Part I

Origin and Evolution of Wheat

Chapter 1

Domestication of Wheats

1.1 Introduction

Wheats are the universal cereals of Old World agriculture (Harlan 1992; Zohary and Hopf 1988, 1993) and the world's foremost crop plant (Feldman et al. 1995), followed by rice and corn. It is the most widely cultivated food crop and is the staple food in more than 40 countries and for over 35% of the global population (Williams 1993). The earliest present evidence for the utilization of wheat comes from the Ohalo II site in Israel, where the wild, brittle tetraploid wheat *Triticum dicoccoides*, dated as 19,000 years old, was found, suggesting the initial steps towards sedentism and cereal agriculture (Kislev et al. 1992). Wheat and barley constituted the principal grain stock upon which Old World agriculture was founded. These were among the earliest domesticated crop plants, 10,000 years ago, in the Pre-pottery Neolithic Near East (Harlan and Zohary 1966; Harlan 1976, 1992; Lupton 1987; Evans 1993; Price and Gebauer 1995; Harris 1996; Valdes et al. 1997; Hillman and Colledge 1998; Ladizinsky 1998; Lev-Yadun et al. 2000). Wheat predicated sedentism and was responsible for the increase in the population by enabling humans to produce food in large quantities, thereby contributing to the emergence of human civilization. Today, wheats rank first in the world's grain production and account for more than 20% of the total food calories and protein in human nutrition. Wheats are now extensively grown across the temperate, Mediterranean, and subtropical parts of both hemispheres of the world, from 67 °N in Norway, Finland, and Russia, to 45 °S in Argentina. However, in the subtropics and tropics, the cultivation of wheat is restricted to higher elevations. The world's main wheat-producing regions are in temperate and southern Russia, the central plains of the United States, southern Canada, the Mediterranean basin, north-central China, India, Argentina, and south-western Australia.

Wheat cultivars are superior to most other cereals in their nutritive value (Zohary and Hopf 1993). Besides 60–80% starch, their grains also contain 8–15% protein, which may rise in elite wild genotypes up to 17–28% (Avivi 1978, 1979; Avivi et al. 1983; Grama et al. 1983; Nevo et al. 1986a; Levy 1987). The gluten proteins in the seed endosperm impart to wheat dough stickiness and unique bread-baking qualities. Wheats were and are the staple food in the ancient and modern world for billions of people.

Modern wheat cultivars belong primarily to two species: (1) hexaploid bread wheat, *Triticum aestivum* (2n = 42 chromosomes), and (2) tetraploid, hard or durum-type wheat, *T. turgidum* (2n = 28) used for macaroni and low-rising bread. Other species are relict. Wheats are almost fully self-pollinated; hence genetic diversity is represented in the wild by numerous clones and in cultivation by some 25,000 different cultivars. Cultivated primitive wheat forms have hulled grains, whereas advanced cultivated wheats are free-threshing. Likewise, wild wheats have brittle ears that disarticulate at maturity into individual spikelets. Each spikelet, with the wedge-shaped rachis internode at its base, constitutes an arrow-like device that inserts the seed into the ground (Zohary 1969). By contrast, all cultivated wheats have non-brittle ears that stay intact after maturation, depending on humans for reaping, threshing, and sowing (Figs 1.1, 1.2). The non-brittleness and nakedness of cultivated wheats depend on the Q locus (Luo et al. 2000), located on chromosome 5 of genome A, and it may have arisen from the *q* gene of the hulled varieties by a series of mutations (Feldman et al. 1995).

1.2 Cytogenetic and Taxonomic Background

The tribe Triticeae is economically the most important group of the family Gramineae. It has given rise to cultivated wheats, barleys, ryes, oats, and a number of important range grasses. Hybridization among genera within the tribe has allowed the exchange of genetic material and given rise to polyploidy in the form of amphiploidy. The wheats (genus *Triticum*) comprise a series of diploid, tetraploid, and hexaploid forms, the polyploids having arisen by amphiploidy between *Triticum* species and diploid species of the genus *Aegilops* (Kihara 1954; Riley 1965; Sears 1969; Miller 1987; Kimber and Feldman 1987; Dvorak et al. 1993; Van Slageren 1994; Feldman et al. 1995; Caligari and Brandham 2001; Figs. 1.1 and 1.2).

The wild diploid species, some of which have contributed to polyploid wheats, are presumably monophyletic in origin, though they have diverged considerably from each other. This divergence is particularly evident in the morphologically well-defined seed-dispersal units of the species and their specific ecological requirements and geographic distributions. Cytogenetic data have corroborated the taxonomic classification by showing that each diploid species contains a distinct genome (Kihara 1954). The related chromosomes of the different genomes show little affinity with each other and do not pair regularly in interspecific hybrids, so the result is complete sterility and isolation of the diploid species from each other.

The polyploid species are a classic example of evolution through amphiploidy. They behave like typical genomic amphiploids; that is, their chromosomes pair in a diploid-like fashion and the mode of inheritance is disomic. The allopolyploid nature of the *Triticum* polyploids has been veri-

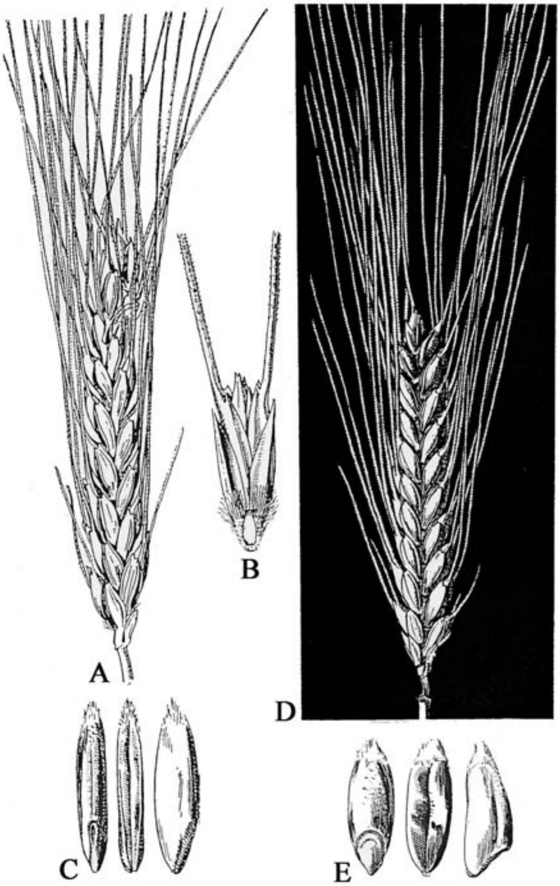

Fig. 1.1A–D. Tetraploid *Triticum turgidum* wheat. **A** Ear (1:1), **B** spikelet (2:1), **C** grain (3:1) of wild emmer wheat, *T. turgidum* subsp. *dicoccoides*. **D** Ear (1:1), **E** grain (3:1) of cultivated emmer wheat, *T. turgidum* subsp. *dicoccum*. (Zohary and Hopf 1993)

fied by cytogenetic analysis of hybrids between species of different ploidy levels. Each polyploid species can be identified as a product of hybridization followed by chromosome doubling.

At the diploid level there are two species of einkorn wheat, *Triticum monococcum* L. and *T. urartu* Thum. The sterility of their hybrids (Johnson and Dhaliwal 1976) indicates that they are valid biological species. *T. monococcum* includes cultivated ssp. *T. monococcum monococcum* (*T. monococcum* L.) and wild ssp. *T. monococcum aegilopoides* (Link) Thell. *T. urartu* presumably exists only in its wild form. At the tetraploid level there are two species, *T. turgidum* L., which includes wild ssp. *T. turgidum dicoccoides* (Korn.) Thell (here designated *T. dicoccoides*) and several cultivated subspecies (Morris and Sears 1967), and *T. timopheevi* (Zhuk., which includes wild ssp. *T. timopheevi*