CHAPTER 2

Sources of evidence for the origin and spread of domesticated plants

The study of the origin and spread of domesticated plants is an interdisciplinary venture based on evidence from numerous sources. Several disciplines, such as archaeology, botany, genetics, chemistry, anthropology, agronomy, and linguistics are involved (for review, *see* Harlan and de Wet 1973), yet the different sources of evidence vary considerably in reliability and relative weight. The modern synthesis leans heavily on two principal sources:

(i) information obtained through examination of plant remains retrieved from archaeological excavations; and
(ii) evidence gathered from living plants, particularly the main traits that evolved under domestication ('domestication syndrome') and the genetic affinities between the crops and their wild relatives.

Since 1950s major discoveries have radically changed our view on the origin of domesticated plants. They have transformed a realm of plentiful speculation and few solid facts into a well-documented field.

In the light of this, the contributions of several classical tools had to be fundamentaly reconsidered. Some sources of evidence, such as N.I. Vavilov's monumental studies of variation and distribution of crops (Vavilov 1949–50; 1987), had to be considerably revised and re-evaluated. Others, such as linguistic comparisons (widely used by de Candolle 1886), appear to have retained some relevance, even today. However, with the flood of archaeological documentation, genetic information, and new techniques from molecular science, those discoveries now carry less weight.

Readers who wish to acquaint themselves with some of the more recent research should consult Pearsall (2000) for archaeobotany, and Hancock (2004) for plant evolution, genetics, and crop sciences. All serve as a good sources for initial orientation.

The following sections review the main sources of evidence on which the modern assessment of crop-plant evolution is based. A list is given in Table 1.

Archaeological evidence

The primary contribution of archaeology to the understanding of crop-plant evolution is by the recovery of plant remains in archaeological excavations, and by identifying to what crop species they belong. The accumulated evidence contributes to answering the following questions:

(i) When and where do we find the earliest signs of domesticated crops?
(ii) How and when did the crops spread to attain their present distributions?
(iii) What were the early cultigens like?
(iv) What were the main changes in the crops once they were introduced into cultivation?
(v) Where and when did these changes take place?

Obviously the key to all answers is the availability of 'fossil evidence'; that is, sufficient amounts of dated, culturally defined plant remains amenable to analysis. The following sections survey the main conditions under which plant material survives in archaeological contexts. These are also listed in Table 2.

Table 1 Sources of evidence on the origin and spread of domesticated plants

I. *Archaeological evidence*

1. *Archaeobotany:* Identification of plant remains retrieved from archaeological excavations in connection with cultural associations and ^{14}C-dating. Determination of the earliest signs of domestication in these plants and their subsequent spread. Changes in crops in time and space. Crop assemblages in various cultures.
2. *Additional evidence*
   (a) Artefacts. Evaluation of: (i) dated tools associated with cultivation, harvesting, and processing of crops; (ii) cultivation artefacts such as irrigation canals, terraces, lynchets, plough marks, and cultivation boundaries.
   (b) Art. Early drawings, paintings, and reliefs of domesticated plants.
   (c) Palynology. Appearance of pollen grains of crops and weeds in dated cores or site contexts.
   (d) Weeds associated with agriculture.
   (e) Examination of ancient DNA extracted from plant remains.
   (f) Chemical analysis. Identification of crops by specific organic residues retained in charred seeds, ancient vessels, charcoal, etc.
   (g) Starch analysis. Identification of plant remains and usage of tools by the remains of starch granules.

II. *Evidence from the living plants*

1. *Search for the wild progenitors.* Identification of the nearest wild relatives of the domesticated crops by use of:
   (a) comparative morphology and comparative anatomy (classical taxonomy).
   (b) determination of genetic affinities by cytogenetic analysis.
   (c) determination of genetic affinities by DNA and protein resemblances.
2. *Distribution and ecology of the wild progenitors*
   (a) Geographic distribution of the wild relatives (including weedy forms).
   (b) Characterization of the habitats and the main adaptations of the wild relatives.
3. *Evolution under domestication*

Main trends of morphological, physiological and chemical changes. The range and the structuring of genetic variation in the crops and in their wild progenitors. Development of crop complexes (wild forms, weedy races, and cultigens). Methods of planting, maintenance, and usage.

4. *Additional evidence*
   (a) Genetic systems: characterization of the main systems operating under domestication, especially reproductive systems (including vegetative propagation).
   (b) Genetic interconnections between cultivars and wild relatives.
   (c) Intentional and unconscious selections.

III. *Other pertinent sources*

1. *Historical information.* Representation of the plants in art, documentation in inscriptions, tablets, manuscripts, and books.
2. *Linguistic comparisons.* Names of crops in various languages.
3. *Circumstantial evidence:* Geological, climatic, hydrological, limnological, dendrochronological, anthropological, and zoological indications on the initiation and spread of agriculture.

Charred remains

Charred (carbonized) remains are the commonest source of plant material in archaeological excavations that are available for analysis. Carbonization occurs on exposure to high temperatures, in most cases due to fires. Such heating (under a limited supply of oxygen) converts the plant's organic compounds into charcoal. Since bacteria, fungi, or other decomposing organisms do not affect charcoal, carbonized plant remains survive in most environments. This includes wet places where ordinary organic material decays rapidly. Carbonized plant remains in archaeological contexts are therefore not products of geological carbonization (true fossils). They represent only 'subfossil' elements charred by fire.

When slowly and mildly charred, wood, seeds, nuts, and sometimes even fleshy fruits, parenchymatous storage tissues, or ears of cereals, can still retain most of their morphological and anatomical features. The morphology and the microscopic anatomical structures are frequently preserved in astonishing clarity. This allows a reliable identification of the plant remains.

Table 2 Preservation of plant remains in archaeological excavations

I. Charred remains

1. Charred during handling:
   (a) near a hearth/oven
   (b) in a drying kiln
   (c) in a storage pit/silo (when cleaned)
   (d) in pottery fired in a pottery kiln
2. Charred by conflagration:
   (a) stored material
   (b) material embedded in daub, unfired bricks, and floors
   (c) thatching material
   (d) scattered or dumped material

II. *Plant impressions*

1. In pottery
2. In bricks and daub

III. *Parched remains*

1. In arid regions:
   (a) in caves
   (b) in tombs and pyramids
   (c) in clay
2. In temperate regions:
   (a) in sealed containers
   (b) in offerings embedded in walls

IV. *Waterlogged remains*

1. In lakes
2. In bogs
3. In wells
4. In sites covered by rising seawater level

V. *Biomineralization (Phytoliths)*

1. Opal
2. Calcium oxalate

VI. *Metal-oxide preservation*

1. Near silver
2. Near copper or bronze
3. Near iron

VII. *Petrified remains*

1. Siliceous mineralization
2. Calcareous mineralization

At fairly high temperatures (between 200 and 400 °C), carbonization causes characteristic deformations. In cereals, the most obvious changes are shrinkage in the length of the kernel together with a relative increase or 'puffing' in its circumference. Size reductions and specific patterns of swelling and/or cracking appear also after the charring of certain seeds. Moreover, some organs do not generally survive charring (e.g. Boardman and Jones, 1989, Märkle and Rösch, 2008, Kislev and Rosenzweig, 1991). Thus, the seed coats in leguminous plants or the glumes and pales in cereals are only recovered on special occasions because they disintegrate into powder in most cases. The intensity of the deformation depends, among other things, on the amount of humidity present in the seed (the drier the grains, the less they are deformed), the spread of the heating, and the temperatures reached.

Substantial information on the effects of heating on the seed of various plants has been gained experimentally by simulation of charring in laboratory ovens. Grains of various cereals and seeds of several pulses and flax have been the main elements tested. A determination of the amount of shrinkage in the seed of various crops also provides a better idea of the actual life-size dimensions of charred seed discovered in excavations (e.g. Märkle and Rösch, 2008, Braadbaart and van Bergen, 2005). Such experiments found that the degree of shrinkage or expansion of seeds vary according to the burning circumstances—temperature, time, degree of sealing from oxygen.

Charred plant material is recovered from the excavated sediment either by direct collection or by separation techniques. There are lucky discoveries of hoards of burnt grains stored in containers or silos, which sometimes contain almost pure grains. In order to recover scattered remains embedded in site deposits, the excavator frequently resorts to separation by flotation. Water flotation is the simplest and cheapest technique, and usually separates the scattered charred remains present in the deposits effectively. This frequently includes relatively large amounts of cereal chaff and wood charcoal as well as other types of plant material that rarely appear in silos. The introduction of flotation in the late 1960s, and especially flotation machines, revolutionized archaeobotany by allowing excavators to search for seeds rather than rely on caches, and also improved the efficiency of such separation.

Impressions on pottery, daub, and bricks

Imprints of grains and other plant parts on pottery contribute to documentation of crop plants in

archaeological sites. Such imprints are found particularly on handmade vessels. Pottery is one of the main diagnostic objects in archaeology, and imprints on pottery therefore have an obvious advantage, since once detected, they can be culturally classified and dated. However, imprints are frequently pressed into gritty, rough pottery (the common type of ceramics in early periods). On such a background the print is rather blurred, and unequivocal interpretation of such findings is often difficult.

Daub and bricks provide another source of plant impressions. Straw, chaff, and similar dry plant material is often added to the wet clay to act as a tempering element. Plant parts can also become embedded in the clay by chance, and even if the organic matter does not survive well, the impressions remain intact in the dried or fired clay. They can serve as negative moulds for casting and reproducing the former inclusions.

Desiccated plant remains

Preservation by desiccation, which blocks the processes of bacterial and fungal decomposition, occurs only under extreme dryness, so this source of evidence is confined to very arid areas. Such desiccated remains can be of particular importance because of their perfect preservation.

Outstandingly rich remains of dried plants have been discovered in Egypt. There, grains, fruits, vegetables, corms, and other parts of plants placed in pyramids and tombs give an excellent account of plant cultivation in the Nile valley during predynastic and dynastic times. During the last decade several later sites, from the Iron Age onward, were discovered along the Red Sea. The finds include soft parts of vegetables, leaves, and flowers, which hardly ever survive under other conditions. Several discoveries of desiccated material were also made in caves in the Dead Sea basin.

Waterlogged preservation

In Europe, valuable information has been obtained by examining plant material sunk in peat bogs or buried in the mud at the bottom of lakes, seas, or wells. Anaerobic conditions in these environments (and the presence of humic acids in bogs) act as effective preservatives, and plant remains in such places frequently retain their most delicate features. Excellent examples of waterlogged preservation have been found in lake-shore dwellings, submerged coastal areas, bottoms of old wells; as well as in the stomach contents of several human corpses retrieved from bogs in Denmark, Holland, and Germany. In some cases, the starch content of waterlogged-seed remains had vanished.

Preservation by oxides of metals

Bronze, silver, and iron occasionally act as effective preservatives for plant material buried close to them. In humid situations they produce metal oxides, which impregnate the plant remains. Because copper-, silver-, and iron-oxides are highly toxic to bacteria and fungi, they block decomposition.

Mineralization

This type of preservation is brought about by filling of cell cavities by inorganic substances or by replacement of the content of cell walls by minerals. The most common is mineralization by calcium carbonate ($CaCO_3$), silica, or phosphate.

Seed coats and fruit shells of several plants undergo natural mineralization. For example, stones of hackberry (*Celtis*) contain large quantities of $CaCO_3$ and the nutlets of several Boraginaceae accumulate silica. They sometimes survive in archaeological deposits without further means of outside preservation.

Phytoliths

Plants deposit the mineral opal ($SiO_2.nH_2O$) between or within their cell walls, which creates minute silica bodies. As the silica is an inorganic material, it does not decompose in the soil/sediment and therefore, it is one of the most dominant botanical finds in archaeological excavations worldwide.

Digested or partly digested remains

Preserved human feces (coprolites) constitute an only partly exploited source of evidence. Since

humans cannot digest cellulose, woody plant fragments, and shelled seed, they frequently retain their features after passing through the alimentary tract. Therefore when feces are charred, desiccated, or waterlogged, they often contain numerous identifiable plant fragments, which indicate the contents of the food in the tested human culture. Coprolite examination has already contributed significantly to American environmental archaeology. In the Old World this source of evidence has not yet been exploited extensively, although some results are already available (e.g. Hillman 1986; Dickson *et al.* 2000).

Chemical tests

Tar compounds present in charred plant remains and organic residues precipitated in ancient vessels can be identified by gas liquid chromatography, infrared spectroscopy, and other tests used by organic chemists. Such detection is possible even when these substances survived in minute traces. Significantly, some of these chemical compounds are specific to a single crop species or a single plant product. They can be used as diagnostic traits for crop identification (e.g. Evershed 2008).

Evidence from the living plants

Several principal contributions to the understanding of the crop-plant evolution are made by the study of the living plants.

A major contribution is the identification of the *wild progenitors* from which the various domesticated plants could have been derived. Once the wild ancestry of the crop has been determined the following examinations can be carried out:

(i) comparison of the cultivated varieties ('cultivars') with their wild counterparts in order to determine the main morphological, physiological, chemical, and genetic changes that took place under domestication;
(ii) assessment of the range and the structure of genetic variation (chromosomal, protein, and DNA polymorphisms) present in the wild progenitor and those found in the domestic derivatives;
(iii) assessment of changes in adaptation. Answers can be sought to the following questions: Which adaptations, that are vital under wild situations, have broken down under domestication? What are the new 'syndromes' that have evolved under domestication? Which selective forces are responsible for these changes?
(iv) delimitation of the distribution areas of the wild progenitors. This often provides information on the place of origin of the crops.

A second major contribution comes from examination of the crops and the ways they are handled, particularly under traditional ('primitive') systems of agriculture. Such studies include:

(i) patterns of variation in each crop and their geographies;
(ii) methods of cultivation and uses;
(iii) genetic systems operating in the various crops and the breeding traditions used; and
(iv) examination of the interconnections between the domesticated varieties and their wild relatives. The role of weedy races accompanying the crops is significant for this topic.

The following sections survey the main tools used for identification of wild progenitors. They also deal with some of the complications and problems involving the use of the wild relatives for elucidation of crop-plant evolution.

Discovery of wild progenitors

A principal goal in the study of the living plants is the identification of the wild progenitors of the crops; that is, the wild stocks from which the domesticated plants could have evolved. Plant domestication is a relatively recent evolutionary event. Therefore, one can expect that most wild ancestors are still alive and include forms similar to those that existed in pre-agricultural times. Indeed, the wild progenitors of the majority of the world's main food plants have already been identified. Many of them became known only during the last thirty-five years.

Several complementary tests are available for the identification of the wild progenitors of crops. They

all seek to determine which of the wild species, usually grouped together with the crop in the same biological genus, is most closely related to the domesticated plant.

(i) *The classical taxonomic approach* recognizes the wild progenitor by its close morphological resemblance to the crop. It sorts out the wild progenitor from among all the other wild taxa grouped in the crop's genus by its closest morphological and anatomical affinities to the cultigen. This is the oldest method. In some cases morphological comparison provides sound clues for the determination of ancestry. However, in numerous cases the wild background is taxonomically complex. Moreover, many crops exhibit a bewildering morphological variation, very different from the patterns present in wild plants, and this can be confusing in relationship analysis. Critical evaluation in such cases necessitates genetic verification; which can be obtained through cytogenetic analysis and by comparative molecular (DNA and/or protein) tests.

(ii) *Cytogenetic analysis* aims at elucidating the chromosomal affinities between the domesticated plant and the wild species. It also tests whether or not these wild taxa are separated from the crop (and isolated from one another) by hybrid sterility or other reproductive isolation barriers. Since evolutionary domestication is a recent development, the crop and its wild progenitor should retain a considerable amount of homology in their chromosomes. In contrast, other species grouped in the genus were probably formed long before the beginning of agriculture. As a result, they could have diverged considerably in their chromosomal constitution.

The principal tool of cytogenetics is a program of crosses between species followed by examination of inter-specific hybrids. Chromosome pairing in meiosis indicates the degree of chromosomal homology between the two parents. In most crops (particularly in grain crops), the cultivars show full homology and complete inter-fertility with only one of the wild species in the tested genus. Such a wild (congeneric) type is recognized as the ancestor (wild progenitor) of the crop. Together they comprise the 'primary' gene pool of the crop. In contrast, other members of the genus are frequently chromosomally distinct and are separated from the crop by strong reproduction isolation barriers such as cross-incompatibility, hybrid inviability, or hybrid sterility. Such species are often called 'alien species' and their chromosomes 'alien chromosomes'. They comprise the 'secondary' and 'tertiary' gene pools of the crops (Harlan and de Wet 1971, p. 107; Harlan 1992a).

To summarize, fully fertile hybrids showing normal chromosome pairing in meiosis point to close genetic relationship between the tested parents and implicate the wild plant in the ancestry of the crop. Lack of chromosome homology and the presence of strong reproductive isolation barriers indicate long-established genetic divergence and rule out the tested wild plant from being a progenitor of the crop.

Chromosome analysis of domesticated plants has frequently also to deal with complications due to *polyploidy*; i.e. the formation of new subspecies (or even new species) by doubling of chromosome numbers. Evolution by polyploidy is common in the plant kingdom. Many wild plants (including progenitors of domesticated plants) are not standard diploids but polyploid entities. One class comprises auto-polyploids which increased their chromosome number from the standard of two dosages (diploid condition) to three sets (triploids), four sets (tetraploids), or even higher levels. Such increases are not uncommon among vegetatively propagated crops (corm and tuber plants, ornamentals, and some fruit trees). A second class includes allo-polyploids; i.e. types formed by inter-specific hybridization followed by chromosome doubling. This combines the genetic contents of two (or even more) donor species in a new hybrid species. Bread wheat is a product of such fusion under domestication (pp. 47–48). Cultivated tobacco and the New World cottons had a similar mode of origin. In such crops, a special cytogenetic test known as 'genome analysis' helps to elucidate the polyploid origin and to identify the parental stocks, which donated their chromosomes to the new polyploid entities.

(iii) *Advances in molecular biology* provide critical tools for assessing the range of variation, and finding the structuring of genetic variation (genetic polymorphism) in crops and their wild relatives. This information can be used for determining the genetic

affinities and phylogenetic relationships between the cultivars and their wild relatives. As major breakthroughs in this field occurred since the publication of the third edition of this book some ten years ago, it receives extensive treatment in the present edition.

Since the 1960s, critical results have been obtained by testing protein variation in crops and their wild relatives, particularly enzyme variants (isozyme and allozyme polymorphism) and/or variability in storage proteins deposited in seeds (Soltis and Soltis 1989). Proteins are the primary products of the genes, and therefore their variability reflects differences in the hereditary material. Gel electrophoresis separation makes it possible to discern variation and differences in numerous proteins. Lately, detecting protein variability has become an outdated technique although it is time- and cost-efficient. Its relatively low output makes this technique less attractive than DNA-based marker systems.

Since the late seventies, large-scale analysis of DNA variation became possible in a wide range of techniques. The first major breakthrough for variability analysis was the development of restriction fragment length polymorphism (RFLP) technology. Restriction enzymes cleave the DNA strands at specific sites ('restriction' sites') into identifiable fragments. Individuals with identical site arrangements yield identical DNA fragments, while those that carry mutations in these sites produce different fragment patterns. Because restriction sites along the DNA strands of genes are numerous, polymorphism in these sites is enormous both within and between populations of crops and their wild progenitors (e.g. Havey and Muehlbauer 1989).

Another major breakthrough was made by development of the polymerase chain reaction technology (PCR), by which quantities of DNA fragments, large enough for variation analysis, are amplified from minute samples of target DNA and their specific primers. Indeed, PCR is used in almost all DNA polymorphism analyses. In the mid-nineties, combining PCR and RFLP resulted in a most popular technique, namely AFLP (amplified fragment length polymorphism, Mueller and Wolfenbarger 1999). Although it is still relatively expensive, this method is highly reliable and informative, and indeed many of the recent elucidations on crop origins such as wheats, barley, and chickpea were available through this procedure (Heun *et al.* 1997b; Badr *et al.* 2000; Özkan *et al.* 2002; Nguyen *et al.* 2004; Duc *et al.* 2010). Another technique that uses arbitrary primers for the PCR and needs minute amounts of genetic material is random amplified polymorphic DNA (RAPD). It is a straightforward method, but is relatively less reliable and informative. However, it reveals genetic diversity easily, as found, for example, in flax and in lentils (Sharma *et al.* 1996; Fu *et al.* 2002).

Another highly informative technique known as microsatellites, involves short DNA repeats that show high variation in repeat-number between individuals (Varshney *et al.*, 2005). Also known as SSR (simple sequence repeat), this method produces highly unique patterns that in fact are the basis for individual DNA fingerprinting in many different organisms including crops (Molina-Cano *et al.* 2005) and humans.

Direct DNA sequencing of the genetic text at target sites may also reveal variability between individuals. In general, it retrieves phylogenetic information from diversity in specific loci in the DNA, as manifested (for example) in the *sad2* locus in flax (Allaby *et al.* 2005), or the *btr1/2* loci in barley (Komatsuda *et al.* 2007).

Remarkable advances in sequencing technology have recently enabled comparisons of large DNA sequences that accordingly embed variations or point mutations in the form of single nucleotide polymorphisms (SNPs, Rafalski 2002). Such point mutations are abundant throughout the genome. They reflect DNA variability and were used recently to study diversity between and within crops and their ancestors as done for example in barley (Kanazin *et al.* 2002).

Today, the bewildering array of DNA markers and the ability of automatic sequencing of genes of interest in hundreds of individuals can be carried out in a very short time. This revolutionized our ability to trace and assess genetic and evolutionary relationships and construct reliable phylogenetic trees for crops and their progenitors.

Distribution of the wild progenitors

The wild relatives can frequently provide critical information about where domestication occurred.

In many crops, the progenitors occupy limited geographic territories—much smaller distribution areas than those of their domesticates. Because domestication is a recent development, it is safe to assume that the distributions of the wild forms (weeds excluded) have not undergone drastic changes since the beginning of cultivation. Delimitation of the wild relative's distribution thus marks the territory in which the crop could have been taken into cultivation. The narrower the distribution area, the more accurate the placement.

Fortunately, the distribution of the wild progenitor of emmer wheat—a principal Old World 'founder crop'—is confined to the Fertile Crescent (Map 4, p. 42). It is thus possible to plot, fairly accurately, the area where Neolithic agriculture could have started. The archaeological records have fully corroborated this supposition. The delimitation of the place of origin of the chickpea is even more precise. Its wild ancestor is endemic to south-east Turkey (Map 10, p. 88). However, not all wild progenitors have such a limited distribution. Some (e.g. the wild relatives of the foxtail millet, oat, flax, and numerous fruit trees) are distributed over extensive territories. The use of their distributions for the determination of places of origin is much less accurate.

Weeds and domestication

Some crops seem to have entered cultivation not directly but by first evolving weedy forms. The establishment of tilled fields (as well as other disturbed habitats) gave an opportunity to numerous *unwanted* plants to invade the newly made habitats and to evolve as weeds. Weed evolution went hand in hand with crop cultivation and from the very start the control of these invaders seems to have been a major problem in agriculture. Noxious weeds are plants that have successfully adapted themselves to the ecology of the tilled ground. They are independent only because they retain their wild mode of seed dispersal, and germinate and develop in spite of the efforts of the cultivator to eradicate them. But if any such weeds turns out to produce a valuable commodity, it can eventually change its relationship with humans. The cultivator may follow the rule 'if you can't beat them, join them', and start to utilize the weed by intentionally planting its seed, harvesting its fruits, and selecting the better yielders. Several Old World crops are such 'secondary crops', i.e. plants that entered domestication through the back door of weed evolution (Vavilov 1949–50, 1987). They were added to the crop assemblage only after the establishment of the principal seed crops. Well-documented cases are those of the oat, *Avena sativa* (pp. 66–69), and of the gold of pleasure, *Camelina sativa* (p. 111). Several other plants seem to have followed a similar evolution under domestication.

Classification and botanical names

Orientation in crop plant evolution is frequently complicated by inconsistencies in species delimitation and by proliferation of botanical names. As already noted, cultivated plants are, as a rule, very variable. Furthermore, evolution under domestication commonly involves drastic modifications in organs and traits that stay fairly uniform in wild plants. Traditional taxonomic treatments of crops suffered from over-splitting, since they were based almost entirely on morphological comparisons. Frequently, inter-fertile crop varieties were ranked as separate species and called by different botanical names because they looked so different. For example, classical cereal taxonomists recognized twelve to fifteen species of cultivated wheats (*see* Table 3, p. 29). Barley and common oat were each split into two or more species (Table 5, p. 57). Similar splitting and species ranking characterized numerous other crops.

With the accumulation of cytogenetic information, it has become increasingly clear that the traditional classification of many crops is inadequate and even misleading. Frequently two, three, or even half a dozen 'species' were found to be inter-fertile, chromosomally homologous, and genetically interconnected. Moreover, in many cases the conspicuous morphological distinctions turned out to be governed by single mutations (Table 7, p. 61). Ranking such types as independent species is unjustified. They represent only varieties within species and deserve only intra-specific ranking. In wheats, modern taxonomic revision has reduced the species number to five (Table 3, p. 29). All cultivated barleys are grouped in a single species (Table 5, p. 57), as are all common oats.

The discovery of the wild progenitors necessitated another nomenclature change. Because the

wild plants and their cultivated derivatives are genetically interconnected, they cannot be regarded as fully diverged species. According to internationally agreed taxonomic rules, once a wild ancestor is satisfactorily recognized, the crop and its wild relative cease to be treated as two separate species. Instead, they should be lumped in a single collective species, frequently also including related weed types. In other words, the wild and crop types are considered as subspecies or varieties of a single *biological species* and botanically named accordingly.

However, habits die hard. Old names and traditional classifications are still widely used by many researchers. Wild progenitors, in particular, are commonly referred to as independent species. To avoid confusion, botanical orientation in crops should begin with the following questions:

(i) What are the main cultivated, weedy, and wild elements in the crop complex?
(ii) What botanical names are used by different people for these intra-specific taxa of the crop complex?
(iii) What are the other fully divergent ('alien') species placed in the same genus?

Radiocarbon dating and dendrochronology

Radiocarbon (^{14}C) dating was developed by W.F. Libby at the University of Chicago soon after the Second World War and created a real breakthrough in archaeology (Libby *et al.* 1949). Previously, one could date archaeological remains only by *relative* chronology based on stratigraphy and cultural associations. The introduction of radiocarbon-dating methods brought about *absolute dates* and made possible age comparisons between cultures in the various parts of the world.

Until the 1980s, radiocarbon dating demanded relatively large samples of charred material. Most tests were made on carbon sources (such as wood charcoal or hoards of grain) obtained from secured archaeological contexts. By then, radiocarbon accelerator mass spectrometry (AMS) technique had been developed (Nelson *et al.* 1977).

This technique, based on counting the atoms instead of the decay product, made it possible to reduce the size of the sample to a few milligrams. Consequently, it became possible to date accurately individual charred grains or to reduce the amount of material removed from rare or very important objects. The application of the AMS test is sometimes critical (Harris 1986). Beside dating, radiocarbon serves to detect—and eliminate—errors in chronologically associated samples to the wrong strata or archaeological level. These errors are due to intrusion; i.e. the occasional displacement of plant remains from one layer or context to another as a result of boring by animals or other interferences (Boaretto 2007, 2009). Better precision and accuracy of archaeological dating brought about by several improvements in this field:

(i) the improved techniques of chemical pre-treatment for the elimination of contaminations from the sample material;
(ii) the ability to reduce the size of the sample to few milligrams, extend the range of possible material to be dated, the care taken to date archaeological finds from secure, sealed, contexts;
(iii) the building of a calibration curve up to the range of radiocarbon dating' 50,000 year (Reimer *et al.* 2009).

The principle of radiocarbon dating is based on the measurement of the radioactive ^{14}C isotope concentration in sample material, in comparison to the stable carbon isotope ^{12}C. The production of ^{14}C, due to the interaction of cosmic rays with molecules, takes place in the atmosphere as neutron absorption on ^{14}N atoms.

These ^{14}C forms CO_2 molecules, are then introduced into different natural reservoirs (e.g. hydrosphere, biosphere) by different physical and chemical processes. In these reservoirs the relative ^{14}C and ^{12}C concentration is in equilibrium as long as the exchange with the atmosphere stays open. When this exchange ceases (e.g. when the organism dies), the ^{14}C concentration starts to decrease due to decay of the radioactive ^{14}C. Therefore, the measured concentration of ^{14}C in material examined depends upon the time elapsed from when the exchange with the atmosphere stopped. The radiocarbon age is calculated from the measured ^{14}C concentration using the decay law. The smaller the proportion of ^{14}C in the tested organic remains, the older the sample.

The concentration of ^{14}C in the atmosphere was not constant in the past (Suess 1970), and some fluctuations seem to have occurred in the concentration of this isotope in the atmosphere. This means that age estimates based on conventional radiocarbon timescale are in need of some calibration. More precise dating was made possible by establishing the sequences of annual rings in wood remains of trees (oaks, bristlecone pine), and currently also in corals; and radiocarbon dating of the rings in these sequences. Recently, these sequences have been updated and extended to 50,000 years BP (Reimer *et al.* 2004). By plotting radiocarbon ages against tree-ring ages, calibration curves have been constructed correlating radiocarbon dates with dendro- or calendar times (Fig. 1). Thus by means of dendrochronology, the radiocarbon timescale can be calibrated against annual tree-ring chronology to calendar dates (Stuiver *et al.* 1986; Stuiver and Reimer 1993; Baillie 1995). Joined by other dating methods (U-Th ages from corals), calibration reaches the limit of radiocarbon dating which is 50,000 years (Reimer *et al.* 2009). A relevant part of the current calibration curve is shown in Fig. 1. One can see that except for the last three thousand years, the radiocarbon age represents somewhat reduced estimates. Moreover, the differences increase in time. Thus for radiocarbon dates 3,000–4,000 years before present (BP), calibration adds 200–400 years. For older radiocarbon dates (6,000–9,000 BP), the addition is already 700–1,000 years. For still older radiocarbon dates the calibration differences are even greater.

The result of the calibration process is usually presented in the form of probability distribution of the radiocarbon age (black curve) as it is shown in Fig. 2. The radiocarbon determination, with one standard deviation, is given in the center of the upper side of the plot. The distribution of the radiocarbon determination (red curve on the left-hand Y axis) is projected on the calibration curve (an uneven double blue line on the X axis, in calibrated years BP), to produce the radiocarbon age (solid

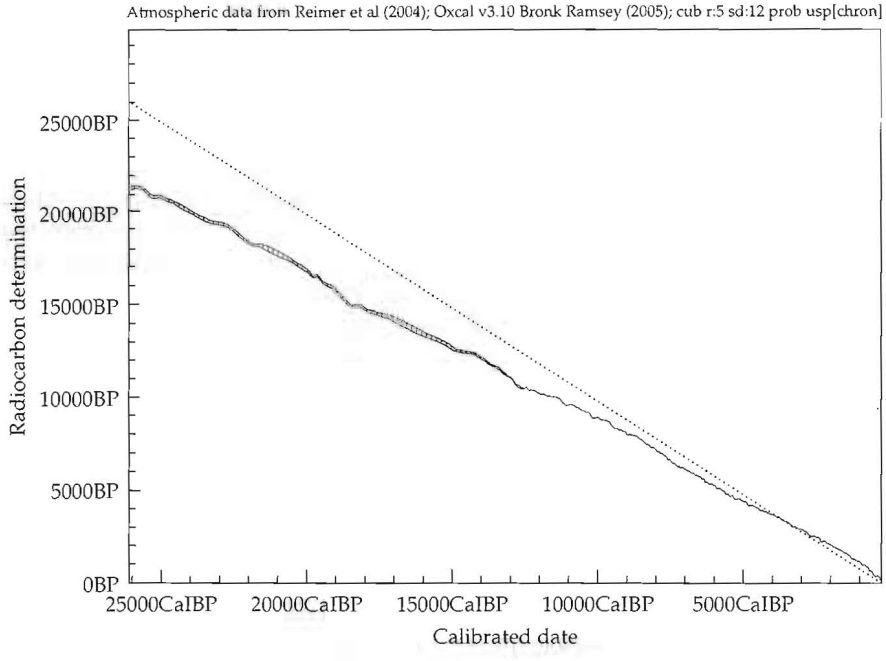

Fig. 1 The radiocarbon calibration curve for the past 25,000 years based on trees and corral annual ring sequences. Adapted from OxCal 3.10 software Bronk-Ramsey 2005 (Bronk-Ramsey 1995; Bronk-Ramsey 2001). The straight thin line represents the ideal 1:1 correspondence between radiocarbon age and calendar age assuming constancy of ^{14}C concentration in the atmosphere. If ^{14}C years were the equivalent to calendar years, all of the data would fall on the diagonal straight line.

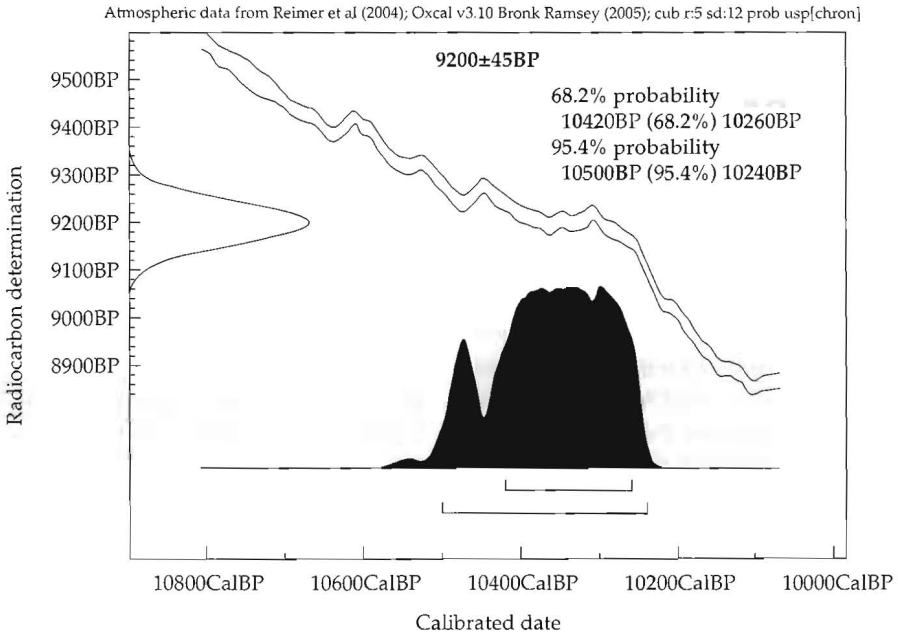

Fig. 2 Presentation of radiocarbon results—probability distribution of a sample that was measured 9200±45 ^{14}C year BP (=Before Present); see text for explanations of this result. The calibration is performed using the software OxCal 3.10 Bronk-Ramsey 2005 (Bronk-Ramsey 1995; Bronk-Ramsey 2001).

black distribution). The probability of dates is given in the top-right corner in two different levels of confidence, 68.2% probability (±1σ) and 95.4% probability (±2σ). For each probability, the range of dates is given, from left to right, with the percentage in the middle representing how much this range covers. When there is more than one range of probabilities for each 1 or 2σ probabilities, each interval appears separately. A straight line is placed underneath the black curve to make it easy to determine the dates as can be seen on the X axis. In case of more than one range of probabilities for each 1 or 2σ probabilities, such straight line is placed under each curve.

It is important to note that radiocarbon dates are given as a probability range, which means the actual dates could be between two *possible* dates, rather than the median dates between them. In addition, as Figs 1 and 2 show, calibration curve is far from being 1:1 straight line, and several wiggles and flat areas can be seen. As a result, due to the fact they fall into a flat area in the calibration curve, several different radiocarbon dates can produce similar ranges. Disturbing such area occur around 10,000 uncal BP—a period of great importance for the understanding of the beginnings of agriculture. These areas in the calibration curve are still widely misunderstood aspects of radiocarbon dating.

As a rule, dates mentioned in this book are calibrated radiocarbon dates before present (cal BP). Therefore, the use of 'BP' and 'cal BP' denote calibrated ^{14}C dates (years before present, i.e. before 1950). BC (years Before Common Era / Before Christ) denotes uncalibrated dates, either from Bronze Age and later radiocarbon dates, when calibration has little impact, when dates drawn from traditional methods of stratigraphic dating, or when calibrated dates were unavailable.

Also, progress of evidences in this book is presented on a timetable moving from older to newer dates, from earliest to recent finds. Therefore, when we separate millennia to first and second halves (i.e. 'the second half of the eleventh millennium cal. BP' or 'the first half of the ninth millennium cal. BP'), the first half will be older and the second one,the younger.