding companies were increasingly grown in the United Kingdom (Palladino, 1996). The high yielding and disease resistant French variety Cappelle Desprez came to dominate wheat farming in the United Kingdom throughout the 1960s and was used extensively at PBI as a parent of new varieties to further push greater yields (Figure 1a; Lupton, 2005). The release of the high-quality wheat Maris Widgeon (Figures 1a and 2) in 1964 was a significant exception to this trend but was not grown widely; again, due to the lack of market incentives to grow high-quality wheat at the time. Therefore, the disconnect between PBI and the market requirements continued into the 1960s and meant that high-quality varieties still went underutilised. From the 1960s, introgression of semi-dwarf height reducing genes into wheat breeding programmes around the world and selection for widely adapted varieties was a fundamental part of the 'Green revolution' which enabled greater use of nitrogen fertiliser to increase yields without risk of yield losses due to crop lodging and a shift towards greater harvest index (Baranski, 2022; Hedden, 2003). However, the first semi-dwarf wheat variety (Maris Hobbit) was not released in the United Kingdom until 1978 (Figure 1a).

From the 1980s, a clearer scientific understanding of the major genetic and physiological components of wheat quality at PBI enabled an era of increased focus on high quality wheat breeding. Early rudimentary methods to assess gluten quality include manually washing gluten from wheat dough (Monsivais et al., 1983), the Pelshenke test and the Zeleny test. These tests were developed as simple methods that could estimate the baking performance of newly developed breeding lines. The Pelshenke test included a measure of time taken for a yeasted dough ball to expand, float and disintegrate in water, thus providing information on the gluten quality (Pelshenke, 1930). The Zeleny test quantifies the sedimentation of wheat flour in a dilute lactic acid solution, indicating good dough quality (Zeleny, 1947). These early tests were replaced by higher throughput and more accurate methods such as the addition of sodium dodecyl sulphate (SDS) to the sedimentation tests which could then be more closely related to dough quality regardless of confounding effects of starch degradation (Preston et al., 1982) and use of near infra-red reflectance spectrometry (NIRS) technology directly on grain or flour samples to rapidly and accurately measure protein content (Corbellini & Canevara, 1994). At this time, PBI scientists knew that wheat gluten quality was largely regulated by the high molecular weight glutenin subunit genes (Blackman & Payne, 1987; Payne & Lawrence, 1983). These are located on chromosome 1 from each of the A, B and D genomes of hexaploid wheat (*Glu-1A*, *Glu-1B*, and *Glu-1D* loci). With this knowledge, breeders could make selection for gluten quality based on specific genetic information. These improvements in both testing methods and genetic marker assisted selection meant that much larger numbers of breeding lines could be screened for quality traits and associated beneficial genes at earlier stages of the breeding programme leading to successful release of several high-quality biscuit and bread wheat varieties throughout the 1980s. Initially, the high

**FIGURE 2** Example side and front view images of ears from key early wheat varieties grown in the United Kingdom.

performing quality subunit 1 allele at the *Glu-1A* locus was already present in older high quality PBI varieties including Holdfast and Maris Widgeon. Subsequently, the variety Moulin was released in 1985 and included the 17 + 18 subunit allele at the *Glu-1B* locus that was introduced from a Mexican breeding line from the International Maize and Wheat Improvement Center (CIMMYT) (Figure 3). Red Fife was identified and used as the new source of gluten strength by Biffen at the start of the 20th century without explicit knowledge of the underlying glutenin profile (Humphries & Biffen, 1907). However, inheritance of Red Fife's 5 + 10 allele at the *Glu-D1* locus that contributes the greatest value for gluten quality was not directly selected from Holdfast to Maris Widgeon at this early stage (Figure 3). It was not until much later that varieties were released in the United Kingdom with the same 5 + 10 allele derived less directly from other European material. The spring wheat Maris Dove was released in 1971 which inherited the 5 + 10 allele from German material where the allele was much more frequent (Belderok et al., 2000) but likely originated from Canadian Red Fife (Figure 3). Mercia was later released in 1984,

**FIGURE 3** Pedigree visualisation of the routes that beneficial high molecular weight glutenin alleles were introduced and combined into UK varieties.

inheriting the allele from the French variety Flanders and was selected based on physical SDS sedimentation tests rather than direct genotyping for the 5 + 10 allele. Solitaire, released in 1985 with 5 + 10 inherited from Dutch and Swedish material, also combined with the other introduced beneficial 17 + 18 allele at the *Glu-1B* locus but did not contribute much as a parent of later varieties (Figure 3). However, Rialto (1991) inherited 5 + 10 from German varieties, similarly to Maris Dove, as well as 17 + 18 directly from Moulin (Figure 3) and is an ancestor of many later high-quality winter wheat varieties. Similarly, via its descendant Cadenza, Maris Dove became the ancestor of many later high-quality spring wheats (Fradgley et al., 2019).

Although these alleles took several routes into the UK wheat gene pool, deeper analysis of the wheat pedigrees suggests Red Fife as the ancestral source of the 5 + 10 allele through each route (Figure 3; Payne et al., 1987; Lukow et al., 1989; Foot & Angus, 2005; Fradgley et al., 2019).

However, this period of successful development of high-quality wheat varieties at PBI would not last. The introduction of Plant Breeders' rights in 1964 enabled several private breeding companies to coexist with the dominant PBI (Galushko & Gray, 2014), but with the privatisation of the PBI in 1987 and the International Union for the Protection of New Varieties of Plants (UPOV) act of 1991, that allowed breeders to claim greater royalties on farm saved seed, a much larger number of private plant breeding companies came to compete in the UK wheat varietal development and release market. In contrast to southern Europe, the particularly strong administration of the royalties system in the United Kingdom has made it a valuable target market for large breeding companies operating programmes across Europe. Management of the variety recommended lists produced by the then publicly funded National Institute of Agricultural Botany (NIAB) was later transferred to commercial breeding industry and farmer levy funded bodies including the British Society for Plant Breeding (BSPB) and the Home Grown Cereals Authority (HGCA), now the Agriculture and Horticulture Development Board (AHDB), and the four distinct wheat quality classes were more clearly defined by NABIM; now UK Flour Millers. As a result, since the 1990s, the United Kingdom has had readily available high-quality varieties with optimum HMW glutenin profiles, combined with a statutory/regulatory framework with clearly defined quality classes enabling clearer incentives and premiums for high-quality wheat varieties. Despite this, the focus of commercial UK wheat breeding has continued to have been on increasing yield as the economically important trait ensuring return on breeding investment (Galushko & Gray, 2014; Lupton, 2005).

### 2.3 | Changes in wheat processing redefine wheat baking quality and nitrogen fertiliser use

Alongside evolving agricultural practices and developments in commercial wheat breeding, modern bread processing technologies were also invented and adopted. This further changed the requirements for UK wheat baking quality and the demand for different end-uses. In a similar manner to that in which roller mills redefined the wheat grain quality requirements and preference for white bread among consumers towards the end of the industrial revolution, the Chorley wood baking process (CWBP) was developed in 1961 (Figure 1a) and revolutionised the mass production of bread. The CWBP involves high speed mixing under high pressure to aerate the dough, rapid fermentation and addition of dough 'improvers' (including enzymes, oxidising agents and emulsifiers) (Cauvain & Young, 2006). These methods enabled much faster processing times and efficiency for industrial production of supermarket bread. The new wheat quality requirements for this method included several more specific criteria to ensure high uniformity and processing efficiency in the new centralised mass-production system but also reduced the required protein content in flour blends to achieve sufficient loaf volume using this method to as low as 11 or 12% (Blackman & Payne, 1987; Stewart, 2013). This meant that bread could be baked using a greater proportion of lower protein UK wheat in blends with higher protein imports and promoted increasing yields of milling wheat varieties at the expense of protein content to reduce reliance on imports (Figure 1b). However, the resulting shift in the yield to protein trade-off has also had implications for crop nitrogen fertiliser use efficiencies – much greater nitrogen fertiliser rates are required to compensate for otherwise lower protein, as well as to meet the higher yield potential of modern varieties.

Under Statutory law, refined white wheat flour in the United Kingdom has been supplemented with calcium and iron since 1998 and more recently with folic acid (Figure 1a), in an attempt to provide sufficient quantities of these nutrients to consumers via inclusion in a food type (wheat products) that make a large contribution to diets (Lockyer & Spiro, 2020). Although whole grain flour contains three times the concentration of key micronutrients compared to refined white flour (Fradgley et al., 2022), 90% of breadmaking flour milled in the United Kingdom is refined white flour (UK Flour Millers, 2023). There is also concern over apparent declines in micronutrient density of modern wheat varieties over recent decades of breeding. Similarly to how grain yield and protein have a negative genetic trade-off, the yield dilution effect has also reduced wheat grain mineral concentrations as yields have increased (Davis, 2009; Fan et al., 2008; Murphy et al., 2008). Nevertheless, there has been no incentives from the UK milling and baking industry to allow plant breeders in the United Kingdom to include nutritional value as a breeding target or promote the health benefits of whole grain cereals (Mann et al., 2017). Therefore, the nutritional components of wheat quality have also been neglected due to lack of value in the supply chain. Like overall quality they have also suffered indirect negative impacts from the focus on maximising yield gains and processing requirements.

## 3 | CURRENT STATUS IN THE UK

Despite the UK's strong potential to produce high yielding milling wheat for human consumption and the plant breeding industry's past successes in responding to the prevailing requirements of the milling and baking industry, delivery of high-quality milling quality wheats by the commercial wheat breeding industry has been considered by some to be a market failure (Galushko & Gray, 2014). Although there are strong financial incentives to breed and produce high quality milling wheat, since the early 1980s less than half of the wheat produced in the UK has been for domestic human consumption end-use (Figure 4). A review of the current UK AHDB Recommended List (a list compiled annually for each end-use quality class to inform farmers' variety choice; AHDB, 2022) shows that there are almost three times as many feed wheats as high-quality milling varieties available to UK farmers. Although the two varieties with the greatest seed production in 2021 were both milling wheat varieties, all milling wheat varieties together were only 32.5% of all certified seed produced. In short, the UK remains a typical example of a high income country that has an increasing focus on non-food uses of wheat (Figure 4; Ray et al., 2022).

However, with the United Kingdom producing mostly feed wheat and over 80% of flour milled in the UK coming from home-grown crops (UK Flour Millers, 2022), the UK could easily be self-sufficient in milling wheat whilst reducing acreage of feed wheat. In comparison to the United Kingdom, wheat yields in major quality wheat exporting countries, such as Australia, Canada, the United States, Ukraine and Russia, are typically less than one half that of the United Kingdom and France (Figure 1b; FAO, 2022), but much more readily achieve high grain protein content. In the United Kingdom, yields of high-quality wheats that are suitable for milling and bread baking end-use are generally no more than 10% lower than feed wheat varieties (AHDB, 2022). Although wheat in the United Kingdom is produced with some of the highest nitrogen fertiliser inputs globally (FAO, 2022), wheat for direct human consumption end-uses can be produced at high yields on a much smaller land area which largely accounts for the smaller carbon footprint of bread made from home-grown compared to imported wheat (Espinoza-Orias et al., 2011).

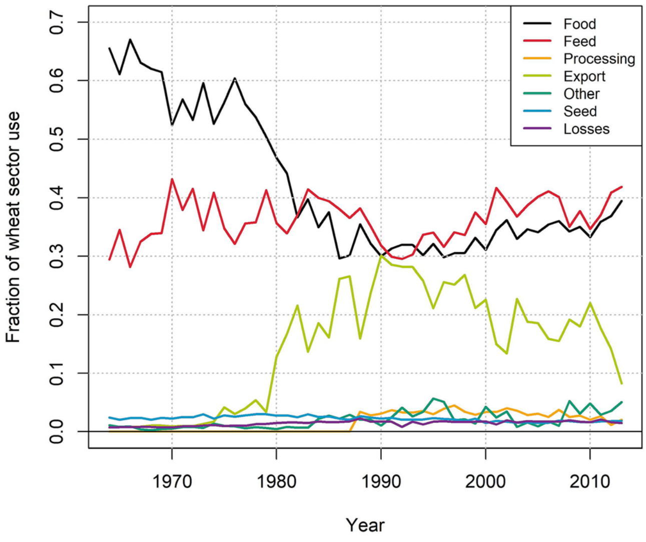

**FIGURE 4** Trends in proportion of UK-grown wheat by different end use types. Data sourced from supplementary material of Ray et al. (2022).

Furthermore, climate change impacts for the UK in the near future are likely to remain largely positive for grain yield (Harkness et al., 2020; Slater et al., 2022) and quality traits (Fradgley, Bacon, et al., 2023). Further developing exports of more sustainably produced UK milling wheat, rather than the feed wheat that currently comprises the majority of UK exports, may also contribute to global food security and sustainability.

## 4 | FUTURE OUTLOOK AND RECOMMENDATIONS

Farmers' decision-making processes for variety choice are largely influenced by management of risk in their production system. Investing more into growing a high-quality wheat variety, particularly in terms of the additional nitrogen fertiliser costs, can result in greater economic returns if the required quality criteria are met after harvest and a premium grain price is achieved. However, management of this risk is largely dependent on quality characteristics of the wheat variety grown so plant breeding plays a major role in influencing trends in farmers' decision-making regarding variety choice and crop management. We propose that recent developments in plant breeding will be key to addressing the wider agronomic, environmental and socioeconomic challenges outlined above.

### 4.1 | Mendelism and 21st century plant breeding

Applying a Mendelian approach to plant breeding in the early 20th century, Biffen had only limited success at breeding high quality UK wheat varieties without knowledge of the specific genetic control of HMW glutenin subunits. The later successes of the PBI, once optimum HMW glutenin profiles could finally be intentionally combined, was fortunately only possible because gluten strength traits are highly heritable with only a few major genetic effects and generally inconsequential environmental effects or variety by environment interactions. Most of the progress in wheat quality breeding has been achieved through improvements in gluten strength traits, but this is unusual in comparison to many of the other more quantitative wheat quality traits for which much less progress in breeding has been made (Fradgley, Bentley, et al., 2023).

Bernardo (2016) outlined how the many trends and 'bandwagons' in genetics and crop breeding have gone through the 'hype cycle'. Utilising the wealth of genomic marker data available, there has been thousands of studies reporting identification of quantitative trait loci (QTL)—small regions of the genome associated with useful variation in a trait of interest. However, only a small fraction of these QTL with large effects have been successfully applied in plant breeding programmes for relatively simple traits such as disease resistance.

It has been much more difficult to find and deploy QTL for more complex and polygenic traits such as grain yield that have been under strong long-term selection and for which the remaining QTL are therefore of only small effect sizes (Scott et al., 2021). Interactions between genetic and environmental effects (G × E) also often mean that identified QTL are rarely stable and validated in subsequent environments. The same trends have been found for many of the other wheat quality traits such as grain protein content, grain specific weight and Hagberg falling number that are more quantitative than gluten strength controlled by a few HMW glutenin genes (Fradgley et al., 2022; Kristensen et al., 2018).

However, more recent developments in tools and methods in quantitative genetics puts modern crop breeders in the unique position to do what previous generations of wheat breeders attempting to reconcile yield and quality traits could not. Wheat breeding now has a wealth of genomic tools at hand to accelerate genetic gain that previous generations of plant breeders did not and costs of genotyping have dramatically decreased (Crossa et al., 2021). Genomic assisted selection methods allow breeders to make selections purely on genetic variation and recycle parental material at earlier stages of the breeding programme. Most notably, quality traits which traditionally are too expensive and time consuming to measure on large numbers of early-stage breeding lines, can be prioritised simultaneously with grain yield and productivity traits.

Although Mendelism prevailed over the more quantitative, statistical genetics theories of biometrics as the accepted model of evolutionary biology at the beginning of the 20th Century (Radick, 2023), today's 21st century breeders are finding greater relevance in more quantitative and statistical genetics models as originally proposed by biometrics. Genomic assisted selection methods such as genomic selection (Meuwissen et al., 2001) use large numbers of genetic markers across the genome to make predictions of trait values so that breeders' selections can be based on the culmination of many inherited genetic effects. This approach has proven highly applicable in commercial breeding programmes for improvement of complex polygenic traits (Crossa et al., 2017). Fradgley, Bentley, et al. (2023) demonstrated that most progress in wheat bread baking quality in the UK has been down to improvements in gluten quality traits, where specific genetic markers were used to select for specific HMW glutenin combinations (Figure 3). However, few improvements in grain specific weight or Hagberg falling number have been achieved. Genomic selection holds great potential for these traits (Fradgley, Bentley, et al., 2023).

## 4.2 | High baking quality at low protein content

It has been shown that UK wheat breeding has successfully enhanced suitability of milling wheat varieties for modern industrial bread baking methods by increasing the frequency of high molecular weight glutenin genes to increase gluten strength while grain protein content has decreased (Fradgley, Bentley, et al., 2023; Shewry et al., 2020). Increased strength of gluten protein now replaces the need for large quantities of weak gluten protein in older varieties. Continued breeding for enhanced baking quality performance at low protein is still an objective for lowering the nitrogen fertiliser requirements of wheat (Shewry et al., 2023), but will require acceptance of such varieties and some adaptation of the bread baking processes by the milling and baking industry. The optimum HMW glutenin profiles have been well defined for baking performance at around 13% protein, but further increasing glutenin strength above what is currently considered optimum may enable reductions in acceptable grain protein content. This could be achieved by making use of more novel alleles of current glutenin and gliadin genes such as the overexpression of the Bx7 at *Glu-B1* (Ragupathy et al., 2008), from the tertiary genepool of wheat ancestors (Delorean et al., 2021), or from dissection of genetic control of the wheat grain proteome (Afzal et al., 2023). However, it should be noted that this approach to further reduce overall grain protein content will not be biologically neutral as it will exacerbate micronutrient dilution (Davis, 2009; Garvin et al., 2006). Consideration of grain protein content and micronutritional quality as quantitative traits alongside grain yield as a component of the forward wheat quality breeding strategy will be important to ensure basic nutritional content including micronutrients can at least be held stable, if not increased (Fradgley et al., 2022; Govindan et al., 2022).

## 4.3 | Breaking the trade-off between grain yield and protein

A key approach to specifically break the trade-off between grain yield and protein content and achieve genetic increases in both traits simultaneously is to employ a selection index for grain yield protein deviation (GYPD), where a positive GYPD is defined as the increased in grain protein content beyond what is expected given the negative correlation between grain yield and protein content (Bogard et al., 2010; Michel et al., 2019; Monaghan et al., 2001). Shewry et al. (2023) demonstrated that modern varieties with high GYPD were particularly valuable for better baking quality at lower protein content due to reduced nitrogen fertilisation. Despite evidence that GYPD has not been optimised in recent decades of wheat breeding in the United Kingdom (Yang et al., 2022), it has been demonstrated that sufficient heritability exists for GYPD (Mosleth et al., 2020; Scott et al., 2021) and simulations of recurrent selection suggests that progress in advancing GYPD to break the yield—protein trade off would be possible, but a highly quantitative approach will be required (Fradgley, Gardner, et al., 2023). Deployment of accelerated breeding methods, making use of genomic selection (Crossa et al., 2017) and speed breeding methods (Cha et al., 2022; Ghosh et al., 2018) to minimise generation times and enable rapid cycling of parental genotypes with high breeding value will aid application of these methods in commercial breeding programmes. Because of the strong genetic association between grain protein and micronutrient content (Davis, 2009; Fradgley et al., 2022), the GYPD selection approach would likely also help resolve the micronutrient dilution problem (Guttieri et al., 2015) and should be an efficient criterion to indirectly select for improved nitrogen use efficiency (Bogard et al., 2010). It has already been shown that progress in conventional recurrent selection breeding for both yield and enhanced zinc and iron content is possible (Govindan et al., 2022). The stability of GYPD trends across differing environments and climates or nitrogen input levels is less well understood, although Michel et al. (2019) demonstrated good accuracy of forward genomic prediction across years.

## 4.4 | A modern synthesis of quantitative genetics and biotechnology

Denison (2015) suggested that trade-off free improvements in crop breeding that have already been optimised by natural selection in ancestral populations will be difficult to resolve. However, application of new breeding technologies to generate or unlock novel genetic effects may be particularly fruitful for enabling breeding progress. Gene editing methods are proving highly useful as a tool for understanding complex gene regulatory networks and molecular biological processes. As an example, recent work taking a more fundamental molecular biology approach found that overexpression of *HOMEOBOX DOMAIN-2* (*HB-2*) protein resulted in a large increase in grain protein content without apparent yield penalties so may be a particularly useful innovation for breaking the trade-off between grain yield and protein content (Dixon et al., 2022). However, bridging the gap between fundamental research and applied plant breeding is often problematic. Applying gene editing technologies as a pre-breeding tool to generate genetic variation that feed into an accelerated breeding programmes could have great potential (Hickey et al., 2019). However, novel genetic effects generated from gene editing in the latest elite material in a crop breeding programme would not be predictable from a genomic prediction model trained on previous cycles of breeding data. Therefore, a priori integration of novel genetic effects in genomic prediction models, such as promotion of alleles by genome editing (PAGE; Jenko et al., 2015) would be required. Like the modern synthesis of Mendelian and population scale Darwinian theory proposed by Huxley (1942), a synthesis of quantitative genetics and more fundamental research employing biotechnologies will be key to their future co-optimisation.

## 4.5 | A broader context

In summary, genomic tools for crop breeding are now cheaply available and enable enhanced selection to break trade-offs between yield and quality that have long been problematic. From a scientific perspective, this tips the balance as far as possible towards breeding for high yielding quality varieties. However, successful application of these scientific methods to applied breeding programmes and wider food systems will require equally innovative regulatory and socio-political incentives.

A better metric for valuing productivity per area of crop land may be required to incentivise positive changes in agricultural practices. Cassidy et al. (2013) proposed that rather than using tonnes of grain per hectare, a metric defining the number of people nourished per hectare should be used. This would greatly favour high yield and quality wheat for human consumption end-use and with enhanced nutritional value rather than wheat for livestock feed. Further changes in global diets including reduced reliance on animal-based proteins will also be required to ensure environmentally sustainable diets (Willett et al., 2019). However, global demand for animal-based protein has continued to rise, and vegetarians and vegans are still a minority even in western countries, such as the UK. Considering the nutritional value of unrefined whole grain cereals in the broader context of complex food systems will also be important (Poole et al., 2021). In short, increasing agricultural productivity will be ineffective in achieving a sustainable food system unless suitability of wheat for end-uses that feed many people is also prioritised through plant breeding and complementary supply and demand throughout the food supply chain.

## AUTHOR CONTRIBUTIONS

Nick S. Fradgley designed and performed the research; collected, analysed and interpreted data and wrote the manuscript. Keith A. Gardner, Matt Kerton, Stéphanie M. Swarbreck and Alison R. Bentley designed the research, interpreted data and wrote the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

## ORCID

*Nick S. Fradgley* https://orcid.org/0000-0002-7868-8795
*Keith A. Gardner* https://orcid.org/0000-0002-4890-301X
*Matt Kerton* https://orcid.org/0000-0002-9587-8523
*Stéphanie M. Swarbreck* https://orcid.org/0000-0001-8355-7354
*Alison R. Bentley* https://orcid.org/0000-0001-5519-4357

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