



Plant breeding and farmer participation



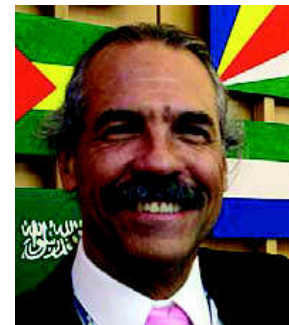
Plant breeding and farmer participation

Edited by

S. Ceccarelli

E.P. Guimarães

E. Weltzien



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Foreword

Participatory Plant Breeding (PPB) originated in the early 1980s as part of a movement promoting the concept of participatory research, in response to criticisms of the failure of post-green-revolution, experiment-station-based research to address the needs of poor farmers in developing countries. Rooted in debate over the social consequences of the narrow focus of the scientific type of research, PPB gained recognition as an activity mostly promoted by social scientists and agronomists based in anti-establishment non-governmental organizations (NGOs). In consequence, rather than being perceived from the beginning as an additional option available to breeders, PPB for a long time had the image of being one of two contrasting types of plant breeding, with PPB being more “socially correct” than conventional plant breeding.

Even now, nearly thirty years later, this view is still common. Few professional breeders accept that farmers can be full partners in a plant breeding programme, even though everyone agrees that it was farmers that domesticated crops about 10 000 years ago and, in some regions of the world, continued to modify and manipulate them to the present day. Even before the re-discovery of Mendel’s laws of inheritance, the work of a number of amateur breeders became an inspiration for Darwin’s theories. In several respects, the relationship with farmers on which PPB is based is similar to the ways in which plant breeders worked with producers in North America and Europe in the early twentieth century. At that time it was commonplace for breeders to spend time interacting with producers, and to test new materials collaboratively in farmers’ fields in order to understand what producers considered to be desirable traits for an improved variety. However, the combination of industrialization of agriculture and formal training for plant breeders created a gap between breeders and farmers, a gap that was exported to developing countries in the post-war era. As the profession of plant breeding lost the habit of interacting closely with producers, concern for how to address farmers’ needs and constraints fell by the wayside. PPB revived this as a central issue, because by the late 1970s it was increasingly evident in developing countries that post-green-revolution “improved” varieties were too often failing to satisfy farmer requirements and were being shunned.

Today there is widespread recognition that the conventional package of new varieties and external inputs, while successful in the more favourable production areas, has often failed to benefit small-scale farmers in marginal areas. As a result, the vital role of PPB as an additional strategy is better understood. Experience has taught that PPB is complementary to conventional plant breeding rather than an alternative type of plant breeding. Demand for a complementary approach has expanded considerably because of pressure to ensure the relevance of research to poor farmers and their diverse agricultural systems, and because PPB allows selection for the specific adaptation required for such a diversity of target environments. Today, about 80 participatory breeding programmes are known worldwide, involving various institutions and various crops. In 2000, an international review of plant

breeding research methodologies concluded that PPB should be an “organic” part of every plant breeding programme aimed at benefiting small-scale farmers in difficult, high-risk environments. In fact, traditional farming and low-input systems, including organic agriculture, are a very heterogeneous population of target environments and not easily served by centralized, conventional plant breeding.

The book demonstrates that PPB is in essence no different from conventional plant breeding, being based on the very same principles of Mendelian, quantitative and population genetics, and therefore has complemented the traditional approach to plant breeding with a number of chapters addressing issues specifically related to the participation of farmers in a plant breeding programme.

The authors of the various chapters have been carefully selected to represent three groups of scientists: the first comprises internationally recognized experts in genetics as related to plant breeding, and in the various aspects of plant breeding (from general methodological issues to more specific issues, such as breeding for resistance to biotic and abiotic stresses, high yield potential, molecular breeding and genotype \times environment interactions); the second group is represented by professional breeders who have actually practised participatory plant breeding with a number of different crops and in a number of socially and climatically different areas, using the range of methods presented by the first group; and, finally, the third is represented by a group of scientists with specific expertise in areas not usually covered in classical plant breeding books, such as variety release mechanisms, seed diffusion, institutional issues associated with PPB, and intellectual property rights. A chapter documenting the impact that participatory plant breeding has had after about thirty years of practice has been chosen to be the logical conclusion of the book.

The book is aimed at plant breeders, social scientists, students and practitioners, with the hope that they all will find a common ground to discuss ways in which plant breeding can be beneficial to all and can contribute to alleviate poverty.

Finally, we would like to acknowledge everyone who has, directly or indirectly, contributed to the book: the CGIAR Participatory Research and Gender Analysis Program (PRGA) for the initial idea of producing such a book, the contributors of the chapters for sharing their scientific experience and for enduring a number of revisions of their respective chapters, Dr P.G. Rajendran for his help in the initial editorial efforts and the Directors-General of our Institutions for their continuous support. Final editing and preparation for publication was done by Mr Thorgeir Lawrence.

Abbreviations and acronyms

AB-QTL	Advanced Backcross QTL Analysis
AFLP	Amplified fragment length polymorphism
AMMI	Additive main effects and multiplicative interaction
AMOVA	Analysis of molecular variance
ANOVA	Analysis of variance
AOSCA	Association of Official Seed Certifying Agencies
ABS	Accelerated Breeding System [for sweet potato]
ASSINSEL	International Association of Plant Breeders for the Protection of Plant Varieties
AVP	Asexually or vegetatively propagated
BC_n	Back-cross generation <i>n</i>
BLUE	Best Linear Unbiased Estimate
BLUP	Best Linear Unbiased Prediction
BPE	Before present era
BSA	Bulked Segregant Analysis
Bt	<i>Bacillus thuringiensis</i> [gene]
BYDV	Barley Yellow Dwarf Virus
CBD	Convention on Biological Diversity
CBP	Centralized breeding programmes
CCN	Cereal cyst nematode
CE	Common era
CGIAR	Consultative Group for International Agricultural Research
CIDA	Canadian International Development Agency
CIE	Commission Internationale l'Eclairage
CIAL	Local agricultural research committees [in Latin America]
CIAT	International Center for Tropical Agriculture
CIMMYT	International Wheat and Maize Improvement Center
CIP	International Potato Center
CPB	Conventional plant breeding
cv	Cultivar [= cultivated variety]
DArT	Diversity Arrays Technology
DBP	Decentralized breeding programmes
dES	Diethyl sulphate [a mutagen]
DF	Degrees of freedom
DH	Doubled haploid
DHPLC	Denaturing high performance liquid chromatography
DM	Dry matter

DPBP	Decentralized-participatory breeding programmes
DUS	Distinctness, Uniformity, Stability
DW	Dry weight
ELISA	Enzyme-linked immunosorbent assay
EMS	Ethane methyl sulphonate [a mutagen]
EPA	Environmental Protection Agency [United States of America]
F_n	Filial generation <i>n</i>
FAO	Food and Agriculture Organization of the United Nations
FDA	Food and Drug Administration [United States of America]
FFS	Farmer field school
FIPAH	La Fundación para La Investigación Participativa con Agricultores de Honduras
FK	Farmer knowledge
FPB	Formal plant breeding
FR	Farmers' Rights
FV	farmer variety [\pm locally selected]
G\timesE	Genotype \times Environment (Interaction)
GGE	Genotype main effect (G) plus Genotype \times Environment (GE) Interaction
GIS	Geographical Information System
GMO	Genetically modified organism
GURT	Genetic Use Restriction Technology
G\timesL	Genotype \times Location
G\timesY	Genotype \times Year
HPLC	High performance liquid chromatography
IAEA	International Atomic Energy Agency
IARC	International Agricultural Research Center
ICARDA	International Center for Agricultural Research in the Dry Areas
ICP	Inductively coupled plasma [mass spectrometry]
ICPOES	Inductively Coupled Plasma Optical Emission Spectrometer
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
ID	Inbreeding depression
IDRC	International Development Research Centre [Canada]
IFPRI	International Food Policy Research Institute
IITA	International Institute of Tropical Agriculture
INCA	National Institute for Agricultural Science [Cuba]
IP	Intellectual property
IPGRI	International Plant Genetic Resources Institute [now Bioversity International]
IPM	Integrated pest management
IPR	Intellectual Property Rights
IRRI	International Rice Research Institute
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
LD	Linkage disequilibrium

LD₅₀	Lethal dose killing 50% of target
LD₁₀₀	Lethal dose killing 100% of target
MAS	Marker-assisted selection
MCA	Multiple correspondence analysis
MET	Multi-environment Trials
MFN	Most favoured nation
MNU	Methylnitrosourea [a mutagen]
MRRS	Modified reciprocal recurrent selection
MS	Mean square
MTA	Material Transfer Agreement
MV	Modern variety
MVD	[FAO/IAEA] Mutant Varieties Database
NARS	National agricultural research system
NDVI	Normalized Difference Vegetation Index
NERICA	New Rice for Africa
NIL	Near-isogenic line
NIRS	Near Infrared Spectroscopy
NIR	Near-infrared [spectrum]
OECD	Organisation for Economic Co-operation and Development
OFSP	Orange-fleshed sweet potato
OPC	Open-pollinated cultivar
PBK	Plant breeder knowledge
PBR	Plant breeder's rights
PC	Principal components
PCR	Polymerase chain reaction
PGR	Plant genetic resources
PPB	Participatory plant breeding
PRA	Participatory rural appraisal
PRGA	[CGIAR] Participatory Research and Gender Analysis [Program]
PRI	Photochemical reflectance index
PSD	Participatory seed dissemination
PVP	Plant Variety Protection
PVS	Participatory varietal selection
PVX	Potato virus X
PVY	Potato virus Y
QTL	Quantitative trait locus
R&D	Research and development
RAPD	Random amplified polymorphic DNA
RCB	Randomized complete block [experiment design]
REML	Restricted Maximum Likelihood
RFLP	Restriction fragment length polymorphism
RFSRS	Reciprocal full-sib recurrent selection
RIL	Recombinant inbred line

RRS	Reciprocal recurrent selection
S_n	Selfed generation <i>n</i>
SD	Standard deviation
SE	Selection environment
SE	Standard error
SFNB	Spot form of Net blotch
SMTA	Standard Material Transfer Agreement
SNP	Single nucleotide polymorphism
SPCSV	Sweet potato chlorotic stunt virus
SPFMV	Sweet potato feathery mottle virus
SPVD	Sweet potato virus disease
SR	Simple Ratio Vegetation Index
SS	Sum of squares
SSR	Simple sequence repeat
SSTW	Small-scale Third World
TGV	Transgenic crop variety
TILLING	Targeting Induced Local Lesions In Genomes
TLC	Thin-layer chromatography
TPE	Target population of environment
TPS	True potato seed
TRIPs	[Agreement on] Trade-Related Aspects of Intellectual Property Rights
UPOV	International Union for the Protection of New Varieties of Plants
USDA	United States Department of Agriculture
UV	Ultraviolet [radiation]
VCU	Value for Cultivation and Use
VIS	Visible spectrum
WARDA	Africa Rice Centre [formerly the West Africa Rice Development Association]
WI	Water index
WIPO	World Intellectual Property Organization
WTO	World Trade Organization
WUE	Water-use efficiency

Contributors

Maria I. ANDRADE

International Potato Center (CIP),
Avenida das FPLM 2698, PO Box 2100
Maputo,
Mozambique

Paolo ANNICCHIARICO

CRA - Centro di Ricerca per le
Produzioni Foraggere e Lattiero-Casearie,
viale Piacenza 29, I-26900 Lodi,
Italy

José Louis ARAUS

International Maize and Wheat
Improvement Centre (CIMMYT),
Apdo. Postal 6-641, 06600 México, D.F.,
Mexico

Jacqueline A. ASHBY

International Potato Centre (CIP), Lima,
Peru

Andrew R. BARR

Affiliate Professor, University of Adelaide,
Waite Campus, Glen Osmond, South
Australia 5064

Javier BETRÁN

Syngenta Seeds,
St. Sauveur,
France

Chittaranjan R. BHATIA

New Bombay 400 703,
India

Zewdie BISHAW

Head, Seed Unit, ICARDA, PO Box 5466,
Aleppo,
Syrian Arab Republic

Flavio CAPETTINI

International Center for Agricultural
Research in the Dry Areas (ICARDA),
PO Box 5466, Aleppo,
Syrian Arab Republic

Salvatore CECCARELLI

formerly with The International Center
for Agricultural Research in the Dry Areas
(ICARDA), PO.Box 5466, Aleppo,
Syrian Arab Republic

Anja CHRISTINCK

Gichenbach 54, D-36129 Gersfeld,
Germany

David A. CLEVELAND

Environmental Studies Program,
University of California, Santa Barbara,
CA 93106-4160,
United States of America

Stan COX

The Land Institute, 2440 E. Water Well
Rd., Salina, Kansas 67401,
United States of America

John DODDS

Dodds and Associates, 1707 N Street NW,
Washington DC 20036,
United States of America

Donald N. DUVICK (DECEASED)
formerly with Department of Agronomy,
Iowa State University, Ames, Iowa,
United States of America

Jorge ESPINOZA
International Potato Center (CIP)
Apartado 1558, Lima 12,
Peru

Yusuf GENC
Molecular Plant Breeding Cooperative
Research Centre, University of Adelaide,
Waite Campus, PMB 1,
Glen Osmond SA 5064,
Australia

Robin D. GRAHAM
School of Agriculture, Food and Wine,
University of Adelaide, Waite Campus,
PMB 1, Glen Osmond SA 5064,
Australia

Stefania GRANDO
International Center for Agricultural
Research in the Dry Areas (ICARDA),
P.O. Box 5466, Aleppo,
Syrian Arab Republic

Wolfgang GRÜNEBERG
International Potato Center (CIP)
Apartado 1558, Lima 12,
Peru

Bettina I.G. HAUSSMANN
International Crops Research Institute for
the Semi-Arid Tropics (ICRISAT),
BP 12404, Niamey,
Niger

Julia M. HUMPHRIES
Department of Clinical Pharmacology,
Flinders Medical Centre,
Bedford Park SA 5042,
Australia

Sally HUMPHRIES
Department of Sociology and
Anthropology, MacKinnon Building,
University of Guelph, Guelph, ON,
Canada, N1G 2W1

Humberto RÍOS LABRADA
National Institute of Agricultural Sciences,
Havana, Cuba

Pierre J.L. LAGODA
Plant Breeding and Genetics Section, Joint
FAO/IAEA Division, Vienna,
Austria

Graham H. LYONS
School of Agriculture, Food and Wine,
University of Adelaide, Waite Campus,
PMB 1, Glen Osmond SA 5064,
Australia

Mirosław MALUSZYŃSKI
Department of Genetics, University of
Silesia, Katowice,
Poland

Jesús MORENO-GONZÁLEZ
Centro de Investigaciones Agrarias de
Mabegondo, Xunta de Galicia,
Spain

Robert MWANGA
National Crops Resources Research
Institute (NCRRI), Namulonge,
Box 7084, Kampala,
Uganda

Karin NICTERLEIN

Food and Agriculture Organization of the United Nations (FAO), Research and Extension Division, 00153 Rome, Italy

Heiko K. PARZIES

University of Hohenheim, Institute of Plant Breeding, Seed Science and Population Genetics, D-70593 Stuttgart, Germany

Fred RATTUNDE

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), BP 320, Bamako, Mali

Matthew P. REYNOLDS

International Maize and Wheat Improvement Centre (CIMMYT), Apdo. Postal 6-641, 06600 México, D.F., Mexico

Raoul A. ROBINSON

Retired Agricultural Botanist 445 Provost Lane, Fergus, Ontario, Canada, N1M 2N3

Ignacio ROMAGOSA

Centre UdL-IRTA, Universitat de Lleida, Lleida, Spain

Conxita ROYO

Institut de Recerca i Tecnologia Agroalimentàries (IRTA), Area de Conreus Extensius, Centre UdL-IRTA, Alcalde Rovira Roure 191, 25198 Lleida, Spain

Pratap K. SHRESTHA

Local Initiatives for Biodiversity, Research and Development (LI-BIRD), P.O. Box 324, Pokhara, Kaski, Nepal

Gustavo A. SLAFER

ICREA (Catalonian Institution for Research and Advanced Studies) and Department of Crop and Forest Sciences, University of Lleida, Centre UdL-IRTA, Av. Rovira Roure 191, 25198 Lleida, Spain

Daniela SOLERI

Department of Geography, University of California, Santa Barbara, CA 93106-4060, United States of America

Susanne SOMERSALO

Dodds and Associates, 1707 N Street NW, Washington DC 20036, United States of America

Yiching SONG

Center for Chinese Agricultural Policy (CCAP), Chinese Academy of Sciences, Institute of Geographical Sciences and Natural Resources Research Jia 11, Datun Road, Anwai, Beijing 100101 China

Iwona SZAREJKO

Department of Genetics, University of Silesia, Katowice, Poland

Anthony J.G. VAN GASTEL

Harspit 10, 8493KB, Terherne, Netherlands

Ronnie VERNOOY

International Development Research
Centre (IDRC), 150 Kent Street, PO Box
8500, Ottawa, ON,
Canada, K1G 3H9

Daljit S. VIRK

CAZS-Natural Resources, Bangor
University, Bangor LL57 2UW,
United Kingdom

Kirsten VOM BROCKE

Centre de Coopération Internationale
en Recherche Agronomique pour le
Développement (Cirad) c/o ICRISAT,
BP 320, Bamako,
Mali

Eva WELTZIEN

International Crops Research Institute for
the Semi-Arid Tropics (ICRISAT), BP 320,
Bamako, Mali

John R. WITCOMBE

CAZS-Natural Resources, Bangor
University, Bangor LL57 2UW,
United Kingdom

CHAPTER 1

Crop domestication and the first plant breeders

Stan Cox



1.1 INTRODUCTION

If the story of modern humans from the beginning to the present day could be compressed into a feature-length movie, the era of crop domestication would occupy a scene approximately six minutes long, starting about ten minutes from the movie's end. During that scene, the action would be scattered and sporadic; the domestication of any individual crop species would almost always occur in only a single locality and occupy only about 15 seconds to 2 minutes of the film.

In that brief era, in those rare places where today's crops were born, every farmer was a plant breeder. And through succeeding millennia, as agriculture spread across the surface of the planet, much of settled humanity came to participate in plant breeding.

Studies of ancient artefacts and botanical remains, ancient DNA, phytoliths, living plant populations, and the agricultural practices of surviving indigenous societies have converged to provide us with a vivid but still incomplete account of the first plant breeders' genetic revolution. Conventional wisdom based on those studies tells us that domestication was preceded by a period of archaic cultivation, during which people encouraged the growth of particular species and harvested their seed or other plant parts; that when people began to sow a portion of their harvested seed, they selected—automatically and unconsciously—for genes of domestication, such as those curtailing seed dispersal and dormancy; and that, as our ancestors developed a mutual dependency with domesticated plants, they became intentional and versatile plant breeders, selecting for a wide range of desired traits in species grown for grains, roots, tubers, fruits, vegetables or fodder.

Conventional wisdom usually gains its status by being accurate in its generalities but off the mark in some of its specifics. As we will see, that is the case with crop domestication. My purpose in this chapter is not to summarize the 'where' and 'when' of domestication, species by species, nor is it to analyse theories on the origins of agriculture. Those tasks would entail the boiling-down, if not the over-cooking, of a vast and fascinating literature (e.g. see Zeder *et al.*, 2006; Sauer, 1993; and Harris and Hillman, 1989). Rather than attempt to summarize that literature, I briefly tabulated in Table 1.1 what is believed to be true, both geographically and chronologically, about the domestication of today's major crops.

Keeping in mind that humanity's brief experiment with domestication involved people in every quadrant of the globe, I will concentrate on the 'how' and 'why' of domestication, on questions about the first plant breeders themselves and the species they transformed: Why did they domesticate some species and not others? How did their farming practices change gene frequencies in plant populations? How long did domestication take? Why did people select for particular traits: unconsciously, intentionally or indirectly? How did their actions affect the genetic structure and diversity of today's crop species? And, finally, what kinds of skills and knowledge did they pass down to the farmer-breeders of more recent times?

Any effort to answer those questions must draw upon examples from the available literature, in which today's major crops, largely cereals and grain legumes, feature most prominently. Although no set of examples can represent the full geographical and botanical range of domestication, I have attempted to rely upon those people,

TABLE 1.1
Species domesticated in each of eight world regions, with approximate age of the oldest evidence of domestication

Region	Species	Common name	Age of the oldest evidence of domestication (years BPE)
West Asia	<i>Hordeum vulgare</i>	Barley	10 500
	<i>Triticum turgidum</i>	Emmer Wheat	10 500
	<i>Cicer arietinum</i>	Chickpea	9 500
Africa	<i>Sorghum bicolor</i>	Sorghum	8 000 ^a
	<i>Pennisetum glaucum</i>	Pearl Millet	? ⁽¹⁾
Eurasia	<i>Brassica campestris</i>	Rape	3 500
East Asia	<i>Oryza sativa</i>	Rice	7 000
	<i>Glycine max</i>	Soybean	4 000
New Guinea	<i>Musa</i> spp.	Banana	7 000 ⁽²⁾
	<i>Saccharum officinarum</i>	Sugar Cane	?
South America	<i>Ipomoea batatas</i>	Sweet Potato	4 500
	<i>Arachis hypogaea</i>	Groundnut	4 500
	<i>Solanum tuberosum</i>	Potato	4 500
	<i>Manihot esculenta</i>	Cassava	4 500
	<i>Phaseolus vulgaris</i> ⁽³⁾	Common Bean	7 500
Mesoamerica	<i>Zea mays</i>	Maize	7 500
	<i>Gossypium hirsutum</i>	Cotton	7 500
North America	<i>Helianthus annuus</i>	Sunflower	3 000

NOTES: (1) Wendorf *et al.* (1992) found archaeological evidence that wild millet and sorghum were being used in the Sahel 8000 years before present. The sorghum specimens showed evidence that they were in the process of domestication.

(2) Denham *et al.*, 2003. (3) Independently domesticated in Mesoamerica as well. Species listed are among the world's 20 most widely grown crops, on a land-area basis (FAO, 2005). Information is from Sauer (1993) unless otherwise indicated.

places and plants that best illustrate the important features of domestication.

1.2 SELECTION AMONG SPECIES

There is little doubt that certain species were 'pre-adapted' (Zohary, 1984) for domestication. Either entire populations or individual plants within populations had to attract the attention of humans before they could be manipulated. With exceptions, plants or populations that exhibited unusually large or numerous edible parts; self-pollination (in sexually propagated species); ease of propagation (in vegetatively propagated species); or delayed seed dispersal (e.g. chickpea: Ladizinsky, 1979) caught the eyes of early cultivators. Bar-Yosef and Kislev (1989) listed characteristics of certain wild cereals (relative to other wild plant species) that attracted early west Asian domesticators: larger grain, local

abundance, annuality, lower seed dormancy, diploidy, harvestability and relative ease of seed dehulling.

A common characteristic among crop ancestors was their weediness: their tendency to thrive in disturbed, fertile soils like those associated with human habitation. The circumstances of domestication are, of course, different for every species. In some places, people started out by harvesting conveniently large stands of annual grasses; in others, variations on the so-called 'rubbish heap' theme were at work (Hawkes, 1969). Many crop ancestors were just as responsible for seeking out humans and human-made environments as were people for tracking down the plants. Indeed, according to Hawkes (1969), it "must have seemed little short of miraculous to find that plants needed for food sprang up by their very huts and paths".

In west Asia, however, those destined to become the first agriculturists tended to make their homes near reliable water sources, whereas they gathered wild grains from stands that were often some distance away (Willcox, 2005). Also relying on the west Asian domestication experience, Abbo *et al.* (2005) labelled the rubbish-heap hypothesis 'environmental determinism' that "tends to underestimate the role of human initiative in the Neolithic transition".

One thing is certain: the original domesticators did not adopt just any species that showed up at their doorstep. Then, as now, people had strong ideas about the usefulness of some plant species and the unacceptability of others. Plants with the most to offer were domesticated long ago, while others that were sufficiently weedy, but less desirable, repeatedly presented themselves to humans, only to be ignored or targeted for eradication (Hawkes, 1969).

Prehistoric people gathered and ate foods from a huge range of plant species, but once they began domesticating, it was *annual* plants that they transformed. Among the staple crops in Table 1.1 that yield edible reproductive biomass, the banana is the lone herbaceous perennial. Herbaceous, *grain*-producing, perennial species are not to be found at all among the world's crops plants (Cox *et al.*, 2002). Herbaceous perennials generally produce less seed in a season than do annuals. Also, rapid climatic change across the Asian continent at the end of the Pleistocene dramatically increased the availability of those annual, seed-producing species that attracted the attention of cultivators (Whyte, 1977). The difference in seed production between annuals and perennials is a result of contrasting selection pressures during the two groups' evolutionary histories. Selection pressure applied in yet a different direction by plant breeders can

increase seed yield and produce perennial grain crops (DeHaan, Van Tassel and Cox, 2005), but only if the right combination of breeding objectives is established.

When we think of how many civilizations built on annual cropping have fallen not to the sword but to the plough (Hillel, 1991; Lowdermilk, 1953) and the soil degradation that continues to haunt agriculture today, we can only lament the fact that the domesticators did not focus more on erosion-resistant perennial species. Apparently, ancient gatherers did utilize the seed of perennial species as food. Weiss *et al.* (2004) identified charred seeds from 3 perennial and 12 annual species of small-grained grasses that people were consuming 23 000 years ago at a site in what is now Israel. Bohrer (1972) discussed traditional methods of harvesting seed from assorted perennial grasses in Poland, Mongolia and North America. Harlan (1989a) listed a wide range of perennial grasses that people living south of the Sahara have harvested for food. Perennial lymegrass (*Leymus arenarius*) was probably cultivated by Vikings before barley reached Scandinavia (Griffin and Rowlett, 1981). Yet no domesticated perennial grain species were handed down to us by the first plant breeders.

Perennials did not compete well with annuals in disturbed soil and would not have followed people back to the fertile, churned soil around their dwellings; if some plants did happen to make their way there, they would have been overwhelmed by repeated disturbance and competition from weedy annuals. More importantly for Neolithic domesticators, farming and plant breeding were one and the same activity. As a result, they inevitably carried plant populations rapidly through sexual cycles, thereby fulfilling an essential requirement of gene-frequency change. Perennial plants re-growing

from vegetative structures would have been much more vigorous than either volunteer seedlings or intentionally sown plants; therefore, even if people tried to cultivate perennials, they would have felt little incentive to sow new generations from seed.

As we shall see, the act of sowing harvested seed applied strong selection pressure. Selection for non-shattering was strengthened when people began tilling new land year after year to sow their seed, perhaps as a part of shifting cultivation to avoid build-up of non-domesticated weeds (Hillman and Davies, 1990). Stands of perennial plants on undisturbed land would have been much less vulnerable to weeds, much more poorly adapted to shifting cultivation, and therefore less susceptible to domestication. One harvest method that spurred selection for seed retention in the annual cereals—uprooting of the plant (Bohrer, 1972; Hillman and Davies, 1990)—is very difficult with most perennials.

Woody perennials of the Mediterranean and west Asia—including olive (*Olea europaea*), grape (*Vitis vinifera*), fig (*Ficus carica*) and date (*Phoenix dactylifera*)—were domesticated in the same region as cereals, but by descendants of the first plant breeders, several millennia after agriculture had been well established (Zohary and Spiegel-Roy, 1975). Fruit-producing trees and vines did not have to compete with annual counterparts for humans' attention. They were vegetatively propagated, and, even today, most sexual progeny derived from them are “not only economically worthless, but often regress towards the mean found in spontaneous populations, showing striking resemblance to the wild form” (Zohary, 1984). The lack of far-reaching genetic changes in Mediterranean tree crops is also manifested in their failure to spread very far beyond their original climatic range, in

contrast to annual domesticates from that region (Zohary and Spiegel-Roy, 1975).

Of course, early farmers also practised selection in vegetatively propagated herbaceous species. As with woody species, they selected clones with desirable characteristics – often the results of unusual mutations – and distributed them far and wide. Occasional hybridization or somatic mutation fuelled some continuing selection; for example, spontaneous yam (*Dioscorea* spp.) clones selected for cultivation by present-day farmers in Benin either are wild or are hybrids between cultivars and wild yams (Scarcelli *et al.*, 2006; Mignouna and Dansi, 2003). But with only rare sexual recombination, there was little opportunity for the degree of domestication seen in grain crops (Zohary, 2004).

The earliest plant breeders' disproportionate attention to seed-propagated annual plants has been replicated by most modern students of plant domestication. That preference will be evident in the range of examples on which the following sections draw.

1.3 INITIAL SELECTION WITHIN SPECIES

It is widely recognized that crops were not domesticated simply through gathering or cultivation. Even the most intensive harvesting of cereals does not apply sufficient selection pressure to domesticate a crop fully. Intentional sowing, in contrast, applies strong, unconscious selection pressure (Zohary, 2004). Alleles for non-shattering, lack of dormancy, reproductive determinacy and increased fertility of formerly sterile florets are all favoured by the sowing-harvesting-sowing cycle (Harlan, De Wet and Price, 1973).

In the west Asia of 10 000 years ago, wild cereals grew naturally in large fields of near-monoculture, but they were not a food source that could simply be browsed

at one's convenience. The time between full ripening and total loss of seed through shattering was only a week or two, and with hot dry weather, the period was shortened to two or three days (Zohary, 1969). Gatherers would have needed to be as timely in their harvest as today's farmers, but the harvest season was lengthened somewhat by differences in time of maturity among different cereal species and by elevation differences in the hilly Levant. Staggered harvests would have allowed people to amass large quantities of grain with a relatively long shelf-life. At the heart of the wild cereals' native range, people could obtain reliable harvests from naturally re-seeded stands; it is therefore most likely that the west Asian grain crops were first domesticated at the fringes of their progenitors' distributions (Harlan and Zohary, 1966). It was there that people would have found intentional sowing most helpful in maintaining stands of their proto-crops. At the same time, Willcox (2005) emphasized the patchiness of wild wheat stands throughout the area where emmer wheat was domesticated. People may have felt some incentive to sow seed, thereby initiating domestication, in any productive localities in that area where wild wheat was not already growing.

A study by Hillman and Davies (1990) deserves to be discussed at some length, because it takes into account many of the factors that affect methods and rates of domestication in grain crops. They started by calculating that the rare, recessive mutations for non-shattering that were necessary for domestication of the west Asian cereals were likely to have appeared once every 5 to 20 years in a typical-sized plot tended by an early cultivator. In predominantly self-pollinating wheat and barley, plants homozygous for recessive non-shattering alleles would have appeared the following

season. At that point, they write, "farmers gathering their first seed stocks from wild stands will have been totally unaware of the existence of these tough-rachised mutant forms, and they would have remained oblivious of them as long as the crop stayed in its essentially wild state."

Beating spikes or panicles into a basket is the most time-efficient way to harvest wild grain crops (Hillman and Davies, 1990), but it does not apply selection pressure for non-shattering. Harlan (1967) famously collected wild cereals at the rate of 1 kg/hr by hand-stripping of spikes, but that method would not select effectively against shattering either (Hillman and Davies, 1990). Sickling or uprooting ripe or partially ripe crops does apply selection pressure, because it shakes loose some seed from wild-type plants, seed that is lost to the harvester. Hillman and Davies (1990) found experimentally that a consistently low 40 percent of wild-type seed was recovered by sickling or uprooting. Under those conditions, selection would strongly favour genes for non-shattering.

In their simulations, such strong selection intensity, combined with the high degree of self-pollination typical of wheat and barley, would have resulted in complete fixation of a recessive non-shattering gene within 20 to 30 harvest seasons, if people sowed seed each year on 'virgin land'. They further predicted that even if early farmers inadvertently relaxed the selection pressure by harvesting less fully ripened plants or repeatedly sowing on the same land, domestication would have been completed within two to four centuries. It is no wonder that we know so little about the mechanics of domestication, according to Hillman and Davies (1990). If it came and went as quickly as they envisioned it, the process was "unlikely to be preserved on

most Mesolithic or Neolithic [archaeological] sites as a recognizable progression”.

Having assumed in their analysis that initial domestication was entirely unconscious, Hillman and Davies (1990) then demonstrated that even if Neolithic farmers had practised intentional selection, they could not have greatly speeded up the process. With conscious selection, people could have done no better than halve the length of time required for domestication, because they could have started selecting only when the mutants were frequent enough to be obvious, perhaps at a frequency of 1 to 5 percent of the stand. By that point, the frequency of mutants had already passed through a lag phase and was poised for a rapid increase in frequency, even under unconscious selection.

What if, because of a thunderstorm or perhaps an excessive delay in harvest, the only intact spikes from which new seed stocks could be recovered were those of mutants? Could domestication have occurred in a single season? Hillman and Davies (1990) discounted this possibility, based on variation in ripening time and the likelihood that birds or other animals would find the isolated spikes before humans did. Nevertheless, any environmental factor that hastened shattering could have increased the selection pressure and speeded up domestication.

Hillman and Davies's argument begs the question of why early cultivators resorted to sickling or uprooting, if beating is the most time-efficient harvest method for wild cereals. They suggested three reasons that sickling or uprooting apparently was preferred at some point: (1) it recovered more seed per unit land area (which, as people became more settled, may have become a more important criterion than seed quantity per unit time); (2) it permitted utilization of the straw for fire-lighting and brick-making;

and (3) it may simply have become customary during a series of wet summers when wild cereals did not shatter as readily and the beating method of harvest was inadequate.

When wild cereals of west Asia shatter, their morphologically distinct basal spikelet remains attached to the culm. That spikelet would have been recovered by harvesters who sickled or uprooted plants, but not by those who gathered already-shattered spikelets from the ground. Basal spikelets might also have been left behind by hand-stripping, but that technique requires that grain be harvested before it is fully ripe, to avoid loss through shattering. Among wild barley and wild emmer remains from four archaeological sites greater than 11 000 years old, Kislev, Weiss and Hartmann (2004) found no basal spikelets and a miniscule number of unripe grains. These observations, they maintained, point to ground collecting as the original harvest method among pre-agricultural people of the region. The authors experimented with ground collection, finding that at any time during the region's rainless summer they could pick up large clumps of spikelets by grasping the upward-pointing awns.

Kislev, Weiss and Hatmann (2004) reasoned that after the first autumn rains, ground gatherers would have noticed seedlings sprouting from spikelets, and that sight would have inspired them to sow a portion of their harvested seed. Of course, sowing of ground-collected seed would have selected not *against* but *for* shattering. Kislev, Weiss and Hatmann (2004) do not speculate on how the transition to sowing of non-shattered seed occurred, but a scenario based on their results comes to mind. In collecting seed from the ground, people would have been moving slowly through stands of wild cereals long after full ripening. Any tough-rachised mutant

with its spike still intact atop the culm may have attracted their interest, and they may well have collected it for sowing in a special plot; if that happened, it would have been a very early case of intentional breeding.

Using lentil (*Lens culinaris*) as a model, Ladizinsky (1987, 1993) showed how domestication of west Asian legumes might have followed a sequence different from that of cereals. He noted that wild lentil (*L. orientalis*) plants are tiny, requiring that an estimated 10 000 plants be gathered in order to obtain one kilogram of clean grain. Therefore, lentils could not have been a major part of the gatherers' diet, as were cereals, which could be gathered much more quickly (Harlan, 1967). Furthermore, Ladizinsky argued, there would have been no incentive for sowing; an incipient lentil farmer would have had to sow their entire harvest simply to produce another crop of equal size. That is because each wild lentil plant produces only about ten seeds, of which only one seed on average will germinate the first year, given the seeds' strong dormancy.

Lentils and perhaps other pulses differed from cereals, argued Ladizinsky (1987, 1993), in that at least partial domestication had to precede sowing. Through intensive harvesting, people would have drastically curtailed natural reseeding, thereby leaving fields more open to fast-germinating mutants and selecting against seed dormancy. Once dormancy was largely eliminated and people were able to sow seed to good effect, selection pressure for indehiscent, non-shattering pods would have been feasible. But traditional harvesters in southwest Asia uproot lentil plants before full maturity, then sun-dry and thresh them—a process that largely avoids shattering. If that was the harvest method in Neolithic times, selection for non-shattering would have been much weaker in legumes than in cereals.

Zohary (1989) forcefully rejected Ladizinsky's model, arguing that legume and cereal domestication followed very similar paths, starting with cultivation and sowing of the wild progenitors. He maintained that wild lentils can produce not ten, but rather 40 to 70 seeds per plant when well tended in fertile soil; therefore, people might well have found sowing to be worthwhile. Ladizinsky (1989a) responded that the fields of early, inexperienced cultivators would not have been very conducive to high yields, and that conditions would have been more like those encountered by wild legume stands than those in Zohary's (1989) tilled, weeded and well fertilized experiments.

Some researchers have concluded that domestication was a rapid process in the crops they have studied, certainly when compared with evolution through natural selection. Harter *et al.* (2004) estimated that in sunflower, "genetic composition of the domesticates has changed at least 50-fold faster than the wild populations since they diverged." Wang *et al.* (1999) calculated that it took approximately 300 to 1 000 years to completely fix the crucial domestication gene *tb1* that telescopes the lateral branches in maize. Other studies indicate a somewhat slower process. Jaenicke-Despres *et al.* (2003) found that as far back as 4 400 years ago, modern mutant alleles of the genes *tb1*, *pbf* (prolamin box binding factor) and *su1* (starch debranching, which affects tortilla quality) were common. But that was almost 2 000 years after the date of the oldest known archaeological evidence of maize domestication. Based on archaeological evidence from northern Syrian Arab Republic and southeastern Turkey, Tanno and Willcox (2006) argued that "wild cereals could have been cultivated for over 10 000 years before the emergence of domestic varieties", partly because Neolithic cultiva-

tors may have taken care to harvest grain before any of it began shattering. That would have reduced the selection pressure on alleles for non-shattering. Fuller (2007) argued that during the domestication of rice, einkorn and barley, selection for grain size proceeded faster than selection for non-shattering, but that grain-size increases were much slower in pearl millet and leguminous crops. Surveying the archaeological data, he found significant grain-size increases in Asian cereals within a matter of centuries, a result, he reasoned, of the advantage large seeds had when early cultivators sowed them deeply in tilled soil. In contrast, he concluded, shattering was not fully eliminated for 1 000 to 2 000 years.

Gepts (2002) concluded that models based on a few genes can estimate only the minimum duration of the domestication process, whereas archaeological data provide a 'reality check'. Physical remains often indicate that domestication took much longer than would be predicted by genetic models.

Whether farmers' transformation of various wild plants into crops went quickly or slowly, it was not always permanent. False starts on the road to domestication may have been common. At sites in west Asia and North America, groups of people practised relatively intense cultivation of wild progenitors, and even partially domesticated some species before eventually abandoning them; those orphaned plant populations did not contribute to the founding gene pools of today's crops (Weiss, Kislev and Hartmann, 2006). In one dramatic example of that phenomenon, domestic rye may have arisen 10 000 years ago in the Syrian Arab Republic and Anatolia, only to disappear for several millennia before being re-domesticated in Anatolia and Europe (Willcox, 2005).

1.4 THE DOMESTICATION BOTTLENECK AND GENE FLOW

The number of domestication events experienced by individual species has long been a favourite topic of debate among researchers. Blumler (1992) and Zohary (1999) have argued that multiple domestications within a species have happened only rarely. They pointed out that genetic variation is much greater in most wild progenitors than in derived domesticates. They also noted the rarity of parallel domestication in related taxa above the species level. For example, people selected einkorn wheat (*Triticum monococcum*), pea (*Pisum sativum*: Ladizinsky, 1989b), emmer wheat, maize and chickpea from their wild ancestors while leaving sympatric, phenotypically similar, closely related species undomesticated.

Matsuoka *et al.* (2002) detected a single domestication event in maize by analysing microsatellite variation. Based on amplified fragment length polymorphism (AFLP) variation, Heun *et al.* (1997) concluded that einkorn was domesticated only once, in southeastern Turkey, but that result has been challenged on archaeological and climatic grounds (Hole, 1998; Jones, Allaby and Brown, 1998). Willcox (2005) summarized archaeological evidence indicating that einkorn, emmer and barley all experienced multiple domestications.

Noting that evidence for single versus multiple domestication events in Andean crops such as amaranth and peppers is inconclusive, Blumler (1992) cited several factors that render it "seldom if ever possible to rule out multiple independent invention": the progenitor species may have diversified after domestication of the crop; loci used in comparing the wild and cultivated types may be linked to loci affecting traits of domestication or ecological adaptation; or sampling by researchers may be unknowingly

biased. In a simulation study, Allaby and Brown (2003) showed that analyses relying on anonymous genetic markers might provide seemingly conclusive evidence that a species was domesticated through a single event when it was in fact domesticated more than once.

The people of South America and those of Mesoamerica probably took the common bean through two separate domestications (Sauer, 1993). Xu *et al.* (2002) concluded, on the basis of chloroplast DNA variation, that the soybean had a polyphyletic origin, but cluster analysis of nuclear random amplified polymorphic DNA (RAPD) markers indicated that local differentiation of soybean occurred in farmers' fields after domestication was complete (Xu and Gai, 2003). In any case, the soybean passed through a very tight domestication bottleneck (Hyten *et al.*, 2006). Barley is unusual among the west Asian cereals in harbouring a high level of genetic polymorphism. Ladizinsky (1998) concluded that early cultivators must have selected at least 100 non-shattering mutant plants in order to capture the level of variability seen in barley. Because the crop is highly self-pollinated, post-domestication gene flow from its wild progenitor *Hordeum spontaneum* cannot have accounted for the high degree of variability that is evident today (Ladizinsky and Genizi, 2001).

Whatever the initial number of domestication events, it is clear that because of genetic drift the diversity of most crop species is low compared with that of their wild ancestors. Drift results from a genetic 'bottleneck', usually at the point of initial domestication—the well known 'founder effect' (Ladizinsky, 1985). A bottleneck could also be caused by some later event, but generally would have to occur very early in the history of the crop, before peo-

ple had a chance to distribute it over a large geographical area.

The founder effect often occurred when domestication depended upon rare mutants, but it was most severe when natural amphiploids (doubled interspecific hybrids) were domesticated. A rare amphiploid taken under human care, as was bread wheat, would have represented a gene pool consisting of a single plant—the tightest possible genetic bottleneck (Cox, 1998).

Tenaillon *et al.* (2004) found that loss of diversity in maize relative to teosinte was only 20 percent for putatively neutral loci, compared with 65 percent for loci affected by selection for traits of domestication. They estimated that the bottleneck that caused this mild contraction of variability had a ratio of population size to duration ranging from approximately 2 to 5. That is, the bottleneck population might have consisted of 10 000 plants over 2 000 generations, or perhaps 2 000 plants over 1 000 generations. Based on data from the *Adb-1* locus, Eyre-Walker *et al.* (1998) estimated a bottleneck size/duration ratio for maize of approximately 2; assuming that domestication took 300 years—similar to the duration estimated for einkorn wheat—they envisioned a bottleneck population of only 600 plants.

Sunflower apparently went through a 'substantial' domestication bottleneck, with inbreeding levels of Native American landraces varying from 0.3 to 0.5 (Harter *et al.*, 2004). Abbo, Berger and Turner (2003) counted three successive bottlenecks that tightly restricted the genetic variability of the chickpea crop from its earliest days onward: the highly restricted distribution of its wild ancestor *Cicer reticulatum*; the founder effect resulting from domestication; and an early shift by west Asian farmers from autumn to spring sowing of chick-

pea (to avoid crop loss due to the *Ascochyta* blight disease). That shift required selection of plants without a vernalization requirement. This third bottleneck, which, they argue, occurred early in the crop's history, affected chickpea uniquely among the major west Asian crops. However, it reminds us that many species may have passed through bottlenecks caused by intense, early farmer-directed selection for traits other than seed non-dispersal and lack of dormancy.

Haudry *et al.* (2007) found that domesticated emmer wheat showed a 70 percent loss of nucleotide diversity relative to its progenitor *Triticum dicoccoides*. Durum wheat, derived by further selection from emmer, showed an additional diversity loss, for a total loss of 84 percent. Bread wheat's diversity unexpectedly showed only a 69 percent loss relative to *T. dicoccoides*, suggesting extensive introgression from tetraploid wheats during the 8 000 years since the origin of bread wheat.

Finally, we should take note of a much more recent, possibly catastrophic, bottleneck. Clement (1999) documented 138 Amazonian plant species—the bulk of them either fruits, nuts or vegetables—that were in 'an advanced state of domestication' at the time of the first contact with Europeans five centuries ago. Because these species had become to some extent dependent on humans for their propagation, Clement maintains that the cataclysmic post-1492 loss of 90 to 95 percent of the area's human population resulted in an approximate 90 percent loss of genetic diversity in plant species then under cultivation.

Introgressive hybridization between domesticates and their wild or weedy relatives has often expanded genetic diversity, counteracting the effects of the domestication bottleneck. Hybridization among domestic, weedy and wild populations is

often an important source of new variation in crops (Harlan, De Wet and Price, 1973; Small, 1984). People tend to remove from a field those weedy hybrids that do not suit their needs, and those weeds tend to be less competitive in the natural environment as well. However, when weeds managed to backcross to crop plants, their less weedy-looking progeny might well have escaped the early cultivator's hand or hoe, remaining in the domesticated population and exchanging genes with it. Weeds often migrate over larger areas than domesticates and jump from one domesticated population to another, exchanging genes along the way (Small, 1984).

Sang and Ge (2007) attempted to reconcile seemingly contradictory evidence regarding the origin of the two rice subspecies *indica* and *japonica* by showing that the current genetic situation could have arisen from either one or two initial domestications, followed by gene flow from the two potential wild progenitors or between the partially domesticated subspecies, or both. It follows, they wrote, that introgression practised by modern plant breeding programmes is, in effect, "the continuation of domestication".

Weeds unrelated to the crop have at times enticed humans to adopt and domesticate them as secondary crops. The ancestors of oats (*Avena sativa*) and rye (*Secale cereale*), for example, caught the eyes of cultivators while growing as weeds in European wheat and barley fields (Holden, 1976).

Through analysis of microsatellites, Matsuoka *et al.* (2002) determined that the genetic diversity of maize was expanded greatly by introgression from teosinte. Wilkes (1977) found maize farmers in the Nobogame Valley of Mexico encouraging the growth of teosinte near and even within their maize fields. They told Wilkes

that the teosinte germplasm makes kernels ‘more flinty and stronger’. Nobogame was the only area in which Wilkes found hybridization intentionally fostered, and, interestingly, it was the only place where the flowering times of maize and teosinte were somewhat synchronized. In other areas, people weeded out teosinte, but, at least in Chalco, they fed it to cattle as fodder, then inadvertently returned its seed to the field when applying manure. It is possible that such mechanisms also played a part in the introgression of teosinte genes into maize in the early phases of domestication.

Gene flow into crops has been important in crop evolution, but there is a much larger flow in the opposite direction: from the domesticate into the wild form. That would probably have been the case in Neolithic grain fields as well. Migration of large amounts of wild pollen into fields of self-pollinated crops was limited, and because pollen from the wild conveyed dominant genes for shattering, hybrid progeny were not likely to be collected or planted by farmers (Ladizinsky, 1985). At the same time, there is much evidence that genes regularly migrated out of fields and into wild populations (Ladizinsky, 1985; Harlan, De Wet and Price, 1973). Many studies have estimated hybridization rates by looking for crop-specific alleles in populations of the crops’ wild relatives growing at various distances from cultivated fields. They generally find surprisingly high rates, even hundreds of metres away (Ellstrand, 2003).

Differences among crop species in the sizes of their founding populations and subsequent opportunities for gene inflow from the wild have profoundly affected the levels of genetic diversity available to present-day plant breeders. Here, the

contrast between bread wheat and grain sorghum is instructive (Cox and Wood, 1999). Hexaploid bread wheat may well have originated from only one or two hybrid plants with genomic constitution ABD (Cox, 1998; Haudry *et al.*, 2007). The tetraploid ancestor (AB) had experienced only limited introgression from diploid plants, mostly of the A-genome species. Subsequent gene flow from AB into ABD wheat plants occurred to some extent (Haudry *et al.*, 2007), but gene flow from the extremely diverse D-genome donor *Aegilops tauschii* into bread wheat was either non-existent or extremely rare until it was done by twentieth-century plant breeders (Cox, 1998). Therefore, throughout the entire bread wheat species, there is limited genetic variability in the A and B genomes, while its D genome contains only a tiny fraction of the diversity found in *Aegilops tauschii* (Reif *et al.*, 2005).

In contrast, people of Africa have always grown grain and fodder sorghum in areas where the crop comes into close contact and interbreeds with wild sorghum races (Doggett and Majisu, 1968). They probably domesticated sorghum in various, widespread locales on multiple occasions, after which it was exposed to a continuous inflow of variability from the wild and weedy gene pools. As a result, grain sorghum today harbours vastly more genetic diversity than does bread wheat (Cox and Wood, 1999).

1.5 GENETIC CONSEQUENCES OF SELECTION

Van Raamsdonk (1995) proposed that most domesticated crops were developed through one of four genetic models (Table 1.2). The models differ in the role of ploidy and the degrees and mechanisms of reproductive isolation. Differences in genetic and

cytogenetic mechanisms meant that the key role of the domesticator varied from model to model (Table 1.2). For instance, with some crops, people functioned as matchmakers, bringing species into contact for the first time; in others, they enforced reproductive isolation.

Domestication tends to intensify the degree of inbreeding in seed-propagated species (Zohary, 2004). The inflorescences of tomato, chili and eggplant (*Solanum melongena*), among other species, were unconsciously selected by domesticators to have shorter styles, which promoted self-pollination (Rick, 1988; Pickersgill, 1969). Artificial selection can push largely self-incompatible populations toward self-compatibility (Rick, 1988), as is believed to have happened in types of *Brassica oleracea*, including summer cauliflowers (Thompson, 1976). Here, there is a kind of ratchet effect: disruption of

self-incompatibility systems is easily accomplished, whereas selection in favour of self-incompatibility would have been genetically complex and very difficult (Rick, 1988).

Inbreeding is a powerful accelerator of unconscious selection for traits governed by recessive genes. The fixation of genes for non-shattering that might have required only a few centuries in highly self-pollinated wheat and barley would, with 100 percent cross-pollination, have taken more than 8 000 years (Hillman and Davies, 1990)!

Each of two recessive alleles at different loci in domesticated rice that reduce seed shattering resulted from single-nucleotide substitutions (Li, Zhou and Sang, 2006; Konishi *et al.*, 2006). Five of six well studied domestication genes in maize, wheat, rice and tomato exhibit differences in regulatory regions between the wild and domestic alleles

TABLE 1.2

Four models proposed by van Raamsdonk (1995) by which the genetic mechanisms of crop domestication can be classified, along with his lists of crops that exemplify each model and some crucial points at which humans intervened in the domestication process under each model

Domestication model	Examples	Crucial actions by domesticators
Reproductive isolation between a diploid domesticate and its diploid wild ancestor is caused by internal barriers, post-zygotic barriers, external reproductive barriers or apomixis.	Soybean, common bean, chickpea, lentil, cowpea (<i>Vigna unguiculata</i>), lettuce (<i>Lactuca sativa</i>), citrus fruits (<i>Citrus</i> spp.)	Selection for self-pollination and against weedy hybrids; fostering of genetic drift
Development of crop-weed-wild complexes in which genetic information is exchanged more or less freely among diploid domesticates and their sexually compatible wild progenitors.	Maize, rice, barley, grape, sorghum, pearl millet, foxtail millet (<i>Setaria italica</i>), radish (<i>Raphanus sativus</i>), beet (<i>Beta</i> spp.), chili (<i>Capsicum</i> spp.), quinoa (<i>Chenopodium quinoa</i>)	Adoption of weeds that invade cultivated land; toleration or encouragement of weeds that can backcross to less wild cultigens
One or more rounds of hybridization and polyploidization occur among wild species prior to domestication.	Cotton, sweet potato, groundnut, tobacco (<i>Nicotiana</i> spp.), cucumber (<i>Cucumis</i> spp.), coconut (<i>Cocos nucifera</i>), alfalfa (<i>Medicago sativa</i>)	Selection at the polyploidy level
Interspecific hybridization involving at least one domesticated species is followed by polyploidization. Resultant amphiploids are reproductively isolated.	Bread wheat, potato, banana, coffee (<i>Coffea arabica</i>), yam (<i>Dioscorea</i> spp.)	Bringing formerly isolated plant populations into contact; selection and propagation of rare amphiploid plant(s) found in or near cultivated fields.
In some cases, domestication occurs through a combination of mechanisms from more than one of the above models.	Sugar cane, oat, <i>Brassica</i> spp., tomato (<i>Lycopersicon esculentum</i>)	—

(Doebley, Gaut and Smith, 2006). Whatever the nature of their mutations, alleles initially selected by domesticators often showed the simplest modes of inheritance. Many genes governing traits of domestication are recessive or additive, and would have been expressed more strongly among the progeny of plants that tended to self-pollinate most frequently. An increased tendency to inbreed may also have been an indirect result of selection for higher grain yield; self-pollination ensures seed and fruit development, especially if the new crop was transported out of the range of its natural pollinators.

Inbreeding also leads to greater within-line uniformity, but it is hard to imagine uniformity being a direct selection criterion for early domesticators, as it would have required that they plant out the progeny of individual plants in separate plots. It is almost certain that they practised mass selection, not progeny testing. But genes promoting self-pollination might have been favoured in very small populations maintained in isolation. Such isolation could have resulted from individual preferences, or perhaps community customs, such as a belief in parts of Guatemala that plants should be grown only from seed produced on the same plot of ground (Pickersgill, 1969). 'Colour coding' (Wilkes, 1989) based on endosperm pigmentation may have helped farmers maintain small, genetically isolated maize populations.

Strong selection to reinforce inbreeding did not occur in crops that were propagated vegetatively; in them, self-incompatibility and out-crossing remained common (Zohary, 2004; Rick, 1988). Through clonal propagation, cultivators could produce large, genetically desirable populations. In contrast to seed-propagated species, in which human selection for improved grain harvests also reinforced meiotic stability,

selection in vegetatively propagated species allowed, or even encouraged, variations in chromosomal number and structure, disrupting reproductive development to varying extents (Zohary, 2004).

In a simulation study, Le Thierry d'Ennequin *et al.* (1999) predicted that to fix a full complement of alleles for domestication, either linkage among loci or a significant degree of reproductive isolation is essential. By their models, in predominantly self-pollinating species subject to little migration, people easily fixed alleles at unlinked loci through selection; however, in species with a high degree of out-crossing, human selection favoured blocks of linked domestication genes.

Empirical experiments have demonstrated that linkage among domestication loci is common, regardless of breeding system (Paterson, 2002). In crosses between pearl millet and its wild progenitor *Pennisetum mollissimum*, Poncet *et al.* (1998, 2000, 2002) found linkage among genes affecting spike characters—important components of the domestication syndrome—but not among genes affecting vegetative characters or total grain yield. Burke *et al.* (2002) mapped 78 quantitative trait loci (QTLs) affecting 18 traits in a cross between sunflower and its conspecific wild progenitor. The domestication-associated loci were spread across 15 of 17 linkage groups, but were highly clustered within those groups. Both pearl millet and sunflower are highly cross-pollinated. In rice, a selfing species, QTLs affecting domestication traits also tended to be clustered in linkage groups (Cai and Morishima, 2000).

Wright *et al.* (2005) found that 2 to 4 percent of the genes in maize have probably undergone artificial selection. Much of that selection, especially for the genes involved in plant growth and auxin response that are responsible for the dramatic differences in

plant morphology between teosinte and maize, appears to have occurred during initial domestication. Those growth-pattern genes were clustered, whereas genes affecting amino acid composition were not.

In wild progenitors, significant numbers of agronomically beneficial alleles are often embedded in linkage blocks with other, deleterious, genes. Such desirable alleles tended to be left behind during domestication. For example, in a tetraploid wheat population, Peng *et al.* (2003) found 24 percent of positive QTL effects to be coming from the wild *Triticum dicoccoides* parent. By breaking up such linkage blocks, modern-day breeders can utilize genes that were 'hidden' from early domesticators.

Gepts (2002), surveying studies of domestication traits in maize, pearl millet, common bean and rice, found an average of 2.2 to 5.3 loci per trait. Those loci accounted for only about 50 percent of the total variation per trait, and loci affecting all traits were spread among 3 to 5 linkage groups per species, indicating rather diffuse genetic control. Paterson (2002) found similar patterns in the QTL-mapping literature on sorghum, rice, maize and tomato. He concluded that loci with larger statistical effects were probably biologically significant as well, because they occurred in similar genomic regions in different crop species (Paterson, 2002; Paterson *et al.*, 1995).

During domestication, people may have unknowingly favoured plants or populations with a higher inherent rate of recombination per unit of physical chromosomal length. A comprehensive survey showed that mean numbers of chiasmata per bivalent were significantly higher in 46 crop species than in 150 wild species (Ross-Ibarra, 2004). This result was in accord with theory, the bulk of which predicts that an increased rate of recombination is

favoured during periods of rapid evolutionary change, of which domestication is an extreme example. Ross-Ibarra found no support for the alternative possibility: that species with higher recombination rates are 'pre-adapted' to domestication.

Even under domestication, the recombination rate is under stabilizing rather than unidirectional selection, because the same high rates that help break up repulsion linkages also speed up the decay of co-adapted gene complexes (Dobzhansky, 1970). Indeed, Ross-Ibarra's comparison of crop and wild species provided evidence for selection against excessive recombination. There are, of course, other mechanisms for maintaining favourable multilocus combinations, including paracentric inversions (Dobzhansky, 1970) and self-pollination (Clegg, Allard and Kahler, 1972).

1.6 INTENTIONAL SELECTION

Although crops were domesticated through largely unintentional selection, there is little doubt that the domesticators quickly became aware of their own ability to change the phenotypic composition of their crops from generation to generation. Genetic modification, once initiated, spread in ever-widening ripples through plant genomes. Sowing spurred unconscious selection for traits like non-shattering; changes caused by unconscious selection prompted observant farmers to practise intentional selection; and intentional selection for one trait often affected other traits as well, through linkage and pleiotropy. Studies of a grain-quality trait in rice show that human selection at a single locus can exert very strong selection pressure on a large chromosomal region surrounding it, causing a so-called 'selective sweep' that can affect other traits much more strongly than would natural selection (Olsen *et al.*, 2006).

From the dawn of agriculture until the twentieth century, farmers acted as plant breeders, working almost exclusively through mass selection; that is, by ensuring that some individual plants made a proportionately greater genetic contribution to the following generation than did others. Natural out-crossing would have been frequent enough, even in highly self-pollinating species, to generate useful genetic recombinants. Early plant breeders worked without the benefits of progeny testing or replication, both of which can enhance gain from selection, but they had two other important factors working in their favour: time and ecosystems. Even small gene-frequency changes from year to year translated into large improvements when they continued over vast numbers of growing seasons. And plant populations upon which people exerted gradual selection in a particular locality, through the full range of weather conditions and pest, pathogen, weed and intercrop populations that the locality had to offer, were bound to be resilient and reliable food producers.

When people applied direct selection pressure for some traits, whether intentional or unconscious, they put indirect selection pressure on others. For example, attached glumes increase seed dormancy, so selection for non-dormancy may have increased the frequency of free-threshing plants. Deep sowing may have favoured larger-seeded genotypes (Fuller, 2007), which, in turn, would have had lower grain protein concentrations via dilution. Selection for greater allocation of resources to reproductive growth (higher harvest index) could have increased susceptibility to pests (Rick, 1988). Because plant parts growing from the same meristematic regions exhibit allometric growth, selection to increase the size of one organ generally

affected others; for example, selection for larger spikes in the cereals produced wider leaves and thicker culms as well.

Smartt (1969) catalogued the many traits for which early domesticators applied selection pressure in species of *Phaseolus*: a reduced number of lateral branches (to avoid excessive tangling in fields where beans were meant to climb maize plants); more robust leaves and stems; larger flowers; increased photoperiod sensitivity; increased pod and seed size; greater permeability of the testa; and reduced pod dehiscence. However, in examining four cultivated species, he found that not all of those traits were affected in every species.

Chang (1976a, b) noted a similarly increased size of vegetative organs and kernels in rice, along with a more extensive root system; higher tillering capacity; synchronization of tillering; more panicle branches; a longer grain-filling period; tolerance to non-flooded conditions; and loss of pigmentation. However, increases in kernel size and harvest index associated with domestication of rice were less than those in most other cereals (Cook and Evans, 1983). In several species of chili (*Capsicum*), people rejected erect-fruited wild plants in favour of mutants with pendant fruits, which were hidden under the foliage canopy and therefore protected from bird damage (Pickersgill, 1969).

Maize is often recognized as a crop that underwent some of the most remarkable morphological changes during domestication, but, as in most crops, the most obvious transformation was in its reproductive structures. In the words of Iltis (2000),

Cover the ears, and it sometimes takes a specialist to tell teosinte from maize ... But compare a many-rowed, 1000-grained ear of maize to a 2-rowed, 5-to-12-grained ear of teosinte – and be perplexed! How

could such a massive, useful monster be derived from such a tiny, fragile, inedible, useless mouse?

Perhaps just as surprising is the finding that morphological differences between maize and its wild ancestor are under relatively simple genetic control (Doebley and Stec, 1993).

Maize is not the only species whose reproductive structures evolved into monstrosities under the guiding hand of early breeders. For example, pearl millet's wild ancestor has heads measuring no more than 10 cm in length, but from it, early breeders selected cultivars with heads up to 2 m long (Harlan, 1989b). In bringing about the visually dramatic domestication of the sunflower, Native Americans selected for the fusion of many smaller heads into fewer, larger ones. People worldwide selected for often dramatically larger reproductive structures in vegetable and fruit crops.

Plant breeding theory, as well as observation of crop domesticates, tells us that the first breeders had their biggest impact on traits that (i) were of the most intense interest to the people who used the plants for food; (ii) were under relatively simple genetic control; and (iii) had a relatively high heritability on a single-plant or single-propagule basis. Therefore, humans altered the appearance and food quality of the harvested product more rapidly than they did traits such as yield per unit area. Contrasting intentional selection with the unconscious selection that preceded and paralleled it, Harlan, De Wet and Price (1973) wrote:

Deliberate selection adds new dimensions to the process [of domestication]. Human selection may be more intense and absolute and is often biologically capricious or even whimsical.

They went on to list a bewildering array of food products and processing tech-

niques, all of which were certain to reveal genetic variation in the crops upon which they were practised.

Human selection for nutritional quality of crop domesticates occurred in the context of other crops that were evolving simultaneously. The most commonly cited example is the complementarity of amino acid profiles in cereals and legumes. Selection among and within species was a matter of health, even life and death. Indeed, Wilkes (1989) declared an 'ethnobotanical rule', stating that when "crops are consumed and not sold, a reasonable level of nutritional adequacy has evolved and been maintained". Neither the single-minded selection for high grain yield per unit area nor the pursuit of high-lysine maize would have occurred to a Mesoamerican farmer of 3 000 years ago.

Plant breeding requires differential phenotypic expression. For example, people could not venture very deeply into the domestication and improvement of a species as a food source if its consumption always resulted in serious illness or death. Indeed, the process by which the sweet almond was derived from its cyanogenic ancestor is still shrouded in mystery (Ladizinsky, 1999). People could begin selecting for lower toxicity once they accomplished at least partial breakdown of toxins through cooking. Other strategies were developed farther back in the human family tree. Geophagy—consumption of clays—is practiced by at least eight primate species (Johns, 1989). People commonly eat clay along with wild potatoes (Johns, 1986) and yams (Irvine, 1952) to de-toxify them, and the practice might have provided latitude for early domesticators to distinguish among different degrees of bitterness without falling too ill too often. Once foods were rendered edible via such practices, selection for lower

toxicity might have been furthered simply through dilution, as people selected for greater root or tuber size (Johns, 1989).

In the potato, there is a remarkable coincidence between toxic thresholds and human capacity for detection. The plant's most common glycoalkaloid is toxic in concentrations above 200 ppm (Johns and Keen, 1986), and tubers with a concentration of greater than 140 ppm are considered unpleasantly bitter by North Americans (Sinden and Deahl, 1976). In contrast, the Aymara Indians of the Andes classify potatoes with concentrations above a range of 200 to 380 ppm as bitter (Johns and Keen, 1986). Because several wild and cultivated *Solanum* species are crucial sources of calories in the Andes, the Aymara and other indigenous people may have developed a taste for somewhat riskier genotypes. Selection for improved nutritional quality can also work against improvement of other traits. For example, potato populations selected for lower glycoalkaloid concentrations had lower resistance to potato leafhopper (Sanford *et al.*, 1992).

In a seeming paradox, cyanogenesis (the production of poisonous hydrocyanic acid) is more common in crop plants than in the plant kingdom as a whole. Jones (1998) noted that 16 of the world's 24 leading crop species (by total production) are cyanogenic in some plant part(s) at some stage of growth. Cyanogenesis, Jones observed, is an important mechanism of resistance to pests. People looking to become cultivators, given a wide range of plant species from which to choose, would probably have been attracted to plants that had not already been damaged or largely consumed by other species. Having the unique ability to eliminate cyanogenic glycosides by grinding, steeping and cooking, humans took advantage of plants that could not

be consumed by rival species. Reducing the mean toxicity to a safer level allowed them to detect and exploit genetic variation within species.

Toxins aside, the simplification of diet that followed the expansion of agriculture appears in itself to have caused a decline in overall human health (Kates, 1994). Gepts (2002) even implies that had regulatory agencies existed in Neolithic times, domesticated plants might well have failed to receive approval!

Selection for food quality involved more than nutritional considerations. Where muscle and fuel power were resources not to be squandered, genotypes that produced food with lower energy requirements for processing and cooking may have been more highly valued. For example, Harlan (1989b) described how modern cultivators in Mali select sorghum heads with softer grains for ease of pounding, but also keep hard-seeded, more insect-resistant types, for longer-term storage.

In some cases, people may have utilized the progenitor of a crop for one purpose only to find, once they became more familiar with the species, that it possessed one or more other traits that warranted its full domestication. For example, many East Asian plants may have been used for medicinal purposes before being domesticated for food production (Chang, 1970). Bohrer (1972) maintained that the wild grasses that eventually gave rise to cereal crops were originally cut or uprooted for use as animal fodder. However, Hillman and Davies (1990) disputed that idea, arguing that at the time and place of west Asian crop domestication there were no domestic cattle and few domestic sheep or goats. The squash (*Cucurbita pepo*) may have been domesticated first for its seed, or for its hard gourds to be used as containers; once

fleshy vegetable genotypes were selected, people may have stopped growing the gourd types to prevent the appearance of bitter squashes through cross-pollination (Heiser, 1989).

Iltis (2000) concluded that teosinte was first grown by Mesoamericans for its green shoots and sugary pith and not for its grain, which remained enclosed in a hard fruit-case. Later, through increased contact with teosinte as a snack or vegetable, an alert cultivator may have noticed an extremely rare, ‘grain-liberating’ mutant—on possibly a single occasion—thus kicking off the process of maize domestication.

Amplifying Iltis’s hypothesis, Smalley and Blake (2003) suggested and then defended a possible sequence of events by which teosinte domestication proceeded: (1) people began casually harvesting and chewing the sweet stalks and shoots of *Zea* plants; (2) they found that they could extract more juice by mechanical mashing; (3) to preserve the juice, they adopted fermentation techniques already in use with other species; (4) they spread maize far and wide, as a new resource for making alcoholic beverages; and, finally, (5) to expand *Zea* cultivation, they began sowing harvested seed. Once that sequence proceeded as far as step (5)—along with the discovery of the free-kernel mutant—domestication of *Zea mays* as a grain crop would have followed quickly. But the time between its very first utilization by chewing and its full domestication as a grain may have been as long as 2 500 years (Smalley and Blake, 2003).

Perhaps too often, researchers tend to portray the era of crop domestication as one of constant struggle against scarcity and hardship. DeBoer (2003) commented that the possibility of people first having utilized maize for sweet and fermented products.

...injects desirous human agents into the account, a palliative for the stern ‘food crises’ and ‘population pressures’ that haunt our angst-driven prehistories. How charming it would be to have a snack-and-party crowd, hassled by only an occasional aggrandizer or two, at the base of the Neolithic!

The initial domestication of crops prompted expansion of farming into new environments, where people continued selection under different conditions, while perhaps repeating the domestication process with new species. Although the ability to accumulate a large excess of grain during a brief harvest season provided, in itself, a strong incentive to settle in one locality for at least a good part of the year [as Flannery (1969) asked regarding a hypothetical community of Neolithic gatherers, “...after all, where could they go with an estimated metric tonne of clean wheat?”], people eventually and inevitably migrated. The ability to take with them a food source that doubled as the means of sowing future crops allowed people to expand agriculture into previously unsettled areas, where the crops encountered new selection pressures and the people encountered new species of plants.

Abandoned fields created by early shifting cultivation in tropical forests may have provided environments in which useful wild plants could survive and grow unusually well, possibly to become domesticates themselves (Piperno, 1989). Barley’s early maturity allowed farming at very high altitudes; pearl millet’s drought-hardiness extended agriculture into parts of India and Africa that receive 200 mm or less of annual rainfall; and maize brought more people into the sparsely populated, mid-altitude hill country of India and Pakistan (Harlan, 1972). However, once settled in new environments, thanks to a reliable

staple crop, people have not always sought out additional species for domestication; rather, monocultures are common on the fringes of agriculture (Harlan, 1972).

1.7 CONCLUSIONS

In recent decades, institutional plant breeders have come to realize the importance of integrating breeding methodology with farmers' knowledge. Doing so has benefits for breeders—whose selection goals become more embedded in the 'real world'—and for farmers, who come to appreciate better their own ability to change gene frequencies of their crops in favourable directions. This would appear to bring us full circle, to a time like that of agriculture's earliest days, when breeding and farming were fully integrated. But today's agriculturalists also have ten millennia worth of hard-won farming and breeding knowledge on which they can draw by working together.

The first plant breeders lived in pre-historic times, so they left us no direct accounts of the methods they used to domesticate and improve crops. As we have seen, many of our hypotheses about their activities are influenced by our knowledge of the methodologies that farmer-breeders have used in historic times. That is no accident. By extrapolating recent methods back to the origin of agriculture, we are acknowledging a 10 000-year-long, unbroken thread of skills and knowledge that is derived from growing plants for food while simultaneously breeding them for the future. Nevertheless, we should not forget that by coming to rely largely on domesticated plants and animals, we humans have also lost vast amounts of knowledge of other species and ecosystems; there is much that we could re-learn from hunter-gatherer societies of the present, the recent past and the days before agriculture.

Keen observation and use of genetic variation in plant species has been a hallmark of societies that depend directly on those plants, whether the people in those societies were hunter-gatherers, the originators of agriculture, or today's subsistence farmers. As the millennia have passed, knowledge has expanded and methods have evolved, but that thread remains intact. Today's institutional plant breeders also benefit from that accumulated knowledge. Although modern breeders' methodologies are often very different, they are rooted firmly in the past. They also utilize that major part of the first plant breeders' unwritten knowledge that survives in code, the genetic code of the plants themselves.

Had the original crop domesticators been familiar with the principles of genetics, the crop species that they handed down to history might have been even more profoundly transformed. Had they understood the hazards of genetic erosion or pest and pathogen epidemics, they might have domesticated a wider range of species and avoided the genetic bottlenecks that restricted variation in many crops from the very beginning. And could they have foreseen the devastating consequences of soil erosion and water contamination under long-term annual cropping (Cox *et al.*, 2006), they might have mounted an effort to domesticate resource-efficient perennial food crops.

Nevertheless, that relative handful of people was responsible for the most important turning point humanity has yet experienced, laying the foundation for the material and cultural world that surrounds us today. But in the evolution of agriculture, it has not been the case that superior knowledge and techniques continuously replace inferior ones. Knowledge survives from every era, all the way back to the origin of crops (and even well before), so that farmers, plant breeders

and all others who work in agriculture can draw upon it in the years ahead.

As it has turned out, the first plant breeders brought about changes in our own species that equal any they achieved with plants, and the plant breeding traditions they established have brought humanity, only in the past century, to a point at which we can study why and how they carried off their revolution, and learn from the answers.

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