Response to Challenge: William Farrer and the Making of Wheats

Farrer Memorial Oration, 1979

L. T. Evans
Division of Plant Industry, CSIRO, Canberra

Summary

Analysis of William Farrer's correspondence with The Australasian *in 1882–83, the turning point towards his subsequent career as a plant breeder, suggests that Darwin's book on* 'Domestication' *played a crucial role in the genesis of Farrer's innovative approaches.*

Farrer's achievements are considered in terms of his response to a series of challenges. The first was the breeding of rust resistance in wheat, and his interactions with N. A. Cobb; secondly, breeding for quality in wheat, and his unique and productive collaboration with the chemist F. B. Guthrie; thirdly, Farrer's approaches to the adaptation of wheat to Australian conditions, and his comprehensive and clear conception of the plant characteristics for which he was selecting; finally, the challenge of raising the yield of wheat crops grown under low input conditions.

Increases in the yield of wheat crops since the earliest times and in other countries are examined in order to assess how much of the increase has been due to the efforts of plant breeders in raising the yield potential, and how much to improved agronomy and growing conditions. The physiological basis of increased yield potential is then analysed before considering the question of how much further wheat yields can be increased.

Finally, Farrer's work is evaluated in relation to the aims and approaches of modern wheat breeding which he anticipated in so many ways.

Memorial awards like the Farrer Medal, which require the medallist to sing for his supper, confer a double privilege. There is, first of all, the privilege of joining a long line of distinguished predecessors in the sure knowledge that nothing succeeds like a successor. The second privilege is the incentive such an award gives one of getting to know much better the man whose memory is honoured by the award, particularly when his works are a deep well from which intellectual refreshment can still be drawn, as in the case of William Farrer. On both counts, I am most grateful for the award.

We see Farrer every day on our two-dollar notes, and might therefore be tempted to believe that his life and work are sufficiently well known. Indeed, the last Farrer Memorial Orator, Walter Ives, began by suggesting that everything worth saying about Farrer has long since been said. My aim, by contrast, is to persuade you that there is much still worth learning about Farrer, before I move on to consider some aspects of wheat improvement since his day, and of what Farrer himself referred to as 'the making of wheats'.

William James Farrer (1845–1906)

The Initial Challenge

Almost one hundred years ago, in November 1882, Farrer was working as a surveyor near Dubbo. He had recently married and had acquired a small property near Tharwa, which he called Lambrigg (or Hill of Lambs) after his mother's home in Westmorland, and which included some sandy flats suitable for wheat growing by the Murrumbidgee River. Lambrigg was not large enough to provide a living, so Farrer was away from home surveying stock routes around Dubbo. He saw many wheat crops, and he saw most of them crippled by rust. A notion of how to deal with the rust problem occurred to him and he outlined it in a letter to *The Queenslander* published on 17 November 1882.

This first letter from Farrer came in for some scathing comments in *The Australasian* of 16 December 1882, which noted that the author was unknown to them and pointed out that his idea 'of raising rust-proof varieties of wheat has been discussed without any practical outcome for an indefinite length of time'. Farrer was stung, and responded with a second letter to *The Queenslander* of 10 March 1883. This was reprinted in *The Australasian* on 31 March with editorial comment to the effect that the subject was rather hackneyed. But by now Farrer's

Farrer's home, Lambrigg, as photographed in November 1979. This aspect of the house remains essentially as it was in Farrer's day. Even the apricot tree is thought to date from his occupancy.

hackles were up, and he wrote three further letters, published in *The Australasian* on 21 April, 5 May and 26 May, 1883.

Many years later, for example in his paper to ANZAAS in 1898 and in letters to colleagues overseas, Farrer made it clear that this controversy with *The Australasian* was the turning point in his career. In his ANZAAS paper (Farrer 1898) he writes:

> 'It was the consideration I gave to the subject during that controversy which convinced me that an opening existed here for useful work, and that work I determined to take in hand if ever an opportunity should be given me. The principles on which the work should be carried on were then seen clearly, and everything which has been done since has been nothing more than a natural development of the views which were formed then'.

Given the crucial nature of this controversy, you may imagine my surprise at finding that these early letters of Farrer to *The Australasian* have not been catalogued, let alone quoted or analysed by his biographers, and I shall spend part of my time on them as they are well worthy of study.

Farrer had published a largely theoretical booklet on 'Grass and Sheep Farming' in 1873, three years after coming to Australia, but it did not attract much notice. He also lost his money in mining speculation at about the same time, and had to give up his hopes of an agricultural career. I mention this because in his second letter, published in *The Australasian* on 31 March 1883, he indicates that he read about improvements in wheat milling 'some few months ago' but says 'I was not specially interested in wheat at that time'. So his first letter was clearly not the result of prolonged consideration. Indeed, he adds that 'it was made, I confess, without much special thought having been given to the matter'.

Yet Farrer's first letter was quite prophetic. He argued that rust-proof wheats could be found on 'the strong probability that an analogy exists between the rust of the wheat and the American blight of the apple', to which resistance had been selected. After developing this argument, and asserting 'that wheat-growing can yet be established as one of the grand industries of Queensland', he concluded: 'The next process will be the selection from the rust-proof varieties of sorts that are also valuable for their milling properties. I expect that at this stage much might be gained by artificially crossing the different rust-proof varieties'. This first letter, therefore, although written 'without much special thought', identified three major and innovative components of his later work.

Farrer never discussed the origin of these ideas, but the examples by which they are supported suggest to me that a reading of Charles Darwin's book 'The Variation of Animals and Plants under Domestication' could have played an important role. According to Campbell (1933), Farrer was related through the Wedgewoods to Darwin, whose book on 'Domestication' was first published in 1868, the year Farrer graduated from Cambridge as a mathematical 'wrangler'. The second edition, from which Farrer quoted frequently in later life, was published in 1875. Admittedly, no explicit reference to this work is made in his letters to *The Australasian,* but we should remember that Australian scientists were mostly hostile to Darwin's evolutionary views at that time and until the last decade of the century (Moyal 1976).

Farrer, who was always scrupulous in his acknowledgment of the influence of others, may have judged it wiser not to make explicit reference to Darwin in his earlier letters, but the latter's influence on his thinking is very clear in the letter he wrote to the *Sydney Mail* on 14 June 1890. When describing the basis of his selection procedure he says 'These are almost Darwin's own words', and the analogous examples

Farrer mentions of blight-resistant apples, of grape varieties resistant to mildew and to phylloxera, and of increase in the sugar content of beet were all discussed in Darwin's book on 'Domestication'. Since the analogy with blight-resistant apples is mentioned in Farrer's first letter, which also emphasizes the power of selection, it seems quite likely that his original proposals were stimulated by reading Darwin.

In his second letter, provoked by the scepticism of *The Australasian*, he supports his earlier suggestion with the observation that some wheat varieties with flinty straw are less liable to rust. His third letter (21.iv.1883) adds the important observation that single healthy plants are occasionally found in crops of rusty wheat, and that these plants usually have flinty straw and hard grain. He goes on to point out that the recent improvements in milling machinery, enabling it to handle hard grains, therefore make possible the breeding of both higher quality and rust-resisting wheats. Thus, within five months of writing his original letter, and long before he began any plant breeding, Farrer had mapped out his main ideas just as Darwin had outlined his ideas on coral reefs before he saw one. But Farrer might well have let the matter drop had he not been provoked by *The Australasian* to support his ideas with observations in the field which convinced him that 'an opening existed here'.

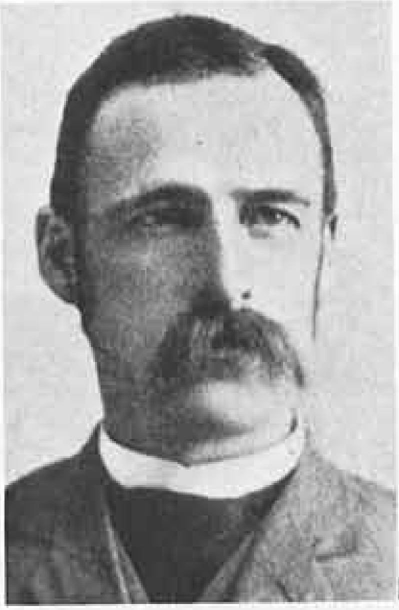
Farrer's responses in his third letter to the newspaper's criticisms are splendid. The paper had suggested that the concept of rust-proof wheat had a charm like the invention of perpetual motion, but that both were parasitic. Farrer thought this 'rather rough to begin with', and quickly disposed of the analogy. He then asked if any systematic attempt had been made to find a rust-resisting wheat and asserted 'If no such attempt ever has been made, well, it is quite time one was made . . . because a thing has never been done before is not sufficient reason in these times of progress for our not making an attempt to do it.'

Here, then, was the challenge which first stimulated Farrer to begin, three years later, the making of Australian wheats at Lambrigg. We should probably be grateful to *The Australasian* for its rather unimaginative and intemperate editorial comments, which were not unlike those it had visited on von Mueller a few years previously over his Directorship of the Melbourne Botanic Gardens.

Response: Rust Resistance in Wheat

Farrer's opportunity to develop his early proposals came in 1886 when he was able to resign his position as surveyor in the Lands Department. For the next three years he grew and observed a large number of wheat varieties on about one hectare at Lambrigg. Then in 1889 he began his extensive crossing program. He may, indeed, have been making his first crosses exactly 90 years ago — using his wife's hairpins as tweezers — because his earliest varieties usually began flowering in October (Russell 1949). Almost certainly, they were the first wheat crosses made in the world with the explicit objective of breeding for resistance to rust.

The next year, 1890, was one of the worst years for rust ever experienced in Australia, and a series of bad rust years allowed Farrer to make progress in identifying lines with some resistance to rust. His progress was, however, hindered by the occurrence of two different rusts and some initial uncertainty as to which was the more serious. Farrer was not invited to the first Conference on Rust in Wheat held in Melbourne in 1890, but a letter outlining his early work was read out by the Chairman. At the second Conference in Sydney in June 1891, New South Wales was represented by Farrer and by Dr N. A. Cobb, the Colony's plant pathologist, whom Farrer invited to work on his plots at Lambrigg later in the year. Cobb accepted and concentrated his studies on the earlier appearing, and more serious looking, spring or brown rust *(Puccinia recondita)* which heavily infested the leaves and sheaths. At first Farrer deferred to Cobb's judgment as a plant pathologist, and they concentrated their attention on leaf characteristics such as cuticle toughness and stomatal size. However, Farrer's varietal comparisons soon led him to the view that brown rust was relatively harmless and that stem rust *(Puccinia graminis* f. sp. *tritici)* had more impact on grain yield, an opinion reinforced by his American correspondent, M. A. Carleton.



Dr N. A. Cobb, pathologist, Department of Agriculture, N.S.W., who collaborated with Farrer on the problems of rust in wheat.

Dr Cobb disagreed rather forcefully, and relations between the two men became cool, even acerbic, as may be seen from their later exchange of articles on the damage done by crows (e.g. Farrer 1897). Farrer always regretted that he had wasted this early rust year 'being directed to an unnecessary end — to an effort to make varieties to resist our spring rust' (Farrer 1898), but the incident was valuable and taught him to trust his own judgment, and to clarify his breeding objectives.

The progress made by Farrer and his successors in breeding for rust resistance has been described by earlier lecturers in this series (Watson 1958; McIntosh 1976). The mathematician in Farrer would have been delighted by the precision of modern breeding methods for rust resistance, and I doubt whether he would have been too abashed by the subsequent fate of some of his cherished notions. He was always ready to give these up in the face of subsequent experience, as in the case of the association between flintiness of the stem and resistance to rust mentioned in his second letter to *The Australasian.* In his letter to the

The pise cottage which Farrer used as a laboratory and in which Dr Cobb worked when he visited Lambrigg in 1891.

1890 Conference on Rust in Wheat, even before his work with Cobb, he admitted that his observations on rust incidence have 'satisfied me that the liability does not arise from mere mechanical reasons, but rather from a constitutional weakness'.

A succession of dry years reduced the severity of the rust problem, as well as Farrer's opportunities to make progress on it, and he turned increasingly to other plant-breeding objectives. But he never lost the conviction that further progress towards his original goal could be made, given the heritable variation in rust resistance which he had observed in his own plots, and the great power of sustained selection.

A More Subtle Challenge: Quality in Wheat

The improvement of quality in wheat by cross-breeding was mentioned in Farrer's very first letter to *The Queenslander* in 1882. It was an innovative suggestion and Farrer subsequently became the first in the world to put it into practice, at least 10 years before Biffen in England (Macindoe 1976). His interest in improving grain quality may have come partly from his early correlation of flinty grains and flinty stems with rust resistance, as set out in his letter in *The Australasian* of 26 May, 1883. In this he wrote, 'It is the new process of flour-making which has secured for us the chance of getting rust-proof varieties of wheat'. Until that time, hard wheats had been unpopular with Australian millers with the consequence that, as Farrer put it to the fourth Conference on Rust in Wheat (1894), 'we find ourselves growing wheats whose berries are little more than mere balls of starch'.

Once again, Farrer sensed an opportunity and a challenge, which could well have been reinforced by the following passage from the section on wheat in Darwin's 'Variation of Animals and Plants Under Domestication':

'Although the principle of selection is so important, yet the little which man has effected, by incessant efforts during thousands of years, in rendering the plants more productive or the grains more nutritious than they were in the time of the old Egyptians, would seem to speak strongly against its efficacy'.

Farrer was encouraged in this task by the success of European plant breeders in selecting beet for higher levels of sucrose, as mentioned by Darwin, and he referred to this example many times, arguing that gluten in wheat could be increased as had the sugar content of beet. For this work Farrer sought and obtained the collaboration of Mr F. B. Guthrie of the N.S.W. Department of Agriculture, a collaboration which lasted until Farrer's death, and which was far more productive than that with Cobb. Indeed, this combination of plant breeder and chemist was unique at the time (Wrigley 1979), and led to many advances in our understanding of wheat quality, as well as to the release of several varieties of high quality, such as 'Bobs', 'Comeback', 'Jonathon', 'Florence' and 'Cedar'.

The story has been told by several earlier Farrer Memorial lecturers and need not be repeated.

Looking back now, it is remarkable how well Farrer and Guthrie understood the nature of the problem. They took account of the needs of millers, bakers and consumers, as well as of wheat growers. Farrer's keen eye for the effects of grain size, shape and bran thickness on milling, combined with Guthrie's tests, raised the millers' yield. Guthrie was the first to show that flour strength was related to the proportion of glutenins, thereby permitting more effective selection by Farrer for baking quality (Lee 1975; Wrigley 1979). They recognized the need for small mills and microtests of baking quality, and fought hard to get the necessary equipment, even in times when 'so poor does our Government say it is, and so illiberal is its present attitude to our Department' (quoted in Russell 1949).

Although the partnership of Farrer and Guthrie raised the quality of Australian wheats to the point where there was no need to import Manitoba grain, Farrer's (1898) dream of increasing the gluten content of wheat in the way the sugar content of beet had been increased was not realized. In fact, the broad evolutionary history of wheat has been from quite high protein contents in the wild progenitors and early wheats to lower proportions in the modern wheats (Harlan 1967; Dunstone and Evans 1974), but Farrer showed, nevertheless, that the trend towards 'mere balls of starch' could be reversed by a plant breeder determined to do so.

F. B. Guthrie, chemist, Department of Agriculture, N.S.W., with whom Farrer collaborated on breeding for better quality in wheat.

A Challenge Met: Adaptation to Australian Conditions

Farrer's early preoccupation with rust resistance and wheat quality did not blind him to the need for varieties better adapted to Australian conditions. His second letter to *The Australasian* (31.iii.1883) emphasized this aim. In his ANZAAS paper of 1898 (pp. 135–6) he says that he considers it of the first importance to select in the variable (F_2) generation for 'that delicate and obscure, but most important quality or assemblage of qualities which we include in the convenient term of constitutional fitness for the locality.'

Farrer's interest in certain adaptive characteristics such as early maturity and the possession of stiff narrow leaves arose partly from their contribution towards minimizing rust losses, but he recognized that these might conflict with other requirements. In an unpublished letter to B. T. Galloway of 6.xi.1894 he writes:

> 'I like to see the leaf quite narrow and remain stiff and (preferably) erect until quite shortly before or even until heads appear. I also like to see the foliage quite scanty. The drawback, however, attached to narrowness of leaf and scanty foliage, is that the plant has not the means, in large extent of leaf surface, of extracting from the air and winning for its grain so much carbon.'

Farrer's understanding of local adaptation was sharpened by the severe droughts of 1895 and 1896 which, characteristically, he regarded as an opportunity rather than a disaster: 'They put me in possession . . . of some information which is possibly even more valuable than any that a rusty season would have furnished' (1898, p.159). Moreover, he recognized as a major challenge from the beginning of his work the possibility of extending wheat growing not only to 'one of the grand industries of Queensland' but also to the drier inland areas of southern Australia (1898, p.160). For this, his thin sandy soil lying on rock at Lambrigg was more appropriate than it was for work on rust resistance.

Living closely with his plants, and observing them keenly, Farrer soon developed a clear and comprehensive conception of the characteristics which he regarded as most important for adaptation to Australian conditions. Many of these were listed in his papers to the 1891 Conference on Rust in Wheat and to the 1898 meeting of ANZAAS. In both he particularly emphasized sparse tillering, narrow leaves to reduce water loss, and earliness in ripening. His close observation of leaf characteristics is evident in his letter to Galloway, quoted above. Farrer recognized that abundant tillering may be advantageous in the wetter climates and more fertile soils of Europe, but that in Australia such varieties may have 'undertaken too much, and that having expended their strength in making preparation for a large crop, had failed to produce more than a small amount of grain' (1898, p.161). Farrer's analysis of the problem has been amply confirmed, and is still being developed (e.g. Passioura 1977). Passioura and his colleagues are currently attempting to select for increased hydraulic resistance in the root system, to ensure that more soil water is available during grain growth as a result of less being used during vegetative growth of the crop.

Farrer indicated on several occasions that he preferred varieties with short strong stems, not only to avoid being 'laid by rains and storms' but also 'to get sorts that do not waste their strength on the production of straw' (1890, p.24). In view of the attention given in recent years to dwarf wheats, it is perhaps salutary to note that Farrer and his colleagues were well aware of the development in Japan over 100 years ago of dwarf, high-yielding, fertilizer-responsive wheat varieties. Indeed, Horace Capron's report of 1873, in which he noted that 'Japanese farmers have brought the art of dwarfing to perfection . . . no matter how much manure is used it [the stem] will not grow longer, but rather the length of the wheat head is increased . . . On the richest soils and with the heaviest yields, the wheat stalks never fall down the lodge,' was discussed by Professor Shelton at the 1892 Conference on Rust in Wheat (p.62).

In his book 'The Wheat Plant', Percival (1921) singles out Farrer for his 'clear conception of the desired improvements'. I believe Farrer could fairly be said to have had a well-defined ideotype of wheat in mind long before Donald (1968) proposed one, and in fact he had specified most of the desirable traits subsequently listed by Donald. As Darwin said of successful animal breeders in his book on 'Domestication', Farrer 'had first drawn a perfect form, and then given it life'. The other element in Darwin's analysis of success in animal breeding was 'a clear and almost prophetic vision into futurity', which Farrer also had. It was almost inevitable, then, that his goal of wheat varieties adapted to the drier inland should have been attained so triumphantly by his variety 'Federation'.

Such challenges to plant breeders can still be found. Currently, for example, many of the poorer countries in the tropics would like to be able to grow wheat for bread, thereby reducing their expenditure on imports. It is a task Farrer would have relished, and we can only hope that local Farrers will be found where they are needed, as happened in this 'lucky country'.

A Challenge Underestimated: the Raising of Yield

In his address to ANZAAS in 1898, Farrer pointed out that all the wheat improvers in other countries had 'given special and almost exclusive attention to the quality of productiveness of grain' (p.134), and that his own work had differed from theirs in giving primary attention to the other qualities we have discussed so far. Indeed, in the list of desirable attributes he presented in 1891 (p.44), only the eleventh, and last, mentioned yield: 'That the variety itself be productive enough in soil of average fertility and without the aid of manure, to be profitable to the farmer'. Farrer clearly envisaged that Australian wheat was likely to be grown mainly in low input systems, where the scope for increase in yield potential would be limited. By and large he has been right, but it is rather ironical that his most successful variety, 'Federation', reigned supreme in Australia for many years, and was grown abroad until 40 years after his death, largely because of its high-yielding ability. After its release, Farrer felt he should publish a note correcting a statement that 'Federation' was a strong-flour wheat 'because I am quite sure that its career will be more satisfactory if it does not start under false colours.' (1903).

Although Farrer was concerned with raising wheat yields under conditions of low inputs and severe environmental constraints, we must now turn to wheat growing in more favourable conditions overseas in order to assess the scope for increased yield potential.

The wild progenitors of the modern wheats are still to be found in the Fertile Crescent of the Middle East, in environments and settings similar to those of Australia. In fact, when I visited the Rosh Pinna site in Israel where Aaron Aaronsohn first discovered wild emmer wheat in 1906, I was struck by its strongly Australian character since eucalypts now dominate the site. Stands of the wild cereals can be quite dense, and Zohary (1969) has harvested 0.5–0.8 t ha^{-1} of grain from them. Such yields are comparable to those of wheat crops in Western Europe in the Middle Ages, but since that time wheat yields have risen progressively, most rapidly since 1950. Last year the national average yield in England was 5.3 t ha^{-1}, ten times greater than yields of the wild stands or of wheat crops in the Middle Ages.

However, before we congratulate the wheat breeders on this achievement, we need to divide the increase in yield between the improvements in agronomic practice on the one hand and those in genetic yield potential on the other. No wholly satisfactory separation of these two components can be made because they interact strongly, improved genetic potential offering little advantage when agronomic inputs are low, while the benefits of improved agronomy may not be fully expressed in the absence of genetic change. Nevertheless, I believe it helps us to understand the nature of past change and future prospects if we attempt to partition yield increases into genetic and agronomic components. Only by so doing can we begin to assess Darwin's assertion that little improvement has been effected since the time of the old Egyptians.

When Darwin was writing, average wheat yields in England were about 1.8 t ha^{-1}. However, Jacobsen and Adams (1958) have estimated wheat yields in Mesopotamia in 2400 B.C., under irrigation, to have been about 2.0 t ha^{-1}. Data given by Feliks (1963) suggest that cereal yields of up to 3.6 t ha^{-1} could be expected in good years in the pre-Christian period of the Mishna in Israel. Clearly, the yield potential of these early crops, with good husbandry, was high.

By yield potential I mean the upper limit in the capacity of a variety to yield grain in environments to which it is adapted, when limitations to yield by nutrient level, water status, pests, diseases, weeds and lodging are removed. For a series of varieties released over a long period of years, during which the level of agronomy may have improved substantially, the comparisons of yield potential should be made at successive steps up the agronomic ladder. This is, in fact, what is done in national yield trials such as those conducted by the National Institute of Agricultural Botany in the United Kingdom. So I have taken their published results over the past 50 years and, from comparison of the relative yields of successive standard varieties, have compiled figures indicating the changes in yield potential. Such a method, first used by Mackey (1979) for Swedish wheat varieties, may tend to overestimate the successive increases in yield potential, since in its last years when it is being compared with the incoming standard variety, the old standard may be increasingly subject to disease. Fig. 1 shows the results obtained with winter wheats bred in England over the last 70 years.

Since the introduction of 'Little Joss' in 1908 by Biffen, one of Farrer's correspondents, the yield potential of the higher yielding winter wheats has increased by more than 50%. The increase appears to have been approx-

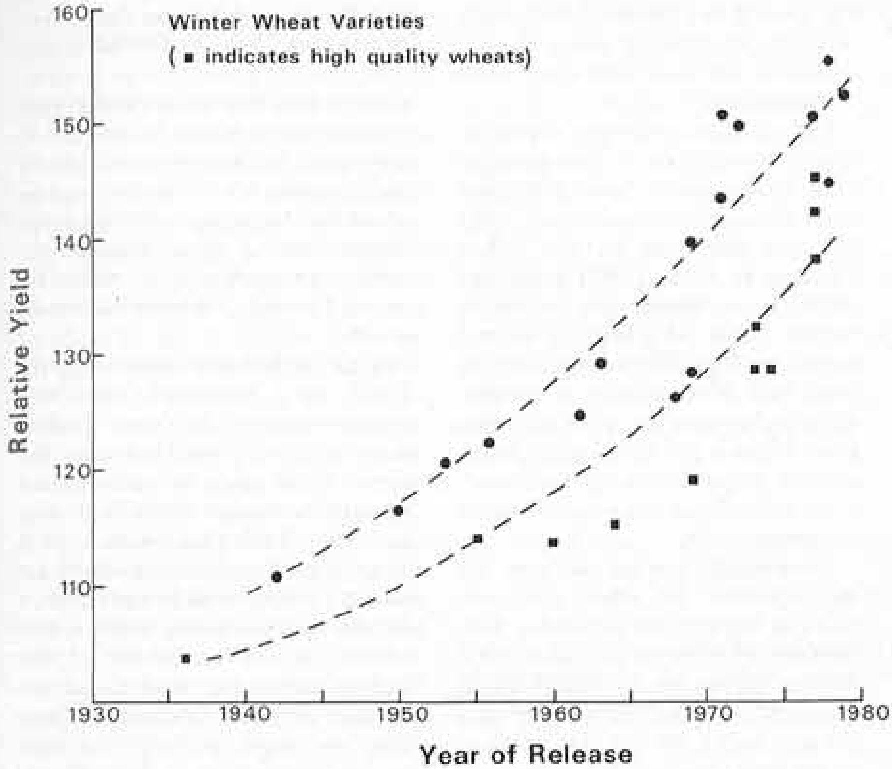


Fig. 1. Estimated increase in relative potential yield of English winter wheats (relative to 'Little Joss' (1908) = 100), based on the results of annual trials conducted by the National Institute of Agricultural Botany.

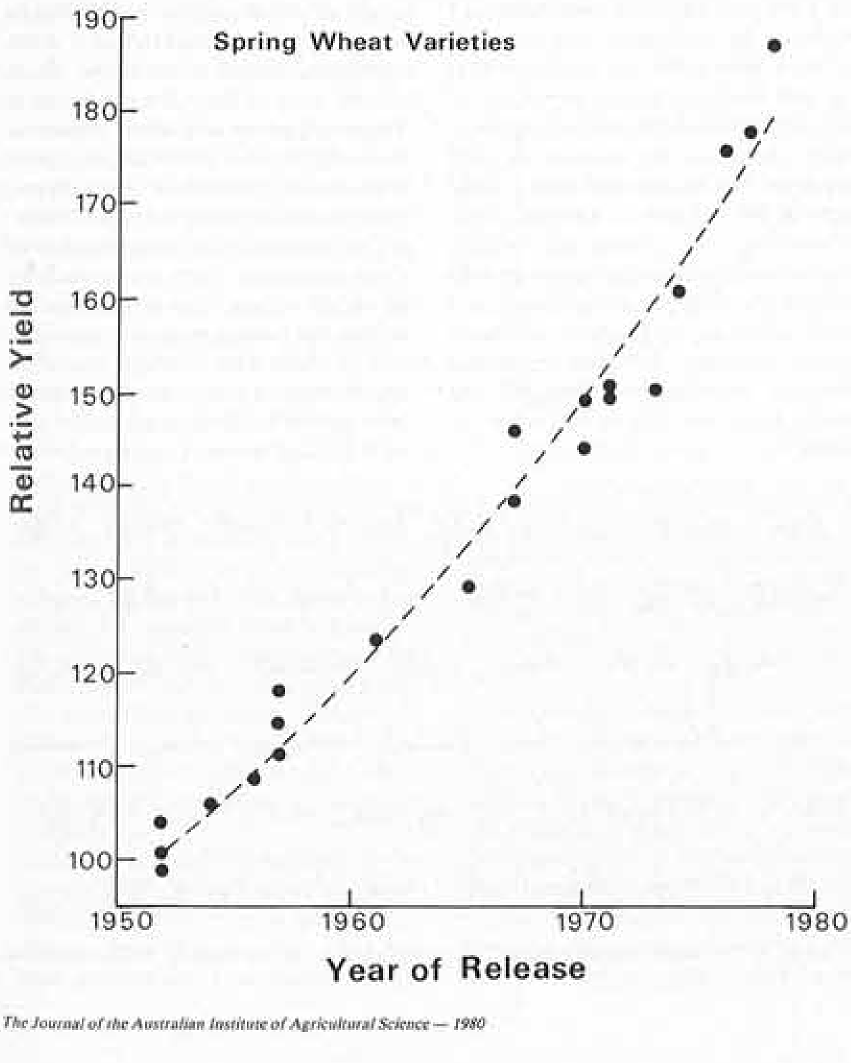


Fig. 2. Estimated increase in relative potential yield of English spring wheat varieties (relative to 'Atle' (1939) = 100), based on annual trials conducted by the National Institute of Agricultural Botany.

imately exponential, at a computed rate of 0.87% per year. The yield penalty on wheats of high baking quality is clear from Fig. 1, but the yield potential of these latter has increased at a computed rate of 0.68% per year. Comparable results for spring wheat varieties are given in Fig. 2.

The increase in the yield potential of the spring wheats released in the United Kingdom over the last 25 years has been almost 90%, with the results conforming fairly closely to the computed rate of increase of 2.23% per year. The much faster rate of increase in the yield potential of the spring wheats may be due to their having been a relatively minor and neglected crop in the United Kingdom until recently. Note also that for neither winter nor spring wheat varieties is there any indication of an approaching yield plateau.

In view of the possibility that the rate of advance in yield potential may be overestimated by this method, last year I undertook with several colleagues at the Plant Breeding Institute in Cambridge a direct comparison of the relative yield potential of 12 winter wheat varieties bred there over the last 70 years. The English climate cooperated, and the crops were not limited by water supply, although they may have been by light. Lodging of the tall, older varieties was prevented by the use of mesh, and diseases were effectively controlled by spraying, so we are unlikely to have underestimated the yield potential of the earlier varieties, the usual problem in such work. In fact, the old varieties performed remarkably well in the absence of disease and lodging (Fig. 3), 'Little

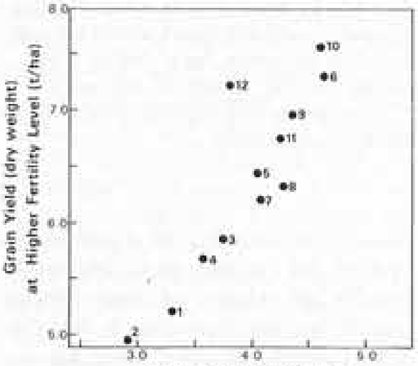


Fig. 3. Grain dry weight yields of 12 winter wheat varieties grown at two levels of soil fertility at Cambridge in 1978, with lodging prevented and diseases controlled. The varieties are numbered in the order of their release, from 'Little Joss' in 1908 (1), 'Holdfast' 1935 (2), 'Cappelle' 1953 (3), 'Widgeon' 1964 (4), 'Huntsman' 1972 (5), 'Hobbit' 1977 (6), 'Mardler' 1978 (7) and 'Armada' 1978 (11) to 'Benoist 10483' (12). The other numbers refer to varieties unnamed as yet. (From Austin *et al.* 1980).

Joss' having a grain yield of 5.9 t ha^{-1} (at 12% moisture) at the higher level of fertility. For comparison, the highest yielding recent variety gave 8.7 t ha^{-1}, about 45% more than 'Little Joss'. These results suggest that use of the NIAB trial comparisons may somewhat overestimate the increase in yield potential, but on the other hand the cloudy weather in 1978 may have led to some underestimation of the yield potential of the newer varieties.

Fig. 3 also shows that there was a fairly close relation between yields of most varieties at the higher and lower levels of soil fertility.

The question concerning the extent to which the increases in yield potential of the newer varieties have contributed to the increase in national wheat yields has been examined for the United Kingdom by Elliott (1962) and Silvey (1978), by combining data on relative varietal yields with that on varietal popularity. Both authors conclude that about half of the increase in national wheat yields since the 1940s has come from breeding for higher yield potential, this proportion having been lower in the earlier years but predominant in more recent years.

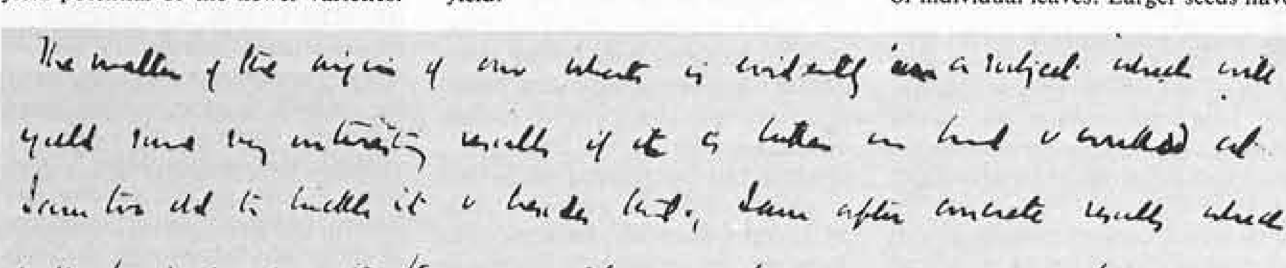
Comparably detailed analyses are not available for other countries. National wheat yields in Sweden have increased by 3.7% per year since 1945, whereas the increase in yield potential estimated from Mackey's (1979) data has been only 0.4% per year. In Mexico national wheat yields have increased 5.2% per year since 1945, whereas I estimate the increase in yield potential to have been 0.9% per year over that period, based on results presented by Fischer and Wall (1976). In these countries, therefore, the increase in yield potential has contributed only a small part of the increase in national yield. However, in countries where agronomic practices and growing conditions for wheat crops are already at a high level, as in England in recent years, increase in yield potential through breeding may become the main route to further increases in yield.

The Basis and Scope for Increased Yield Potential

Before asking how much further yield potential can be increased, we need to understand the physiological basis of past increases. Useful insights can be gained by comparing older and newer varieties, but to get a broad evolutionary perspective it is worth including the wild progenitors of wheat as well.

In an unpublished letter to Biffen written on 4 November, 1905, five months before he died, Farrer (National Library MS.33) wrote: 'The matter of the origin of our wheats is evidently a subject which will yield some very interesting results if it is taken in hand and worked out. I am too old to tackle it and besides that, I am after concrete results which will be valuable to the agriculture of this country rather than matters the importance of which is abstract.' Since then, the origin of wheat has been largely worked out, although the origin of the B genome has still to be satisfactorily established. This cytological detective work has, by no means, been of only abstract value as Farrer suggested to Biffen. Indeed, it has contributed substantially to one of his most cherished objectives, resistance to rust (*cf.* McIntosh 1976).

Our physiological comparisons of these progenitors with wheat varieties of varied vintage may be summarized as follows: During evolution and selection in wheat there has been a substantial increase in grain size, and this has been paralleled by increase in the area of individual leaves. Larger seeds have


The matter of the origin of our wheats is evidently a subject which will yield some very interesting results if it is taken in hand & worked out. I am too old to tackle it & besides that, I am after concrete results which will be valuable to the agriculture of this country rather than matters the importance of which is abstract. In connection with this subject
[illegible]

Extract of an unpublished letter written by Farrer to Professor Roland Biffen of Cambridge on November 4, 1905. (National Library Collection, MS 33).

several advantages for man. For example, milling losses can be reduced, and larger seeds give larger seedlings which compete more effectively with weeds. Nevertheless, we found no increase in the relative growth rate of the seedlings and no increase in the photosynthetic rate per unit leaf area. Indeed, the maximum photosynthetic rate seems to have fallen in the course of evolution in wheat, possibly associated to some extent with the increase in leaf area (Evans and Dunstone 1970; Dunstone and Evans 1974).

Thus increased yield potential in wheat has not come from selection for faster rates of photosynthesis or growth. Rather, it has come largely from changes in the distribution of the accumulating plant matter among the various organs. Darwin was, long ago, impressed by such changes in distribution within the brassicas, but those in wheat have been comparable, although less obvious. An example might be taken from our experiment with English winter wheat varieties, mentioned earlier. The results in Fig. 4 show that the increases in grain yield in these varieties have been associated with equivalent reductions in the weight of leaves and stems, total plant weight being fairly comparable in all varieties. Thus what plant breeders have done, in essence, has been to select plants which invest an increasing proportion of their resources in the organs harvested by man — in this instance, the wheat grain. The harvest index of wheat has therefore risen substantially, particularly since the introduction of semi-dwarf wheats (Fig. 5).

However, it is important to emphasize that such increases in the harvest index depend, to some extent, on an increasing level of agronomic support for the crop. Better control of weeds, for example, makes selection for shorter stems practicable. But varieties selected for higher yield under these conditions may sometimes be at a disadvantage in less favourable conditions, and this could account for the slight upward curvature of the results in Fig. 3.

Given the central importance of the process of photosynthesis to crop productivity, it may seem surprising that higher photosynthetic rates have not been selected for, even unconsciously.

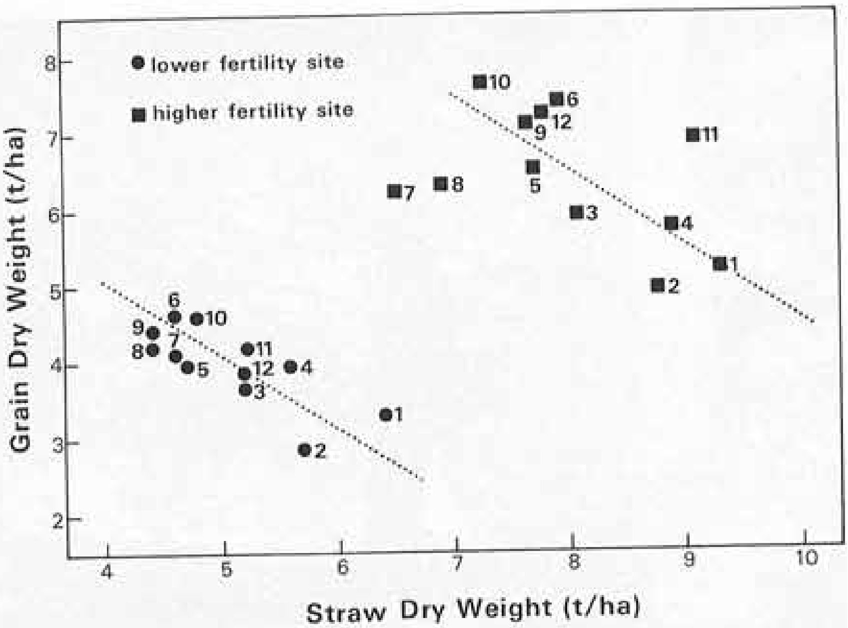


Fig. 4. Grain dry weight plotted against straw dry weight at maturity, at two levels of soil fertility, for the 12 winter wheat varieties in Fig. 3. The lines show a slope of —1.0. (From Austin *et al.* 1980).

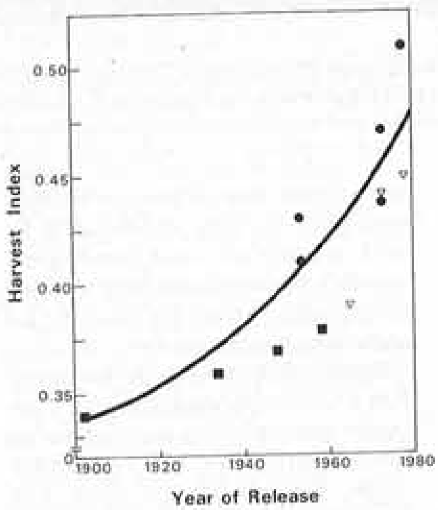
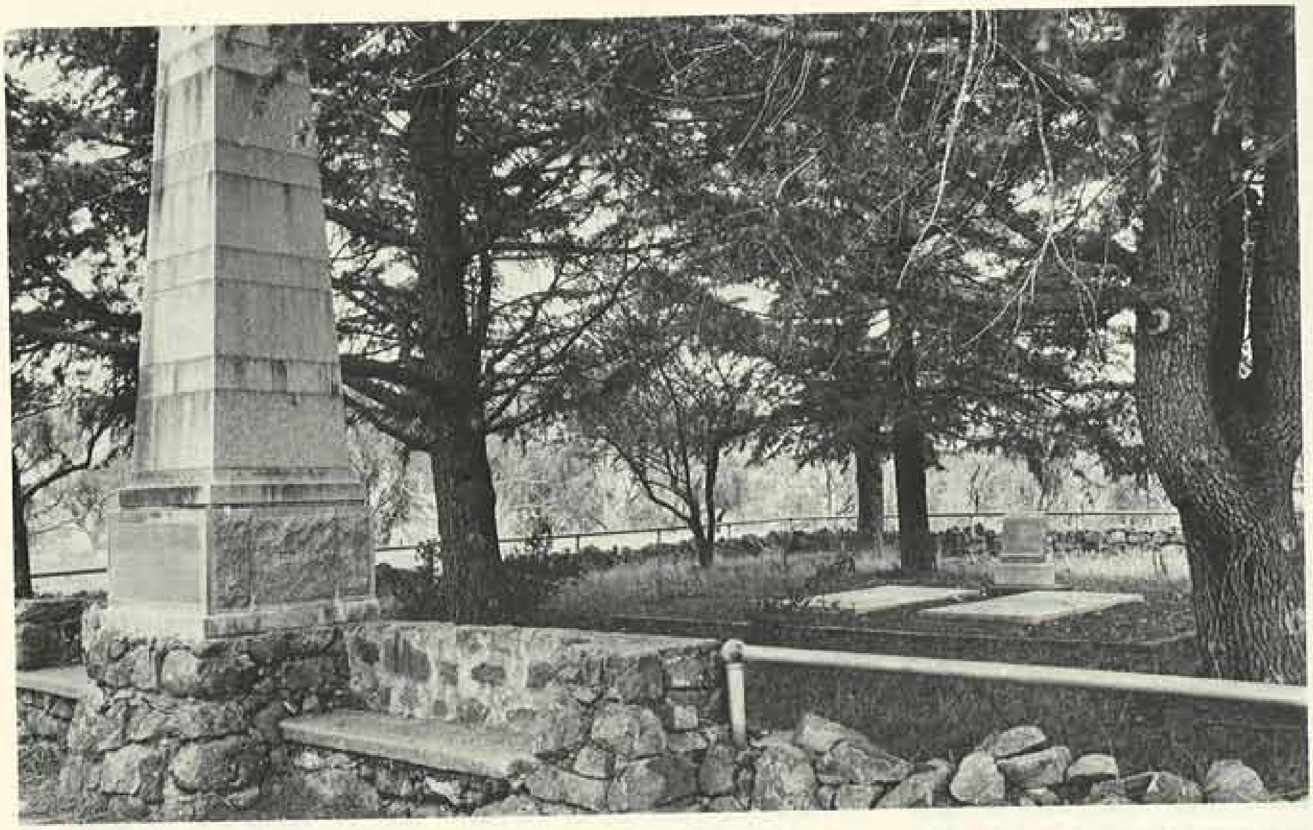


Fig. 5. Trend in harvest index of wheat varieties with year of their release (Data of van Dobben 1962 (■); Fischer, 1973 (▽); Thorne G. , N. unpublished (•))

Our evidence suggests that some counter-productive associations with higher photosynthetic rates in wheat, such as smaller leaves and more rapid senescence, may be involved. Moreover, a shift in the partitioning of photosynthetic assimilates has sufficed to raise yield potential substantially. In any case, the photosynthetic rate may have been more readily raised by the use of nitrogenous fertilizers (*cf* Osman *et al.* 1977), agronomic evolution outpacing genetic change, just as cultural evolution has done in human affairs. In future, however, it may well prove possible to select plants for increased photosynthetic efficiency even though this has apparently not occurred to date. It is this possibility which makes it difficult to predict with any confidence what the upper limit to wheat yields might be.

The present world record yield of wheat is about 14 t grain ha^{-1}, for the variety 'Gaines' grown by W. Huppert in Washington State, U.S.A. This is substantially higher than the annual record yields in England of 10–11 t ha^{-1} and probably owes its advantage to very unusual circumstances. The annual record yields for wheat in England, as for rice in Japan, have shown little change in recent years. Consequently, the gap between national average and record yields is closing. Estimates I have made suggest that wheat yields substantially above the world record of 14 t ha^{-1} are possible, but such estimates depend as much on the degree of innate optimism of the estimator as on his understanding of plant physiology. In case you should ask what is the use of such estimates, let me quote Farrer (1904)



The graves of William and Nina Farrer on the hill behind their home. The inscription on the column to the left reads: *'This memorial to William James Farrer 1845–1906 overlooking the scene of his labours was erected by the Commonwealth as a tribute to his great national work in the breeding and establishment of improved varieties of Australian wheat.'*

on such 'ifs' and 'mights': 'Imagination . . . is a factor of considerable importance in efforts to secure progress, and in this case a glimpse of the possibilities we seem to have before us, even if they have only been imagined, may serve to make the work . . . better understood.'

Farrer, a Modern Plant Breeder

What strikes one most in getting to know Farrer from his writings is how thoroughly modern in outlook he was. He clearly recognized that plant breeding was a numbers game requiring well-defined objectives, many crosses, and rigorous culling, and quoted the greyhound-breeding British peer cited by Darwin as saying, 'I breed many and hang many.' Most of his contemporaries preferred selection within rather than crossing between old varieties. At the fourth Conference on Rust in Wheat in 1894 Professor Shelton said, 'Nature seems to abhor crossing in the wheat plant', while Cobb (1902) wrote, 'There is no prospect that any new varieties will be vastly superior to the old', but Farrer's approach has been vindicated not only by his own results but also by his wheat-breeding successors.

Equally impressive is the breadth of Farrer's crossing program which included the various wheat species as well as barley and rye. His variety 'Bobs' derived from a cross with Nepaul barley, and he made several successful wheat x rye hybrids (first achieved by Wilson in 1873) whose high protein content was known to him from Guthrie's analyses long before the recent interest in triticale developed. Hence the tribute paid to Farrer by Vavilov in 1935: 'There is probably no region where intraspecific and interspecific hybridization of wheat has been so extensive as in Australia' (Vavilov 1951, p.296).

In making so many crosses, such wide crosses, and such complex crosses, Farrer anticipated the future trend of plant breeding, as he did also in the clarity of his objectives and his recognition of the marked influence of environment on varietal performance and susceptibility to disease.

Farrer was the first of the moderns also in the comprehensiveness of his breeding objectives, and particularly in the balanced emphasis he gave to milling, baking and nutritional quality. He would also have been entirely at home with the international exchange of early generation materials which occurs in modern plant breeding. Varieties from all over the world were grown at Lambrigg, whence Farrer distributed the early products of his crosses. In 1894 he wrote, 'I have been sending wheats to Europe and America, and intend to send some shortly to India and France. I hope also to soon be able to start a correspondence with people in different parts of the world . . .' He was, in fact, a one-man international agricultural research centre, and he would have appreciated the strength that such centres have derived from being wholly focused on one or two crops.

Nevertheless, Farrer also recognized

that wheat growing was only one part of Australian agricultural systems, and that the long-term productivity and stability of these would depend on building up soil fertility through regenerative farming practices. He was an early advocate of legume leys and, although he would have been delighted by Australia's subsequent informed use of these, I believe that, were he with us today, one of his greatest disappointments would be that the long-term soil fertility experiments which he initiated at Wagga as an Australian counterpart to those at Rothamsted were discontinued so soon. There is an interesting story, still to be told, about Farrer's frustrations as Wheat Experimentalist, as Campbell (1933) intimates towards the end of his paper.

However, it is as a plant breeder that we honour Farrer each year, so let me conclude with some words from Charles Darwin's 'Domestication', the book which Farrer admired above all others. In describing successful breeders, Darwin writes: 'Indomitable patience, the finest powers of discrimination, and sound judgement must be exercised during many years. A clearly predetermined object must be kept steadily in view. Few men are endowed with all these qualities.' William James Farrer was one of those few.

Acknowledgments

I am most grateful to Mrs Fleur Kelleher for her help in tracking down Farrer's letters to *The Australasian*, and to my colleagues Ms A. E. Grant Lipp, Dr R. A. Fischer, Dr R. M. Gifford and Dr J. B. Passioura for helpful comments. The photographs of Lambrigg, Farrer's grave and his laboratory were taken by Colin Totterdell. I am also indebted to the National Library for permission to reproduce part of Farrer's letter to Biffen (NLC-MS 33).

References

Austin, R. B., Bingham, J., Blackwell, R. D., Evans, L. T., Ford, M. A., Morgan, C. L., and Taylor, M. (1980). A comparison of the yields of old and new varieties of winter wheat at two levels of soil fertility. *J. Agric. Sci. (Camb.) (in press).*

Campbell, W. S. (1933). William James Farrer. *R. Aust. Hist. Soc. J. & Proc.* **19,** 269-85.

Cobb, N. A. (1902). Universal nomenclature of wheat. *Agric. Gaz. N.S.W.* **12,** 1614-29.

Darwin, C. (1868). 'The Variation of Animals and Plants under Domestication.' 2 vols. (John Murray: London.)

Dobben, W. H. van (1962). Influence of temperature and light conditions on dry matter distribution, development rate, and yield in arable crops. *Neth. J. Agric. Sci.* **10,** 377-89.

Donald, C. M. (1968). The breeding of crop ideotypes. *Euphytica* **17,** 385-403.

Dunstone, R. L., Evans, L. T. (1974). Role of changes in cell size in the evolution of wheat. *Aust. J. Plant Physiol.* **1,** 157-65.

Elliott, C. S. (1962). The importance of variety testing in relation to crop production. *J. Nat. Inst. Agric. Bot.* **9,** 199-206.

Evans, L. T., Dunstone, R. L. (1970). Some physiological aspects of evolution in wheat. *Aust. J. Biol. Sci.* **23,** 725-41.

Farrer, W. J. (1890). Rust in Wheat. First Conf. Proc. pp.24-6.

Farrer, W. J. (1891). *ibid.* Second Conf. Proc. pp.39-44.

Farrer, W. J. (1892). *ibid.* Third Conf. Proc. pp.34-7.

Farrer, W. J. (1894). *ibid.* Fourth Conf. Proc. pp.8-9, 14-18.

Farrer, W. J. (1897). The too common crow. *Agric. Gaz. N.S.W.* **8,** 47-52.

Farrer, W. J. (1898). The making and improvement of wheats for Australian conditions. *Agric. Gaz. N.S.W.* **9,** 131-68, 241-50.

Farrer, W. J. (1903). Federation variety of wheat. *Agric. Gaz. N.S.W.* **13,** 977.

Farrer, W. J. (1904). Some notes on the wheat "Bobs"; its peculiarities, economic value, and origin. *Agric. Gaz. N.S.W.* **15,** 849-54.

Feliks, J. (1963). 'Agriculture in Palestine in the Period of the Mishna and Talmud.' (Magnes Press: Jerusalem.)

Fischer, R. A. (1973). Physiologic research as a tool in improving yield potential. Proc. CIMMYT Wheat, Triticale and Barley Seminar, pp.314-8.

Fischer, R. A., Wall, P. C. (1976). Wheat breeding in Mexico and yield increases. *J. Aust. Inst. Agric. Sci.* **42,** 139-48.

Harlan, J. R. (1967). A wild wheat harvest in Turkey. *Archaeol.* **20,** 197-201.

Jacobsen, T., Adams, R. M. (1958). Sand and silt in ancient Mesopotamian agriculture. *Science* **128,** 1251-8.

Lee, J. W. (1975). Fifty years of cereal chemistry since Guthrie. *Proc. R. Aust. Chem. Inst.* **42,** 33-8.

Macindoe, S. L. (1976). Wheat quality since Farrer: 1906 to 1975. *J. Aust. Inst. Agric. Sci.* **42,** 28-33.

McIntosh, R. A. (1976). Genetics of wheat and wheat rusts since Farrer. *J. Aust. Inst. Agric. Sci.* **42,** 203-16.

Mackey, J. (1979). Genetic potentials for improved yield. *In* 'Workshop on Agricultural Pontentiality directed by Nutritional Needs', ed. S. Rajki, pp. 121-43 (Akedemiai Kiado: Budapest.)

Moyal, A. (1976). 'Scientists in Nineteenth Century Australia: a Documentary History.' (Cassell: Melbourne.)

Osman, A. M., Goodman, P. J., Cooper, J. P. (1977). The effects of nitrogen, phosphorus and potassium on rates of growth and photosynthesis of wheat. *Photosynthetica.* **11,** 66-75.

Passioura, J. B. (1977). Grain yield, harvest index, and water use of wheat. *J. Aust. Inst. Agric. Sci.* **43,** 117-20.

Percival, J. (1921). 'The Wheat Plant,' p.463. (Duckworth: London.)

Russell, A. (1949). 'William James Farrer, A Biography,' p.226 (F. W. Cheshire: Melbourne.).

Silvey, V. (1978). The contribution of new varieties to increasing cereal yield in England and Wales. *J. Natl. Inst. Agric. Bot.* **14,** 367-84.

Vavilov, N. I. (1951/1935). Scientific bases of wheat breeding. *In* 'The Origin, Variation, Immunity and Breeding of Cultivated Plants' (ed. K. S. Chester.) *Chron. Bot.* **13,** 169-349.

Watson, I. A. (1958). The present status of breeding disease resistant wheats in Australia. *Agric. Gaz. N.S.W.* **69,** 1-31.

Wilson, A. S. (1875). Wheat and rye hybrids. *Trans. Bot. Soc. Edinb.* **12,** 286-8.

Wrigley, C. W. (1979). W. J. Farrer and F. B. Guthrie: The unique breeder–chemist combination that pioneered quality wheats for Australia. *Rec. Aust. Acad. Sci.* **4,** 7-25.

Zohary, D. (1969). The progenitors of wheat and barley in relation to domestication and agricultural dispersal in the Old World. *In* 'The Domestication and Exploitation of Plants and Animals', eds. P. J. Ucko and G. W. Dimbleby, pp.47-65. (Duckworth: London.)