Introduction

The purpose of this book is to examine the wider scientific and social contexts of modern plant breeding and agriculture. We will begin by examining the historical development of plant breeding over the past two centuries, before focusing on the dramatic changes of the last two decades. Perhaps the best-known recent development in plant breeding is the emergence of genetic engineering, with its attendant social and scientific controversies. But, as we shall see, GM crops and 'agbiotech' (agricultural biotechnology) are just one manifestation of a more extensive series of seismic changes that have profoundly altered the course of plant breeding since the 1980s. Today, in the middle of the first decade of the twenty-first century, plant breeding and crop improvement are at an historic crossroads. On one hand, are the tried and tested breeding methods that underpinned the Green Revolution and enabled us to feed the expanding world populations in the twentieth century. More recently, however, governments across the world have largely dismantled their applied research infrastructures and have greatly reduced the capacity for public-good applications of newly emerging breeding technologies, including transgenesis. Much of this institutional restructuring occurred as part of the ideologically driven privatisation of public assets in the 1980s and 1990s. The resulting depletion of public sector breeding has left a void that was filled by a few private sector companies who applied a new paradigm of crop improvement based on transgenesis – and from this, the agbiotech revolution was born.

As we confront the challenges of increasing populations, economic growth, rising affluence, the spread of environmental degradation, and the depletion of non-renewable resources, twenty-first century agriculture will need all the tools and scientific expertise that plant breeders can muster. Not to mention the appropriate crop management strategies, market freedoms, and social stability that will be necessary to translate the promise of the breeder into the reality of productive and profitable crops for the wellbeing of the farmer. We will see how research into plant science is becoming increasingly remote from its application for breeding. For a variety of different but linked reasons, public sector scientists are largely failing to provide the requisite leadership in the development of practical public-good technologies for crop improvement, especially in developing countries where the need is greatest. One of the main take-home messages of this book is that we must re-engage plant and agricultural science with the rest of society at a whole series of levels. These include better links between basic science and applied technologies, between scientific breeders and their farmer-customers, between the public sector and the private sector, between industrialised countries and the developing world, between inexpensive conventional breeding and the costliest high-tech methods, and between agronomists and managers, and the economists and politicians working in agriculturally related areas of their respective professions.

The book is divided into six parts that first introduce us to the science of plant breeding before describing its changing social organisation and evolution as a mixed public/private venture over the last two centuries. Part I includes a brief account of the origins of breeding and its transition from a farm-based empirical activity to the highly sophisticated scientific programmes of today. We will follow the increasingly successful efforts of plant scientists of the eighteenth and nineteenth centuries to harness their growing knowledge of plant reproduction and development for practical and profitable commercial application. We will see how agricultural innovators became ever more skilled in manipulating those twin pillars of breeding, namely genetic variation and selection. The rediscovery of the principles of Mendelian inheritance and their application to simple and complex genetic traits was the key scientific foundation of twentieth century crop breeding.

The practical application of genetic knowledge to crop improvement in the field was made feasible by the theoretical and statistical tools provided by quantitative genetics after 1918. In the 1920s, chemical and X-ray mutagenesis were first used to create new crop varieties, while the 1930s saw the beginnings of increasingly successful applications of tissue culture in breeding programmes. Soon, scientific breeders could create artificial hybrid combinations from different species, and even different genera. And it was not long before the first manmade crop species, a plant called triticale, was produced. By the 1950s, the technique of wide crossing, coupled with chemically induced chromosome manipulations, had enabled breeders to transfer chromosomes, or parts thereof, from plants that were normally much too distantly related to interbreed. More effective types of radiation mutagenesis, using nuclear sources such as cobalt-60 or caesium-137, were effectively used after World War II to create more than 3000 new crop varieties.

In Part II, we will switch to consider the societal contexts of these scientific developments that led us from the farmer-breeder of the nineteenth century to today's multinational, high-tech agribusiness. During the nineteenth century, it was realised that the most effective method for applying scientific principles to crop improvement was to establish a professional body of trained plant breeders and researchers. In many of the newly industrialising countries, this was achieved by direct government action. Without a doubt, the most comprehensive, effective, and enduring crop improvement network is that of the USA, as originally established by the Morrill Act in 1862, during the depths of the Civil War. The British establishment, in contrast, took a distinctly more *laissez-faire* route to agricultural betterment. Here, there was a gradual evolution of a disparate group of mostly privately funded research centres during the late nineteenth and early twentieth centuries. It was in some of these British research centres that the application of the newly rediscovered principles of Mendelian genetics first propelled crop science into a new era. In the USA, the huge potential of hybrid crops, in terms of both yield and profitability, began to be realised during the 1920s with the introduction of the high-yielding maize varieties that eventually spread across the continent and beyond. For most of the twentieth century, plant breeding and crop science research were very much concentrated in the public sector, with major contributions from universities and specialised crop-focused research centres.

The success of this public sector based paradigm became ever more apparent as increasingly sophisticated breeding technologies were developed. These technologies, developed by public sector plant researchers as free public goods, were called upon to resolve the worsening food crisis as populations in developing countries expanded rapidly during the 1960s. The Green Revolution of the 1960s and 1970s was largely the result of the focused application of such public-good plant breeding, assisted by some US-based philanthropic foundations. Thanks to the work of a few groups of dedicated plant breeders, new high-yielding varieties of wheat and rice were developed, just in time to head off the spectre of mass hunger that haunted the Indian subcontinent and much of Eastern Asia. The spectacular success of the Green Revolution in much (but not all) of the developing world led to the establishment of an international network of plant research and breeding centres, including such vital resources as seed and germplasm banks.

In Part III, we move on to consider the turbulent events of the late twentieth century and the surprisingly rapid unravelling of the hitherto successful public/private paradigm of plant breeding research and development. The 1970s and early 1980s marked the apogee of public sector and public-good international plant breeding. Within a few years, governments around the world began to dismantle their public sector plant science infrastructures, in line with the new privatisation agenda that emanated largely from the UK. Meanwhile, the private sector emerged from the shadows as an increasingly dominant force in the enterprise of crop modification and improvement. Two additional factors facilitated the growth of the private sector: the shift to a more benign regulatory environment for the legal protection of new plant varieties; and the invention of a new set of plant manipulation technologies that would allow the patenting of transgenic (GM) crop varieties. We will go on to follow the fate of some of the rationalised, reduced, or terminated public breeding programmes across the world and the resulting retreat of the vast majority of public sector researchers into more academic studies.

The topic of Part IV is agbiotech. The decade from 1985–1995 witnessed a fundamental shift in the world of plant breeding, as the private sector became the more dominant partner and transgenic technologies were increasingly promoted as the way forward for crop improvement in general. We will analyse the consequences of these important developments for the future of agriculture. I will present the case that it was not so much genetic engineering (transgenesis) itself that has been the root cause of the many public controversies about agricultural biotechnology (agbiotech). Rather, it is the context in which the technology was created, promoted, and then applied to crop manipulation, which was radically different to previous forms of high-tech scientific crop improvement. After World War II, highly intrusive and 'artificial' methods of crop genetic modification had already been developed in the public domain with little or no fanfare or public controversy. These technologies were used freely to create new crop varieties around the world and were especially widely applied in developing countries.

In contrast, transgenic technologies were largely developed and patented by the private sector. Some companies then used the new technologies for the manipulation of a few simple input traits in a few profitable commercial cash crops. In the meantime, however, these technologies had already been widely hailed, by public sector scientists and companies alike, as a radical and revolutionary breakthrough in plant breeding of almost unlimited potential for the future of agriculture. Subsequently, the fact that, notwithstanding the optimistic rhetoric, nothing of any matching public value has so far emerged from transgenesis, has engendered a mixture of public scepticism and distrust about the entire agbiotech enterprise. We will also see how the actions of a few agbiotech companies are currently in danger of sabotaging some rather promising future developments in transgene technology to produce cheap medicines via biopharming.

In Part V, we will discuss alternative methods of enhancing crop production, especially amongst the rapidly increasing populations of the developing world. I will show that there need not be any looming crisis in feeding the world population over the next fifty years. We already have the crops, the breeding expertise, and the organisational skills to achieve this task – providing it is managed properly. I will present the case for a judicious expansion of our use of arable land, especially in parts of South America, where a large amount of non-forested land is available for sustainable crop cultivation. Combined with re-use of fallow, abandoned, and set-aside land, these measures could significantly increase global food production over the next few decades. Other productivity enhancing measures include better on-farm management, improvement of physical and regulatory infrastructure (ports, roads, credit facilities, tax regimes etc.), and the ending of discriminatory tariffs and subsidies. Implementation of these exceedingly practical but relatively unglamorous measures, along with the prospect of continuing yield gains via plant breeding, should ensure that we will be able to 'feed the world' over the next fifty years, without recourse to more nebulous and uncertain 'magic bullet' solutions.

In Part VI, we will look forward to the future of plant breeding in the twenty-first century, whether in the public/private sectors, or in industrial/developing countries. We will discuss the uncertain situation of international organisations like CGIAR (Consultative Group on International Agricultural Research), our endangered global seed banks, and the often heroic, and largely unseen, efforts of breeders in countries from Iraq to Côte d'Ivoire in trying to maintain these precious resources against the depredations of warfare and civil strife and the more benign neglect of increasingly jaded funding bodies. We will then look forward to consider some new options that could allow a reinvigorated public sector to resume its place as a major partner in the global enterprise of crop improvement. The long-term success of international agriculture is dependent on a diverse, mixed ecology of public and private agents and agencies. We need strong, well-resourced public-good ventures, which in turn are balanced and complemented by appropriately regulated, for-profit, private sector ventures that are both innovative and truly competitive.

The current problems of plant breeding have not been helped by the fact that many public sector scientists have largely withdrawn from practical breeding and public debate, to the more secluded and serene realms of basic research. The latter are not so much ivory towers as ivory cloisters of an almost adamantine unworldliness. This withdrawal has left the public arena bereft of many of the voices that could bring some balance into the sterile and polarised discourse on transgenic crops that has plagued the debates of the past decade. It is only by regaining a sense of balance in each of these aspects of crop improvement that we can recapture public confidence, and move forward with a renewed sense of optimism to confront and resolve the many challenges of agriculture in the twenty-first century.

Part I

The science of plant breeding

Here Ceres' gifts in waving prospect stand,
And nodding tempt the joyful reaper's hand.
Alexander Pope (1688–1744)
Windsor Forest (l. 39)

1

Origins of plant breeding

For out of olde feldes, as men seith
Cometh al this newe corn fro yeer to yere;
And out of olde bokes, in good feith,
Cometh all this newe science that men lere.
Geoffrey Chaucer (*c.* 1382)
The Parlement of Foules

Introduction – the development of agriculture

For most of our history, we humans have been omnivores who enjoyed a varied plant and animal based diet that was derived from a hunter-gathering lifestyle. This special relationship has bound people and plants in mutual dependence for well over one hundred millennia. During this period, our Palaeolithic and Neolithic ancestors experimented with many different strategies of plant exploitation, especially during the last hundred millennia when climatic conditions changed repeatedly and other resources such as large animals often became progressively more difficult to obtain.[1] For tens of millennia before the start of formal agriculture, societies throughout the world were engaged in many types of relatively sophisticated management of their favoured food plants. For example, 23 000 years ago, people in the Jordan Valley were already harvesting and grinding wild cereal grains, and baking the flour into bread and cakes.[2] Discoveries of similar grinding implements dating back as far as 48 000 years ago might mean that the management and processing of cereals went on for well over 30 000 years before these plants were ever cultivated as crops.

During this period of informal plant management, our ancestors unwittingly began a process of plant selection that would lead to the domestication of a few genetically amenable species. These plants became the first successful crops, and their formal cultivation was already well under way in several regions of the world by 12 000 years ago, and possibly earlier. Following the development and spread of agriculture, most of our ancestors came to rely increasingly on a much more restricted repertoire of domesticated plants for the majority of their food needs. Even today, most of the world depends on a small, carefully selected group of edible plants. We also use plants for a host of other purposes, such as clothing, shelter, medicines and tools. Although we now believe that the beginnings of the domestication process were probably non-intentional and unforeseen by Palaeolithic and Neolithic proto-farmers, these people soon learned how to improve their new crops by conscious forms of selection and breeding.[3]

Non-intentional selection

Selection can be said to be the backbone of crop breeding. There is little point in assembling or creating a group of genetic variants unless one has an effective mechanism to recognise and select the best adapted or most useful of these variants for further propagation. Such selection could have been either unintentional or deliberate on the part of the early farmers or would-be farmers. To a great extent, all living organisms act in concert with the abiotic (non-living) part of the environment as unintentional agents of selection. This sort of selection is normally negative, i.e. less fit individuals tend to be eliminated from the population. For example, simply by hunting for prey, a carnivore will tend to select those individuals that are easier to capture because they are less well protected, slower, more easily detected etc. As a result, the prey population is selected in favour of fitter individuals who, for example, may have adopted herding behaviour, are more fleet of foot, have acquired camouflage etc. Our ancestors started out as non-intentional agents of selection during the early stages of crop domestication. They then progressed to conscious selection of the relatively small number of favourable traits that were readily recognisable in a crop plant, e.g. seed size, vigour, or yield. In contrast, the scientific breeders of today have access to a battery of screening and selection strategies, many of them automated, that enable them to manipulate hundreds of often invisible traits in our major crop plants.

Most plants in non-agricultural ecosystems have been selected for traits such as indeterminate flowering and easy seed shedding from the parent plant. This minimises the chance of seed loss to herbivores. Several early human societies used techniques of plant management that had the by-product of selecting for a different set of traits. From recent genetic evidence, we know that these new traits enabled a few plant species to develop in the direction of domestication. The concept of non-intentional, or unconscious, selection by humans was first expounded by Darwin,[4] although he had no idea of the mechanism by which the favoured variants could transmit their variations to subsequent generations.[5] More recently, this mechanism of crop selection has been described in detail by Zohary.[6] Non-intentional selection probably led to those initial genetic changes that were the prerequisites to successful cultivation of plants as crops. The simplest form of traditional grain agriculture involves planting the seeds into tilled fields, harvesting the grain-bearing structures, and threshing out the seeds by mechanical agitation. Just by growing a crop in this way, a huge selection pressure is established that favours plants that do not shed their seeds before the harvester is ready.

In the wild, most seeds would be shed from the reproductive structures, but in a tilled field such shed seeds would fall to the ground and therefore would not be saved for re-planting. Gradually, the wild-type seed shedding trait would be lost from the population, which would instead be dominated by a new phenotype, i.e. non-shedding of seeds. This non-shedding phenotype would have been extremely maladaptive in the original ecosystem in which the plant had evolved, but it then became extremely useful under the new conditions of cultivation by humans. Similarly, seeds that germinated immediately upon planting would be automatically selected under the conditions created by cultivation. Wild-type varieties tend not to germinate straightaway. Instead, the seeds enter a period of dormancy that can be of variable duration, hence ensuring that they do not all germinate at the same time and compete with each other.[7] This type of seed dormancy trait is automatically selected against under cultivation and most seed crops have now lost their ability to delay germination.

Other important domestication-related traits that are automatically selected for by cultivation include an erect habit, synchronous flowering, thin seed coats, loss of camouflage colouration, and more numerous and larger seeds. This form of unconscious selection probably made possible the acquisition of most of the domestication-related traits in the early crops. The time taken for these evolutionary developments would have depended on the genetics of the individual crop. For example, if the variation for these traits were largely regulated by a small number of genes, and if these genetic loci were tightly linked, then new domestication-syndrome varieties could appear within a few dozen generations. It is likely that most of the early crops were genetically pre-adapted to cultivation, which means that the first farmers were at least spared some of the initial stages of trait selection. However, there are many other crop traits, the manipulation of which requires the deliberate intervention of humans. Such characteristics include many non-visible traits, such as those regulating seed quality or disease resistance.

Our most favoured plants were, therefore, the species that responded genetically to their prolonged association with human beings. In particular, a few plants were able to evolve some very specific traits that strongly encouraged their continued and more extensive use by their human guardians. These plants formed larger, more prominent seeds, which stayed on the main body of the adult plant and were therefore easier for people to see and collect. They germinated as soon as they were planted, ensuring a full crop each year. A few wild cereals hybridised with each other to produce many different types of starchy grain. This diversity of grains enabled people to select and grow a range of food types from a single family of crops. For example, people have learned to grow several different forms of wheat that are variously suitable for making bread, or cakes, or biscuits, or the many different types of pasta. Genetic evidence suggests that many changes involved in domestication occurred because of some very unusual arrangements of genes in the relatively few plant species that were successfully cultivated as staple crops. It seems that it was their peculiar genetic endowments that determined which plants would go on to become crops, rather than any conscious decision by human cultivators.[8]

In those ancient societies that persisted with agriculturally based plant exploitation, people soon started to manipulate their crops deliberately by a process of empirical breeding. As with the ancient craft of empirical biotechnology, which has given us such products as wine, beer, spirits and leavened bread, the empirical forms of plant breeding needed no knowledge of science to achieve far-reaching biological manipulations of crops. New varieties of wheat, rice and maize were developed, and farmers bred particular landraces of crops that were adapted for their own specific regions, soils and climates. This process resulted in a slow but steady increase in crop yields, and their adaptation to a host of new environments, as cultivation spread far and wide. But there were also many setbacks for farmers, as new diseases, warfare, and local climatic vagaries took their toll on food production. Hence, it is likely that the varieties of major crop staples being cultivated in late-medieval Europe were in many cases only marginally superior in yield to those grown by Neolithic farmers many millennia previously. However, all this was set to change after the sixteenth century, as a combination of scientific enquiry and entrepreneurial activity led to the transformation of agriculture in Northwestern Europe. This second phase of plant breeding occurred during the post-Enlightenment explosion in evidence-based knowledge of the past three hundred years, and we may therefore refer to this as 'scientific plant breeding'.

Variation and selection in breeding

Conceptually, at least, breeding is a fairly straightforward process. The two keys to the successful breeding of anything from a peony to a pony are *variation*[9] and *selection*.[10] In a nutshell, all that any breeder really needs is some degree of genetic variation between the individuals in a given population, plus a means of identifying and selecting the most suitable variants. These more useful variants are then mated or crossed with each other to produce a population that is now composed almost entirely of the newly selected genetic variety. This is how wolves were turned into