

# Contents

## Part I

<b>Origin and Evolution of Wheat</b> .....	1
1 Domestication of Wheats .....	3
1.1 Introduction .....	3
1.2 Cytogenetic and Taxonomic Background .....	4
1.2.1 The Origin of the A Genome .....	6
1.2.2 The Origin of the B Genome .....	8
1.3 Emmer and Durum Wheats: <i>Triticum turgidum</i> .....	8
1.4 Genetic Erosion of Cultivated Wheats and the Need to Restore Diversity .....	9
2 Wild Emmer, <i>Triticum dicoccoides</i> , Wheat Progenitor: Origin and Evolution .....	11
2.1 Origin .....	11
2.2 Classification .....	12
2.3 Ecology .....	14
2.4 Domestication .....	16
3 Centers of Origin and Diversity of Wild Ancestors and Crop Improvement .....	19
3.1 Israel as a Natural Laboratory of Wild Genetic Resources ...	19
3.2 Multidisciplinary Research Program of Wild Emmer Wheat, <i>Triticum dicoccoides</i> , for Wheat Improvement, at the Institute of Evolution, University of Haifa, Israel .....	21

## Part II

<b>Population Genetics of Wild Emmer Wheat</b> .....	23
4 Macrogeographic Population Genetic Studies of <i>Triticum dicoccoides</i> in the Fertile Crescent, Israel and Turkey: Allozyme and DNA Polymorphisms .....	25
4.1 Allozymic Diversity .....	25
4.1.1 General Overview of Molecular Evolution .....	25
4.1.2 Patterns of Allozyme Diversity of Wild Emmer .....	26

4.1.3	Population Genetic Structure of Wild Emmer Wheat	31
4.1.3.1	“Archipelago” Population Genetic Structure of Wild Emmer Wheat	31
4.1.3.2	Spatial Autocorrelation of Allozymes	43
4.1.3.3	Multilocus Structure of Allozymes	43
4.1.4	Adaptive Nature of Allozyme Polymorphisms	44
4.2	RAPD Genetic Diversity	46
4.2.1	Patterns of RAPD Variation and Genetic Diversity	46
4.2.2	Genetic Structure	47
4.2.2.1	RAPD Discriminant Analysis	47
4.2.2.2	RAPD Genetic Distance	48
4.2.2.3	RAPD Spatial Autocorrelation	49
4.2.3	Multiple Regression Analysis of Environmental Variables and RAPD Polymorphisms	50
4.2.4	RAPD versus Allozyme Genetic Diversity Profiles	53
4.3	Microsatellite (SSR) Diversity	54
4.3.1	SSR Genetic Diversity	55
4.3.1.1	Patterns of SSR Diversity	57
4.3.1.2	Summary of SSR Genetic Diversity	58
4.3.1.3	SSR versus RAPD and Allozyme Genetic Diversity Profiles	59
4.3.2	Population Genetic Structure	60
4.3.2.1	SSR Genetic Distance	60
4.3.2.2	SSR Discriminant Analysis	61
4.3.2.3	Genetic Structure of Wild Emmer Wheat Populations	62
4.3.3	Ecological Correlates: Multiple Regression Analysis of SSR Polymorphism on Environmental Variables	63
4.3.4	Diversity and Utility of Wheat SSRs	63
4.3.5	Genetic Diversity of Wild Emmer versus Cultivated Wheat	66
4.4	Ribosomal DNA Diversity	67
4.5	Structure, Function, and Evolution of Ribosomal DNA	71
4.6	Growth Characteristics in Wild Barley, <i>Hordeum spontaneum</i> , Populations from Different Habitats in Israel	72
5	<b>Microgeographic Studies of Allozyme and DNA Polymorphisms in <i>Triticum dicoccoides</i></b>	75
5.1	Divergence of Multilocus Allozyme Structure in Wild Emmer Wheat Across a Dipping Basalt Plateau in the Golan: Qazrin versus Yehudiyya	75
5.2	Microclimatic Stress and Adaptive Allozyme and DNA Differentiation: <i>Sun</i> versus <i>Shade</i> at the Yehudiyya Microsite	77
5.2.1	Allozymic Diversity: <i>Sun-Shade</i> Divergence	78

5.2.1.1	Distribution of Polymorphism Among Loci .....	80
5.2.1.2	Analysis of Genetic Diversity Within and Between Populations .....	81
5.2.1.3	Genetic Differentiation at the Two-Locus Level .....	83
5.2.1.4	Multilocus Organization: <i>Sun</i> versus <i>Shade</i> ..	84
5.2.1.5	Shade Ecology .....	84
5.2.1.6	Neighbor Effects, Population Size, and Migration in Wild Emmer .....	85
5.2.1.7	Multilocus Microclimatic Differentiation in Wild Emmer .....	85
5.2.1.8	Aridity and Lightless Stress Selection in Wild Emmer and Other Organisms .....	86
5.2.2	RAPD Diversity: <i>Sun-Shade</i> Divergence .....	87
5.2.2.1	RAPD Discriminant Analysis .....	88
5.2.2.2	RAPD Linkage Disequilibria .....	91
5.2.3	Microsatellite DNA Differentiation .....	93
5.2.3.1	The Distribution of Alleles at SSR Loci .....	93
5.2.3.2	SSR Genetic Distance .....	99
5.2.3.3	SSR Discriminant Analysis .....	99
5.2.3.4	Linkage Disequilibrium (LD) Between SSR Loci .....	100
5.2.3.5	Genetic Effect on SSR Variation .....	101
5.2.3.6	Mutational Mechanisms for Producing SSR Variation .....	102
5.3	Edaphic, Topographical, and Temporal Factors Affecting Allozyme and DNA Differentiation of Wild Emmer Wheat at the Tabigha Microsite, Northern Israel .....	102
5.3.1	Edaphic Allozyme Divergence .....	105
5.3.1.1	Distribution of Polymorphism Among Loci ..	105
5.3.1.2	Distribution of Alleles .....	105
5.3.1.3	Association with Soil Type .....	108
5.3.1.4	Genetic Summary .....	111
5.3.1.5	Discriminant Analysis .....	111
5.3.1.6	Analysis of Genetic Diversity, <i>He</i> , Within and Between Populations .....	114
5.3.1.7	Genetic Differentiation at the Two Locus Level .....	115
5.3.1.8	Multilocus Organization – Terra Rossa versus Basalt .....	115
5.3.1.9	Natural Selection of Allozymic Diversity ....	116
5.3.2	Edaphic SSR DNA Divergence in Wild Emmer Wheat at the Tabigha Microsite .....	117
5.3.2.1	Distribution of Allelic Diversity at Polymorphic SSR Loci .....	118

5.3.2.2	SSR Permutation Test .....	118
5.3.2.3	SSR Genetic Diversity and Distance Between the Terra Rossa and Basalt Soils .....	120
5.3.2.4	Microsatellite Diversity of Repeat Numbers Between the Terra Rossa and Basalt Subpopulations .....	122
5.3.2.5	SSR Discriminant Analysis .....	124
5.3.2.6	Linkage Disequilibrium (LD) Between SSR Loci .....	124
5.3.2.7	Differential Physiological Response in Wild Barley Across the Edaphically Subdivided Transect at Tabigha .....	125
5.4	Population Dynamics of <i>Triticum dicoccoides</i> in a Natural Habitat in Eastern Galilee: The Ammiad Microsite Study ....	126
5.4.1	General Characteristics of the Ammiad Microsite ....	128
5.4.1.1	Population Dynamics .....	129
5.4.1.2	Phenotypic Patterns .....	129
5.4.1.3	Disease Resistances .....	130
5.4.1.4	High-Molecular-Weight Glutenin Polymorphisms: Spatiotemporal Ecological Factors .....	131
5.4.1.5	Allozyme Diversity: Spatiotemporal Ecological Factors .....	131
5.4.1.6	Spatiotemporal Allozyme Divergence Caused by Aridity Stress at the Ammiad Microsite: Extended Study over the 6 Years .....	133
5.4.1.7	Allozymic Correlations with Rainfall and Soil Moisture over the 6 Years .....	137
5.4.1.8	Genetic Diversity of Allozymic Loci: Summary over the 6 Years .....	138
5.4.1.9	Partition of Allozymic Diversity over the 6 Years .....	138
5.4.1.10	Correlation of Allele Frequencies and <i>He</i> Among Allozymic Loci over 6 Years .....	141
5.4.1.11	Variable Selection of Protein Groups over the 6 Years .....	144
5.4.1.12	Allozymic Diversity and Water Availability in Critical Growth Periods .....	144
5.4.2	SSR Divergence in Wild Emmer Wheat at Ammiad ...	146
5.4.2.1	Distribution of Alleles at Polymorphic SSR Loci .....	147
5.4.2.2	SSR Variation in Repeat Number .....	148
5.4.2.3	SSR Gene Diversity Among the Four Habitats .....	151
5.4.2.4	SSR Genetic Differentiation Among the Four Habitats .....	151

5.4.2.5	Genetic Distances Among the Four Subpopulations .....	151
5.4.2.6	SSR Genetic Diversity in Subpopulations from Eight Subhabitats .....	151
5.4.2.7	SSR Spatial Autocorrelation .....	152
5.4.2.8	Multiple Regression Analysis of Ecological Factors and SSR Diversity .....	153
5.4.2.9	SSR Discriminant Analysis .....	153
5.4.2.10	Linkage Disequilibrium (LD) Between SSR Loci .....	156
5.4.2.11	SSR Multilocus Structure .....	158
5.4.3	Parallel Microgeographic Patterns of Genetic Diversity and Divergence Revealed by Allozyme, RAPD, and Microsatellites in <i>Triticum dicoccoides</i> at Ammiad, Israel .....	159
5.4.3.1	Patterns of Genetic Diversity Among the Four Subpopulations .....	160
5.4.3.2	Genetic Diversity over All Four Subpopulations .....	160
5.4.3.3	Partition of Genetic Diversity Within and Among the Four Subpopulations .....	162
5.4.3.4	Genetic Distance .....	164
5.5	Microsatellite Diversity Correlated with Ecological-Edaphic and Genetic Factors in Three Microsites of Wild Emmer Wheat in North Israel .....	165
5.5.1	Divergence Among the Three Populations of <i>Triticum dicoccoides</i> .....	166
5.5.2	Divergence Between Terra Rossa and Basalt Groups ..	167
5.5.3	Genetic Effects on SSR Diversity .....	170
5.5.4	Effects of Genetic and Environmental Factors on SSR Variation .....	172
5.5.5	Contribution of Genetic and Environmental Factors to SSR Variation .....	173
5.5.6	Determination of Mutational Mechanisms and Edaphic Effect on SSR Diversity .....	174

### Part III

#### Genetic Resources of Wild Emmer for Wheat Improvement ..... 177

#### 6 Genetic Variation in Agronomic Traits ..... 179

6.1	Quantitative Morphological and Physiological Variation in Phenotypes and Genotypes .....	179
6.1.1	Genetic Variation in Phenotypic Agronomic Traits ...	179
6.2	Heat Production in Wild Cereals .....	181
6.3	Abiotic Stress Tolerance and Variation in Physiological Performances: Salt and Drought Tolerance .....	182

6.3.1	Salinity Tolerance .....	183
6.3.1.1	Genetic Polymorphisms in $^{22}\text{Na}$ Uptake .....	183
6.3.2	Drought Tolerance .....	187
6.4	Herbicide Response .....	187
6.5	Grain Protein Quality and Quantity .....	189
6.5.1	The Genetics of Grain Protein Content .....	193
6.5.2	Utilization of High Grain Protein from Wild Emmer .....	194
6.5.3	Wheat Storage Proteins and Glutenin DNA Diversity in <i>Triticum dicoccoides</i> in Israel .....	195
6.5.3.1	Utilization of Glutenin Diversity in Bread-Making Quality .....	195
6.5.3.2	Genetic Differentiation of Higher Molecular Weight Glutenin Subunits .....	195
6.5.3.3	Glutenin DNA Diversity .....	198
6.6	Amino-Acid Resources in <i>Triticum dicoccoides</i> : Polymorphisms and Predictability by Ecology and Isozymes .....	203
6.6.1	Amino Acids in Wild Emmer .....	206
6.7	Amylases .....	207
6.8	The Amylase Multigene Family .....	212
6.8.1	Evolutionary Considerations .....	212
6.8.2	Importance of Amylase Variation for Wheat Improvement .....	213
6.9	Disease Resistance Polymorphisms in <i>T. dicoccoides</i> (Host-Pathogen Coevolution in the Center of Diversity) ....	214
6.9.1	Powdery Mildew, <i>Erysiphe graminis tritici</i> .....	214
6.9.2	Leaf Rust, <i>Puccinia recondita tritici</i> .....	216
6.9.3	Stem Rust, <i>Puccinia graminis tritici</i> .....	217
6.9.4	Stripe Rust, <i>Puccinia striiformis tritici</i> .....	220
6.9.5	Responses of Israeli <i>Triticum dicoccoides</i> to Selected Australian Pathotypes of <i>Puccinia</i> Species .....	221
6.9.6	Resistance to Wheat Soilborne Mosaic Virus (WSBMV) .....	221
6.10	Photosynthetic Characters in <i>Triticum dicoccoides</i> and Their Predictability by Ecological and Genetic Factors .....	225
6.11	Diurnal Rhythms of mRNAs for the Chlorophyll a/b Binding Protein in Wild Emmer Wheat and Wild Barley in the Fertile Crescent .....	229
6.12	Crop Improvement .....	230
6.12.1	Genetically Engineered Plants for Crop Improvement .....	230
6.12.2	Potential and Actual Genetic Resources of <i>Triticum</i> <i>dicoccoides</i> and Future Wheat Breeding .....	231
6.12.3	Utilization of <i>Triticum dicoccoides</i> in Breeding .....	232

**Part IV**

<b>Genome Organization and Genetic Mapping</b> .....	239
<b>7 Genome Structure of <i>Triticum dicoccoides</i></b> .....	241
7.1 Molecular Genetic Maps .....	241
7.1.1 Introduction: Molecular Markers as a Tool for Genetic Mapping .....	241
7.1.2 Marker Polymorphism Between <i>Triticum durum</i> and <i>Triticum dicoccoides</i> .....	242
7.1.3 Construction of the Molecular Genetic Map .....	243
7.1.4 Distribution of Molecular Markers Among the Genomes and Chromosomes .....	252
7.1.4.1 Clustering of Marker Loci .....	252
7.1.4.2 Nonrandom Distribution of AFLP Markers ..	254
7.1.5 Conserved Order of Microsatellite Loci and Structural Changes of Chromosomes .....	255
7.2 Segregation and Recombination upon Crossing <i>Triticum dicoccoides</i> with <i>Triticum durum</i> .....	256
7.2.1 Distorted Monogenic Ratios .....	256
7.2.2 Quasi-Linkage: Nonrandom Segregation of Nonhomologous Chromosomes .....	258
7.2.3 Negative Crossover Interference .....	262
7.3 Coevolution of A and B Genomes in <i>Triticum dicoccoides</i> ...	265
7.3.1 Introduction .....	265
7.3.2 Probing of <i>Triticum dicoccoides</i> Genome with DNA from Its Putative Diploid Ancestors .....	267
7.3.3 Interaction of Two Genomes in the Polyploid .....	269
<b>8 Genetic Mapping of Agronomically Important Traits</b> .....	273
8.1 Resistance to Diseases: High-Density Map of 1B Chromosome Region Harboring Stripe-Rust Resistance Genes <i>Yr15</i> and <i>YrH52</i> .....	273
8.1.1 Introduction .....	273
8.1.2 Why Mapping? .....	274
8.1.3 Updated High-Density Molecular Map of <i>Yr15</i> and <i>YrH52</i> Regions and Preliminary Discrimination of <i>YrH52</i> and <i>Yr15</i> Genes .....	275
8.1.4 Resistance Gene Cluster on Chromosome 1BS .....	277
8.2 Herbicide Resistance .....	279
8.3 Mapping QTLs for Agronomically Important Traits in <i>Triticum dicoccoides</i> .....	284
8.3.1 Introduction .....	284
8.3.2 QTL Detection: The Experimental Design .....	285
8.3.3 Genomic Distribution of QTLs for Agronomic Traits .....	286
8.3.4 Summary of the Revealed QTL Effects .....	293

<b>9 Molecular Evolution and Ecological Stress in Wild Emmer Wheat at Regional and Local Scales: Natural Selection in Action</b>	297
9.1 Overview	297
9.2 Evidence	297
9.3 Theory	299
9.3.1 Evolutionary Forces and Adaptive Complexes	299
9.3.2 Maintenance of Genetic Diversity in Wild Emmer Wheat	299
9.3.2.1 Diversifying and Balancing Natural Selection	300
9.4 Effect of Ecological Selection on Single SSR Locus	301
9.4.1 Mutational Mechanisms of SSRs	301
9.4.1.1 Interaction of Replication Slippage and Recombination	302
9.4.1.2 Functional Perspectives of SSRs	303
9.4.1.3 Microclimatic Selection	305
9.4.1.4 Edaphic Selection	305
9.4.1.5 Topographic and Microgeographic Drought Effects	306
9.4.1.6 Natural Selection and Linkage Disequilibria of SSR Alleles	306
9.4.2 Ecological Selection and Clustering of Allele Size Frequency Distribution	307
9.4.3 Ecological Effect on SSR Mutational Mechanisms	308
9.5 Natural Selection and RAPD-DNA Diversity	309
9.6 Natural Selection and Allozymic Diversity	311
9.7 Random Genetic Drift and Neutral Theory of Molecular Evolution	312
9.8 Gene Flow	314
9.9 Hitchhiking Effect	315
<b>Part V</b>	
<b>Conclusions and Prospects</b>	317
<b>10 Conclusions and Prospects</b>	319
10.1 Wheat as Model Organism	319
10.2 Genetic Diversity of Wild Emmer for Wheat Improvement	319
10.3 Unique Population Genetic Structure and Center of Origin of Wild Emmer Wheat	320
10.4 Genetic Resources	321
10.5 Prospects	321
10.6 Theoretical Perspective	322
10.7 Applied Perspective	322
References	323
Subject Index	353



Evolution of Wild Emmer and Wheat Improvement  
Population Genetics, Genetic Resources, and Genome  
Organization of Wheat's Progenitor, *Triticum  
dicoccoides*

Nevo, E.; Korol, A.B.; Beiles, A.; Tzion, F.

2002, XXII, 364 p. 69 illus., 25 illus. in color., Hardcover

ISBN: 978-3-540-41750-7