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Plant Breeding: Past, Present and Future

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Edinburgh, UK

ISBN 978-3-319-23284-3 ISBN 978-3-319-23285-0 (eBook)
DOI 10.1007/978-3-319-23285-0

Library of Congress Control Number: 2015951092

Printed on acid-free paper

This Springer imprint is published by Springer Nature
The registered company is Springer International Publishing AG Switzerland

Preface

Plant breeders starting work in 2015 will be nearing the end of their careers in 2050. Both years are of significance. The United Nations set eight ambitious Millennium Development Goals to be achieved by 2015, from a 1990 baseline. One was halving extreme poverty rates and included halving the proportion of people who suffer from hunger. The commitment to halve the percentage of hungry people by 2015 has almost been met at the global level and has been achieved by a total of 72 developing countries out of 129, or more than half the countries monitored according to the 2015 report from FAO, IFAD and WFP (2015). The report estimates that about 795 million people (780 million in the developing regions) are undernourished globally, which is a reduction of 167 million over the last decade and 216 million less than in 1990–1992. For the developing regions as a whole, the share of undernourished people in the total population has decreased from 23.3 % in 1990–1992 to 12.9 %. The report concluded that economic growth was a key factor for reducing undernourishment, but had to be inclusive and provide opportunities for improving the livelihoods of the poor. Enhancing the productivity and incomes of smallholder family farmers remains a key to progress. Encouraging as this is, a tremendous amount of work remains to be done to eliminate hunger, and the situation could worsen between 2015 and 2050.

The United Nations predicts that the global human population will continue to rise from the 7.0 billion reached in 2011 to 9.0 billion by 2050, when 70 % of the population will live in urban environments. As a consequence, world food production will need to increase between 70 and 100 % in just 40 years. Once again there are fears of population growth overtaking food supplies, as famously predicted by Thomas Robert Malthus in 1798 in *An Essay on the Principle of Population* (Malthus, 1798), when the population was only around 1.0 billion. Increasing food production to feed 9.0 billion people will be made even more challenging by four factors. Firstly, urbanisation and increasing wealth in developing countries (particularly China) is leading to a shift in diets to meat and dairy products, and these require the use of more farmland than an equivalent plant-based diet. Secondly, first-generation biofuels are using crops and cropland to produce energy rather than food so that even more food will need to be produced from the remaining land. Thirdly, the land area used for agriculture may remain static or even decrease as a result of degradation and climate change, despite more land being theoretically available, unless crops can be bred which tolerate associated abiotic stresses. Fourthly, it is unlikely that steps can be taken to mitigate all of the climate change predicted to occur by 2050, and beyond, and hence adaptation of farming systems and crop production will be required to reduce predicted negative effects on yields that will occur without crop adaptation. These impacts have been analyzed and summarised in the Intergovernmental Panel on Climate Change Report (AR5) published on 31 March 2014 (Climate Change: Impacts, Adaptation, and Vulnerability) and included in its Synthesis Report published on 31 October 2014. Substantial progress will be required in bridging the yield gap between what is currently achieved per unit of land and what should be possible in the future, given the most appropriate farming methods and best storage and transportation of food. Suitably adapted cultivars will also be needed, including adaptation to climate change (e.g. cultivars adapted to different growing seasons and to heat stress).

Breeding suitably adapted cultivars is the challenge for a new generation of plant breeders. They will need to decide what germplasm and which breeding methods to use and the types of cultivar to produce. They will need to appreciate what germplasm has already been utilised and how to find further desirable genetic variants in cultivated species and their wild relatives. They will also need to appreciate which breeding methods have been successful in the past and which ones are still likely to be successful today. In addition, they will need to consider the new opportunities made possible by technological advances in the manipulation of DNA, the chemical basis of heredity.

This book aims to help plant breeders in these endeavours by reviewing past achievements, currently successful practices and emerging methods and techniques. Theoretical considerations are presented when thought helpful and trying to strike the right balance on being as simple as possible but as complex as necessary. On a number of occasions, I suggest that practical breeders may get more out of computer simulations than complex theory. The book assumes an understanding of botany, genetics and statistics and does not attempt to teach these subjects, although reminders are given of facts relevant to plant breeding. However, as I have discovered from teaching undergraduate and postgraduate courses, it is impossible to discuss plant breeding in a meaningful way without presenting some genetic theory, particularly in population and quantitative genetics. Furthermore, the reader may need to consult a *Dictionary of Plant Sciences*, such as the one by Allaby (2012), for the meaning of some terms.

The book is divided into four parts. Part I is an historical introduction, from domestication to landraces and scientific breeding in the twentieth century, finishing with a discussion of future goals. Part II deals with the origin of genetic variation by mutation and recombination of DNA, the recognition and selection of genetic variants that affect qualitative and quantitative traits in a desired way and the implications of genotype × environment interactions for selection. This part concludes with a consideration of genome evolution and polyploidy, including examples of crop species that are polyploids and any implications for breeding. Part III starts by explaining how the mating system of a crop species determines the genetic structure of its landraces and hence the types of high yielding cultivars that have been selected and bred from landraces. Then current practice is reviewed for breeding the four main types of cultivar: synthetic (including open-pollinated), clonal, hybrid and inbred line (including mixtures). Finally the genetic basis of heterosis is examined in the context of choosing between breeding inbred line and hybrid cultivars. Opportunities are taken in this part to introduce important aspects of the nature of plant breeding: population improvement, multistage selection, multitrait selection, inbreeding and crossbreeding, hybridisation strategy and size of programme. Part IV considers the three complementary options for future progress: the use of sexual reproduction in further conventional breeding, base broadening and introgression; mutation breeding; and genetically modified crops. It then concludes with strategies for achieving durable resistance to pests and diseases, something that has so often appeared to be an historical fact or just hope for the future.

In writing the book I have drawn on my experiences over a 34-year period as a plant breeder and geneticist at the former Scottish Plant Breeding Station in Edinburgh and the former Scottish Crop Research Institute in Dundee. Throughout my career I have benefited from discussions with colleagues and the wider plant breeding community, particularly members of EUCARPIA, the European Association for Research on Plant Breeding. I have also benefited from participation in teaching, working groups and editorial work. Recently I edited Volume 7 (*Root and Tuber Crops*) in Springer's *Handbook of Plant Breeding*. In writing this book I have once again received much help and encouragement from Springer, this time from Ejaz Ahmad, Susan Westendorf and Kenneth Teng in particular. The 'handbook' provides detailed information on a wide range of economically important crops and should be of great value to breeders of those crops. In addition, I feel that those new to plant breeding might appreciate a more general review of the subject, its past successes, current practices and future possibilities. I hope that this book goes some way to meeting this objective.

Edinburgh, UK
June 2015

John E. Bradshaw

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Plants

Evolution of Plants

Plant breeding is the genetic improvement of cultivated plants through human selection, a process which began when plants were first brought into cultivation for human use, as early as 13,000 years ago (Balter, 2007). The plant species available for cultivation were the products of millions of years of evolution by natural selection. Our understanding of the history of plant life on Earth comes from an examination of the fossil record of plant remains and biomolecules, complemented with analysis and classification of the patterns of morphological and genetic variation among present-day plants (phylogenetics). The timescale is estimated from geological records and from the rate of production of genetic differences seen today (the molecular clock of phylogenetics). Detailed accounts of plant evolution, together with theories of the mechanisms driving the process, can be found in books such as *The Evolutionary Biology of Plants* by Niklas (1997), the beautifully illustrated *Green Universe* by Blackmore (2012) and *The Evolution of Plants*, *Second Edition*, by Willis and McElwain (2014). Here it is sufficient to list and briefly comment on some key events dealt with by these authors:

1. The evolution of the first forms of life (single prokaryotic cells from protocells with membranes that enclose the chemical reactions that form the basis of life), possibly in tidal pools, by 3.5 billion years ago. At that time, carbon dioxide concentrations were between 30 and 100 times higher than present levels of 360 ppm, global temperatures could have been between 30 and 50 °C (high enough to sustain liquid water on Earth), and oxygen accounted for <0.01 % of total atmospheric concentration.
2. The origin and development of photosynthetic cells; in particular, cyanobacteria (blue-green algae) capable of using light energy from the sun, water and carbon dioxide to synthesise complex sugars (with the release of oxygen) some

2.7 billion years ago. About 2.5 billion years ago, oxygen levels rose significantly to around 2.1 % and remained at that level for the next 2.0 billion years.

3. The formation by endosymbiosis of eukaryotic cells with a nucleus and organelles (mitochondria resembling purple non-sulphur bacteria for energy production and chloroplasts resembling cyanobacteria for photosynthesis); in particular, unicellular green algae approximately 1.87 billion years ago.
4. The acquisition of a multicellular construction; for example, green algae living in an aquatic medium some 800 million years ago (mya), that is, 800 megaannums (Ma).
5. The colonisation of land (and air) by plants from 470 Ma. The initial colonisers were relatively small (<1 m in height) plants; restricted to damp, moist regions; and related to our living bryophytes (mosses, liverworts and hornworts). The atmosphere was very rich in carbon dioxide, between 8 and 15 times higher than present, but still low in oxygen at 4 %. The global average surface temperature was thought to be approximately 21 °C.
6. The evolution of (seedless) vascular plants with conducting tissues for the transport of water (lignified) and food from 430 Ma. The result was large plants filling every ecological niche available, including spore-producing trees from 390 Ma (giant horsetail tree, giant Lepidodendron tree, tree-ferns and the Archaeopteris tree with its particularly advanced vascular system, true roots and megaphyllous leaves). By 360 Ma forests had widespread global distribution. Between 360 and 299 Ma atmospheric carbon dioxide levels rapidly declined from 3600 to 300 ppm, probably as a result of the global expansion of vascular plants. In contrast, there was a remarkable increase in oxygen to above 21 % (current level), with a peak of between 28 and 30 % around 280 Ma.
7. The evolution of naked (fruitless) seed plants (gymnosperms), initially trees, from 350 Ma, with a major radiation of new groups of plants from 290 to 250 Ma (including cycad and ginkgo trees whose pre-pollen microspores produce motile male gametes), and of conifers (cone-bearing and airborne pollen producing) from 250 to 200 Ma. From 299 to 250 Ma, carbon dioxide levels increased from 300 to 1500 ppm and then fluctuated until 140 Ma. Today the tallest known trees at 115 m are coast redwoods (*Sequoia sempervirens*) from California, and the largest due to their girth are giant redwoods (*Sequoiadendron giganteum*) at 84 m and 1486 m^3 of timber.
8. The evolution of the flowering plants (angiosperms) from 140 Ma, the first of which were probably herbaceous, weedy, small shrubs in low latitudes, but could have been aquatic plants. Angiosperms have seeds which are fully enclosed within a new and specialised plant organ, the carpel. Although the most rapid interval of angiosperm radiation was around 100 Ma, the grasses (Poaceae) did not emerge until 70 Ma. Initially they occupied an understory habitat within closed forested vegetation, but by 20 Ma, probably as a result of increasing global aridity, they had become the dominant group of plants in truly open habitat grasslands in many areas, ecosystems that we now describe as tropical and subtropical savannah, temperate grasslands and steppes. Today grasses provide over 50 % of the carbohydrates in our human diet.

Our present-day, angiosperm-dominated, flora is the result of major changes in the overall composition and distribution of global vegetation over the past 66 million years, associated with major extrinsic environmental change. During this period tectonic processes occurred in the Earth's crust, as a result of which the continental plates moved into their present positions, today's prominent mountain ranges formed and new ocean current systems were established. An initially warm (>30 °C) global climate became increasingly cool (towards 15 °C global mean) and arid, culminating in a build-up of ice at the poles, greater temperature gradients from equator to poles and the formation of deserts. Carbon dioxide concentrations fell from about 1200 ppm to around 300 ppm. From about 2.5 Ma recurrent glacial–interglacial cycles have occurred, closely linked to variations in the incoming solar radiation. These result from changes in the Earth's orbit around the sun and the tilt and wobble of the Earth on its axis. Concentrations of atmospheric carbon dioxide fell to averages of around 180 ppm during the glacial periods compared with 300 ppm during interglacial periods. During glacial periods temperate vegetation became isolated in regions where microenvironmentally favourable conditions existed and then re-expanded from these regions during interglacial periods.

Biogeographical maps of the Earth's flora can be found in the book by Willis and McElwain (2014), but we do not need to consider them further. Before starting the history of plant breeding, however, it is worth pausing for a moment to reflect on the extent to which we need plants for our well-being, as this provides the context for their improvement through breeding.

Use of Plants

People use plants for many purposes as seen in Economic Botany Collections such as the ones at the Royal Botanic Gardens, Kew (1998), which now consist of over 76,000 specimens. A few examples will suffice. Plants provide us with basic food in the form of carbohydrate and protein, as well as essential fatty acids, vitamins and minerals. Carbohydrates come from cereals (wheat, rice and maize), tubers (potatoes) and roots (cassava) and proteins from legumes and their pulses (beans, peas and lentils). Vegetable oils for both food and industrial use come from the crushed or pressed seeds of temperate crops such as oilseed rape and linseed, Mediterranean ones like sunflowers and olives and tropical ones like peanuts and palm oil. Plants also provide fodder for our livestock, including grass for ruminants as they can digest the cellulose in plant cell walls. We flavour our food with herbs and spices and sweeten it with sugar, both cane and beet. We make wine from grapes and beer from barley, while tea, coffee and chocolate are popular beverages. We clothe ourselves with plant fibres such as cotton, coloured with dyes like indigo in blue jeans, and use plants for hats, shoes and adornments such as seed necklaces. We are clean and sweet smelling thanks to scented soap made, for example, from palm oil and lavender. We still rely on plants for medicines. The latex of poppy capsules provides morphine and codeine for pain relief, and for many years, quinine from cinchona bark was the best treatment for malaria. Indeed, it can be argued that the settlement of white Europeans in Africa, with its political, economic and social consequences, was only possible through quinine (Hobhouse, 1992). Currently one of the most effective treatments for malaria is artemisinin (qinghaosu in Chinese), a drug extracted from the herb *Artemisia annua* (sweet wormwood), which had been used in traditional Chinese medicine for many centuries before being rediscovered by the Western world in the 1970s (Benson, 2012).

Plants provide us with fuel, traditionally wood to burn for heating and cooking, but increasingly as a fuel for electricity generation together with grasses such as *Miscanthus* × *gigantus*. Today wood harvesting systems include short rotation coppice, for example, willow and poplar; and since the mid-1800s paper has been made from wood pulp, having first been made by the Chinese around 100 BCE (before the Common Era) from plant fibres such as hemp. Whereas wood for fuel makes use of the current growth of trees, fossil fuels (coal, oil and natural gas) are a finite resource from past trees and vegetation. Biodiesel from oilseed crops and bioethanol produced by fermenting plant sugars are modern alternative fuels to diesel and petrol, respectively. Second-generation biofuels are anticipated in which cellulose cell walls are also converted to fuel. Plants also provided the materials for water transport and now rubber for the tyres of modern vehicles. Musical instruments, sports and games equipment and storage containers (baskets and boxes) have all been made from plants, as have traps and nets for hunting and fishing. Finally, we find plants beautiful and use them for decorative purposes.

More details on our uses of plants can be found in *Why People Need Plants* edited by Wood and Habgood (2010). We should, however, never forget that we rely on plants as a whole to capture the sun's energy to make the food we eat and to produce the oxygen we breathe and, perhaps most importantly of all, that photosynthesising organisms have shaped and still shape the Earth's climate.

Part I
Historical Introduction