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Wheat Taxonomy: the legacy of John Percival

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Wheat Taxonomy:
the legacy of John Percival

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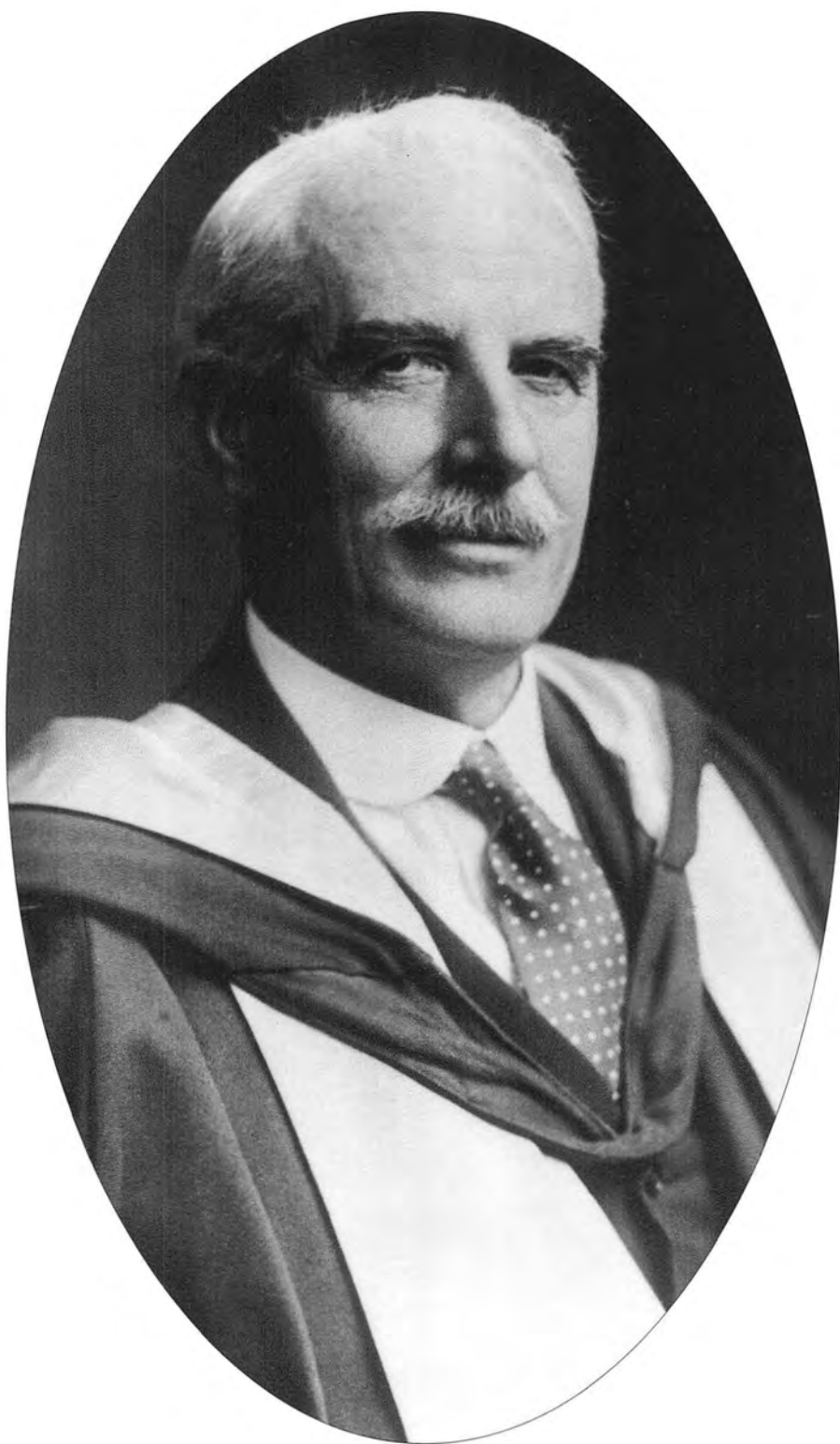
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An edited volume arising from papers presented at
The Percival Symposium:
Wheat – Yesterday, Today & Tomorrow
A meeting to celebrate the life and work of John Percival

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Preface

John Percival (1863–1949) was Professor of Agricultural Botany at the University of Reading from 1907 to 1932 and a driving force behind the creation of agricultural botany as a scientific discipline. His monumental treatment of wheat *The Wheat Plant: A Monograph* (1921) still serves as a standard reference, having been reprinted as recently as 1974. Percival was the consummate agricultural scientist – botanist, taxonomist, geneticist, germplasm collector, curator, breeder, agronomist, historian and teacher.

On the occasion of the 50th anniversary of Percival's death, the University's School of Plant Sciences hosted a meeting to celebrate his life and work. Reflecting the scope of Percival's scientific views, invited speakers surveyed research progress during the last half-century in the archaeobotany, systematics, genetics and breeding of the wheat plant. The two-day event offered a unique opportunity for a multi-disciplinary gathering of experts who shared a common interest in wheat studies.

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Introduction

John Percival – acknowledging his legacy

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John Percival died in 1949, the year that I was born, but his legacy still remains a strong one, not only in philosophical but also in tangible terms. The Department of Agricultural Botany at The University of Reading, of which he was the first Professor in 1909, has flourished and is an active centre for as wide a range of aspects of agricultural botany as John Percival himself encompassed and encouraged. A collection of herbarium specimens (The Percival Collection) that he assembled still exists in different research centres and is actively used today. His internationally acclaimed book *The Wheat Plant: A Monograph* which he first published in 1921, is still widely referenced. This stood alongside a range of books, papers and activity which formed the very basis of the subject of agricultural botany.

Of course, as I am sure John Percival would have insisted, the subject and Department have moved on and developed considerably since his time. I will not detail the history of the Department but simply point out that, from his starting point, it is now one of the three constituent departments of the School of Plant Sciences at the University of Reading, a School which was rated as the top plant science group in the UK in the last Research Assessment Exercise, gaining the top 5* rating. One cannot help but wonder how he would have seen the current work, such as the opportunities that are being opened up by the new technologies in the areas of molecular biology and biotechnology. I am sure, however, that he would have used them to advantage.

John Percival's influence continues in many ways, including our still finding physical evidence of his activities. In only the last few years the unpublished parts of what John Percival himself had entitled *Aegilops species: A Monograph* (an outline of which is included at the end of this volume) were discovered, works that might have gone alongside his masterful *The Wheat Plant: A Monograph*.

The 50th anniversary of his death seemed a very appropriate opportunity to commemorate his life and work. It is an opportunity to see where we are now and where we are going in the future. On this basis a distinguished group of speakers, who represent a wide range of interests that John Percival shared, agreed to present the papers published

in this volume. I am very grateful to them all for agreeing to play such a vital role in this meeting and helping to fulfill this vision.

The first important point was to set John Percival's work in the context of his life. Professor Hugh Bunting, with whom I share the privilege of having held the Chair of Agricultural Botany, of which John Percival was the founding Professor, generously agreed to the request that he speak about Percival the man. This constitutes the first paper with subsequent ones covering important aspects of John Percival's work on wheat, a major but no means exclusive part of his academic contribution

ACKNOWLEDGEMENTS

John Percival – the man:
his life and times

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Abstract

John Percival was born in 1863 in Carperby, Wensleydale, North Yorkshire. He was the second natural son of Edward Chapman, a farmer's son, taxidermist and naturalist, and Elizabeth Percival. Though some of his descendants record that he was always sensitive to the circumstances of his birth, his parents were married in 1869, and a stable family background evidently did much to promote his remarkable later career. At the age of 14, after nine years in a local school, his father's Quaker associations may have facilitated his move to York, where he was apprenticed to the Quaker bookseller and printer William Sessions. With the help of the Quaker families Spence and Cotton, he entered Cambridge in 1884 at 21. After taking a good degree in biological sciences he went on to a three-year voluntary attachment in the botanical laboratories of the British Museum (Natural History).

He was next associated with Daniel Hall in the Cambridge agricultural extension endeavour and with the early years of Wye College, where he established and developed the botanical parts of the degree curriculum in agricultural subjects. As the first Director of the Agricultural Department at Reading, during 1903–9, he was the founding father of the Faculty of Agriculture. In 1909 he was appointed Professor of Agricultural Botany (1909–1932). His interests in the breeding and biodiversity of wheat (including archaeological materials) led him to assemble and classify a collection of 2500 accessions of living wheats from most of the wheat-growing countries of the world. This work brought him international recognition, the lively friendship of N.I. Vavilov, and in due course the degree of ScD Cambridge (1921). From 1916 onwards he had to face a continuing series of family difficulties. Nevertheless his drive to succeed, his phenomenal industry, his vast and well-organized memory, and his essential generosity, courtesy and kindliness, especially to younger people, enabled him to continue his scientific work to within weeks of his death in 1949.

INTRODUCTION

I did not have the good fortune to know John Percival as a man. I therefore offer as my contribution to this symposium, an account of his life and works as a background to the assessments made of him by people who did know him, and to my own assessment. Though I intend this paper to do honour to his memory and justice to his achievements, I have attempted to write a history rather than a eulogy. As far as possible, I have therefore based my account on factual, usually archival sources, mostly in Reading and North Yorkshire, together with census returns and the relevant records of the Society of Friends. Anecdotal and speculative materials, and suggestions based on them, are, I hope, clearly indicated.

John Percival was a North Yorkshire Dalesman. His birthplace, the ancient village of Carperby in Wensleydale, has a Scandinavian name and is listed in Domesday Book.

He was born on April 3 1863 and died on June 26 1949. "The Origin of Species" (of which Percival's copy is said to have been inscribed by Darwin himself) was published in the fourth year before his birth, and the helical structures of the nucleic acid macro-molecules were deduced in the fourth year after his death. His life therefore spanned most of a century of profound and increasingly rapid change and development in biology.

John Percival was the second of four "natural" sons of Edward Chapman (of Thornton Rust in Wensleydale), described as a taxidermist. His mother was Elizabeth Percival of Carperby, who "made her mark" with a cross when she registered his birth. Some of John Percival's descendants believe that the circumstances of his birth weighed heavily on him in later years. A part of my initial purpose was to determine how Percival's career took wing and soared high in spite of the potentially disadvantaged circumstances of his birth.

THE YEARS OF PREPARATION, 1863–1894

Yorkshire

I soon found that the circumstances were far more propitious than might have been expected. Socially, Edward and Elizabeth seem to have established a stable, close and affectionate family which was accepted in the community. Not much more than fifty miles to the north, in Scotland, it could have been recognised legally as a "marriage of habit and repute"; closer to home Elizabeth might have been regarded as a "common-law wife".

Although an initial search found no record of a marriage between Edward and Elizabeth in Aysgarth (the parish which includes Carperby) between 1844 and 1892, they were in fact married on 28 October 1869, six years after John's birth, by the district registrar of Aysgarth. Moreover they remained together until Edward's death in 1896. Elizabeth lived on until 1907. Of their four sons the eldest, James, and the youngest, William, died in 1879 and 1880. After the marriage they had three daughters. All the children seem to have used their father's surname, Chapman, at least in their earlier years.

John reverted later to the Percival surname, but he evidently regarded himself as a member of the family throughout his life. He seems to have enjoyed a constructive

relationship with his father. Later in his life he took a splendid photograph of him, seated with his gun across his knees. Though in 1896 he was living and working in Kent, he was married a few months after Edward's death in that year, in Aysgarth Church, as a resident of Carperby. His will (1940) includes legacies to each of his three sisters, under their married names.

Economically, the circumstances of the family may well have been satisfactory also. Edward's profession and craft of taxidermy was important in those days not merely for preserving the trophies of the chase for domestic ornament (perhaps especially in the houses of the gentry like the landed Chapman family which lived near Edward's home village of Thornton Rust), but as conserving authentic material for scientific record and study (Dufresne, 1820). Many taxidermists described themselves as naturalists (Frost, 1987).

Edward, whose father was a farmer and lead-miner in the Dale, had a substantial reputation for his knowledge of birds. He is described by Harry Speight in *Romantic Richmondshire* (1897) as "the naturalist to whom more than anyone else we are indebted for records of birdlife in Wensleydale". It is not difficult to imagine that young John gained much of his knowledge of, and enthusiasm for, the environments and living organisms of the Dale during excursions with his father.

Edward Chapman's house in Carperby is today the home of Janice Peacock, the granddaughter of John's sister Elizabeth, and her husband Alan. It contains many paintings and other objects (including a gun) which were made or used by Edward or John.

John attended the National School in Aysgarth from 1868 to 1877. W.B. Brierley (who succeeded Percival in 1932 as Professor of Agricultural Botany at Reading), suggested in his Linnean Society obituary (1949, hitherto the principal source of information about Percival's life), that after leaving school he was employed at the York Glass Works, owned at the time by a Quaker family named Spence (which had part of its roots in Nidderdale). No record has been found of him in the surviving records of this firm in 1877 or 1878.

However, in 1879 he appears in the list of attenders (non-members) of the Society of Friends in York, as John Chapman, in the household of William Sessions, a well-known Quaker printer and bookseller, to whom he was later apprenticed. It may be (though we have no firm evidence) that the move to York arose from Quaker connections of Edward and Elizabeth Chapman. Though their names have not been found in any earlier records, Edward is recorded in his later years as a "habitual attender" at Quaker meetings in Carperby (though not a member of the Society), and it is said locally that Elizabeth was a Quaker.

It seems likely that it was during his five years (1879–1884) with William Sessions that John first had ready access to books and developed the habit of reading widely and deeply that continued throughout his life. In 1881 he reverted to his "own" (birth certificate) surname of Percival, perhaps because of a "crisis of identity", or perhaps to satisfy the York census enumerator.

Brierley also tells us that Mrs T.A. (Charlotte) Cotton, a member of the Spence family, enabled Percival (despite his limited preceding formal education) to enter St.

John's College, Cambridge, in 1884, aged 21 years. The record sheet of the admissions interview describes him as a Quaker, and also refers to warm supporting testimony from Fielden Thorp, former headmaster of Bootham, the distinguished Quaker school in York. It is useful to remember that it was only after 1871, when denominational tests were abolished, that Oxford and Cambridge could accept nonconformists as members.

Cambridge and London

In Cambridge Percival devoted four years to Parts I and II of the Biological Sciences Tripos and took his degree in 1888, at 25. His honours grades, both in the second class, suggest that he was still developing as a biologist. Marshall Ward wrote of a "brilliant Cambridge career". During these years he compiled, from earlier sources, a flora of Wensleydale (actually a verified check-list rather than a flora) listing 583 (not 653) species and varieties, all but ten of which he had himself seen in the field (Percival, 1888)[1]. Some of the sheets in Percival's herbarium of Wensleydale flora appear to have been prepared by T.A. Cotton, suggesting a common interest in botany. By continued reading he laid secure foundations in biological and other sciences for his later achievements. Though he was only transiently associated with the Society of Friends, he served a period in 1888 as President of the undergraduate Nonconformist Society.

He then spent three years (1888–91) in London, as a voluntary graduate worker on botanical and plant disease questions in the botanical laboratories of the British Museum (Natural History). The Keeper, Dr W. Carruthers, F.R.S., who was also consulting botanist to the Royal Agricultural Society, wrote that Percival had not only an extensive knowledge of botany but also a large acquaintance with sciences other than botany. During this period his reading covered general as well as scientific literature, and he appears also to have developed interests in music and fine art. Somewhere along the way he became a competent photographer.

In the summer vacation of 1891, at 28, he joined a voluntary class in agricultural chemistry offered in the Chemistry Department at Cambridge, where he did well enough to be appointed a junior demonstrator in the laboratory.

It seems likely that the Spence-Cotton family sustained Percival financially through his seven years in Cambridge and London. We have not found any direct archival evidence of their support, but his friendship with the family lasted for many years, and in time included his grandchildren.

University extension with A.D. Hall

In 1890 new national financial arrangements (the "whisky" money) provided funds for new initiatives in agricultural education. Cambridge set about an agricultural extension programme, led by A.D. Hall, in four counties. In 1891 Percival joined this endeavour in Surrey and Sussex.

In the course of it he met his future wife, Ethel Elizabeth (later also referred to as Suzanne) Hope-Johnstone, a county council instructor in dairy science. She was the daughter of Major the Rev. Edward Hope-Johnstone, a chaplain and naval instructor in the Royal Navy, whose home was in County Kildare in Ireland. As noted above, they

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1   Deborah Millward of Thornton Rust published a centennial review of the Flora (Millward, 1988).

were married on August 17th, 1896 in the parish church of St Andrew at Aysgarth. The witnesses were T.A. and Charlotte Cotton. The only surviving child of John and Ethel, Alan Vivian, was born at Wye, in Kent, in 1899. It is reported that a twin was still-born or else died very early, but I have not sought to confirm this, significant as it may have been emotionally for the young family.

The extension programme, in environments and systems of farming vastly different from those of the North Yorkshire dales, must have expanded considerably Percival's knowledge and understanding of farming. It would also have advanced his ability to communicate with farmers and other rural people about farming as a business rather than a way of life or an application of science.

In 1893 Percival was elected a Fellow of the Linnean Society, of which he was a Vice-President in 1926–7.

THE SOUTH-EASTERN AGRICULTURAL COLLEGE, WYE, 1894–1902/3

In 1894 the Kent, Surrey and Sussex Agricultural College, later the South-Eastern Agricultural College, and now part of Imperial College in the University of London, was established at Wye with A.D. Hall as Principal. Along with three other members of Hall's extension group, Percival joined the staff in the same year, aged 31, as Professor of Botany. He continued at Wye until 1902/3. During some of these years he was vice-Principal.

In his eight years at Wye he established comprehensive lecture courses and practical classes in botany for students of agriculture. Since there was no preceding example for him to follow or adapt, these were truly pioneer courses. He had not only to design them but also develop the teaching material as he went along. One product of this was his remarkable text *Agricultural Botany, theoretical and practical*, of which the first edition (Percival, 1900) appeared in 1900 and the eighth in 1936 (fourth impression in 1945), 3 years after his formal retirement. The work was translated into several languages, reportedly including Arabic. His grandson, John Gregory of San Francisco, records that in 1948–9, the last year of his life, Percival was working on a ninth edition.

The structure of *Agricultural Botany* reflects in part that of the translation (1881) by Dr S.H. Vines, F.R.S. (later Sherardian Professor of Botany at Oxford), who was probably his tutor, of Prantl's German textbook of botany, which may well have been an important introductory part of Percival's botanical diet at Cambridge. Both works open with general descriptions of the vegetative morphology of higher plants followed by outlines of the anatomy (cells and tissues) of plants – two allegedly abstruse topics of which all too many latter-day entrants are ignorant (no doubt because they find them boring). In both books, the third sections are on plant physiology, and the fourth are concerned with classification. In Vines' translation this latter section covers all plant families (including thallophytes) and forms the bulk of the work, but Percival contents himself with ten families of flowering plants which are important in the agriculture of temperate climate, and then goes on to four special chapters covering weeds, farm seeds, diseases of plants and bacteria.

Much of the work, and especially the suite of elegant illustrations, seems to be based on original observation. There was no preceding body of literature on the botany of farm plants from which the material could easily be derived. Perhaps for this reason, *Agricultural Botany* was, from the first, sensitive both to the needs of farmers and their advisers and to the content of the relevant science, as it stood at the time. Whatever criticisms might be levelled today at the content, to have prepared this text in fewer than six years, alongside all the other duties of a trail-breaking managerial post in a new type of institution, was a remarkable achievement. Through it Percival established the subject of agricultural botany as a new and synoptic discipline dependent on, but distinct from, both botany and agriculture.

Needless to say, the content of the book, as it evolved over the years, was reflected in the content of the botanical courses which Percival developed at Wye and later at Reading.

Percival's other technical publications during his time at Wye were concerned largely with scientific aspects of agricultural activities in Kent and the neighbouring counties, including the growing and processing of hops.

In 1895, at Wye, Percival began to collect diverse forms of wheat. This led in due course to the Reading wheat collection, which is more fully considered below.

The Diaspora from Wye, 1902-7

In 1902/3 the staff at Wye included, in addition to Daniel Hall and John Percival, E.J. (John) Russell and Albert Howard. Of these, all but Percival were knighted in due course. Members of the family believe that Percival was offered a knighthood also but declined because of sensitivity about his family background. All four left Wye between 1902 and 1907, to become founding fathers of important new developments or interests elsewhere.

So in 1902, after the death of Sir John Lawes, Hall moved to Rothamsted as Director, to carry forward the long-awaited "marriage of science and agriculture". Russell followed him to Rothamsted in 1907, where he became Director in due course[1]. Howard, who had served briefly in the West Indies, as a lecturer on the staff of the Imperial Department of Agriculture, before coming to Wye, was appointed Imperial Economic Botanist in India in 1903. He was posted first at the Indian Agricultural Research Institute at (old) Pusa in Bengal. Later he was appointed agricultural adviser in the southern States, based at Indore in Madhya Pradesh. There he developed the interest in methods of composting farm wastes which in due course established him as the patron saint of the soils division of the environmental movement. When my engineer uncle Sheldon, who had known Howard in India, introduced us in 1939, the sources of the very large future requirement in the world for extra (not simply recycled) fixed nitrogen to be harvested in cereal and other crops were not on the agenda. Nor was the alleged nutritional superiority of proteins in organically grown food, about which we crossed swords in *Country Life* around 1945.

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1   In which capacity he appointed me to the staff of the Chemistry Department in 1941 to work on the manurial value of bulky organic manures.

The fourth emissary from Wye was John Percival. He was appointed to the staff of University College Reading in 1902.

PERCIVAL AT READING, 1902/3 TO 1909

Building the future faculty

Though we at Reading University usually seem to think of John Percival as our first Professor of Agricultural Botany, he did not assume this more specialised title until 1909. His earlier roles, as Director of the Agricultural Department and lecturer in both agriculture and agricultural botany from 1902/3, and Professor of Agriculture and Director of the Department of Agriculture and Horticulture to 1909, clearly established him as the most important of the founding fathers of the Faculty of Agriculture and Food, now set to become part of a Faculty of Life Sciences.

His tasks in the early years grew naturally from those in which he had succeeded at Wye. They included directing the development of teaching and research in agriculture, and later in horticulture (which had earlier been the responsibility of Frederick Keeble, lecturer in, and later first Professor of Botany at Reading, and afterwards, in his turn, Sherardian Professor at Oxford). He was also responsible for the recruitment of agricultural students, and the design and examination of courses of teaching and practical instruction. He had to see to the provision of buildings, facilities and equipment for lectures and practical instruction in laboratory and field.

His later responsibilities included the establishment and equipment of new buildings for the agricultural and horticultural departments when they were moved from Valpy Street in central Reading to the east cloister on the London Road site. The departments remained at London Road for more than half a century until they found another home in the recycled buildings at Earley Gate which were built to house a regional centre of government during the second war, and are still not completely demolished.

Percival had made it a condition of his appointment that the College should acquire a farm for teaching and research. As a result Lane End Farm at Shinfield (the first of several) was purchased in about 1904/5.

He also organised field trials and observations in the neighbouring counties. This was a natural continuation of the work in the countryside that had begun, at Reading as well as at Wye, in the university extension days from 1891. It led on to close associations, in both teaching and research, with county staffs, some of whom were more or less interchangeably based in the departments of the University and later in the faculty.

His interests in the practice of agriculture are reflected in the few publications I have so far identified in this period. They include papers on malting barley (1903–4), a series of reviews of the soils of Dorset (with Luxmoore, 1906) and a new edition, with Sir William Crookes, of Ville's important early work on artificial manures (1909). During this period Percival did most of the work on his second significant text book *Agricultural bacteriology: theoretical and practical* of 1910 (2nd edition 1920). As in *Agricultural Botany* the text reflects original observations as well as information assembled from the work of others. The scope seems vast and the detail exhaustive.

In 1907 the College transferred the direction of teaching and research in horticulture from Keeble's developing department of "pure" botany, to a new department of agriculture and horticulture, directed by John Percival as the first Professor of Agriculture at Reading. Horticulture became a distinct activity in the combined department, under its own director, in 1909.

In 1908 Percival had built, to his specifications, "The Pyghtle" (66 Northcourt Avenue), in which he lived until some time after his formal retirement. He then moved to "Leighton" on Shinfield Green, perhaps to be nearer to the agricultural botanic garden in which his wheats (below) were grown.

PERCIVAL AFTER 1909

The Chair and Department of Agricultural Botany

In 1909, Percival left the chair of Agriculture in order to move to a newly-created chair, of agricultural botany, so far as I know the first in Britain. His work for the future Faculty of Agriculture and Horticulture, which was formally established in 1913–14, was now sufficiently complete to allow him to devote himself fully to the further development of his chosen field.

At first, the main task of Percival's new department was to continue to provide the botanical elements of the courses for students reading for Reading diplomas and London degrees in agriculture and horticulture. The syllabuses gradually evolved, mainly by adding elements of the advancing sciences of botany. Evolution, adaptation, genetics and plant breeding seem slow to enter the syllabuses, but they get there in the end. Whether the students thought all of them were relevant is another matter. I certainly felt that the vigorous survival of so many of the classical Natural Orders, as late as 1956, was remarkable.

In this work, as it developed and grew over the years, one cannot but be impressed by the teaching loads carried by very few people. When I arrived in Reading in 1956 there was some regret that my predecessor, David Goodall, had cut down one or two surviving series that had each included up to 100 lectures in an academic year. Perhaps it was a degree of nostalgia for those heroic days that led the vice-Chancellor under whom I first served, Sir John Wolfenden, himself a redoubtable teacher, to ask me (after a meeting of the Committee of Deans in which I had argued (successfully) for a departmental staff of ten academics), how it came about that if one person had to learn it all, one person could not teach it all.

Part of the answer was that Percival could indeed teach it all when necessary, and both vigorously and attractively into the bargain. But in his new department he also needed the help of younger people. J.M. Hector divided about five years as plant pathologist between the department and the Reading advisory province, before leaving for South Africa, where I knew him as Professor of Agricultural Botany in Pretoria. Dr A.S. Thomas, later in Uganda, remained on the strength from 1923–6 and was followed by J.S. Waldie, who was a mainstay of the teaching for students of agriculture when I arrived in 1956 and for a number of years after that.

The most notable recruit was Dr Adela Erith ("Brownie"), who entered as a student in about 1914, took a brilliant B.Sc. degree, and was appointed to the staff after the 1914–18 war. She became an honorary daughter in the Percival household until she established her own home in 1935 or 1936 (when Percival moved to Shinfield and his son Alan returned from the United States and set up at Mortimer) in order to care for her widowed mother. As research assistant, lecturer and senior lecturer, she devoted the whole of her academic life to the department that Percival had created. She retired in 1960. Her Ph.D. around 1924 (on white clover) is said to have required a German examiner, whom she travelled to Germany to meet.

In 1956 she managed both the Department and a newly-arrived professor with equal aplomb, though the latter did not win acceptance (or even much tolerance) until he had demonstrated in the field that he had soundly rebuilt his knowledge of the southern English flora and could in addition run up Silbury Hill.

After the first war, Brownie (maybe with Alan's aid) equipped Percival and herself with powerful army-surplus Enfield dispatch-riders' motorcycles so that they could set forth to botanize new areas of England. Mrs Percival is said to have followed by train. Brownie was as competent at maintaining and repairing these two monsters as she was at de-coking the engine head of her Austin 7 – before coming indoors to go on with the embroidery of an evening skirt. (John Percival also liked tinkering with machinery and is said to have taken a motor-cycle to pieces, to find out how it worked, and reassembled it on the lawn of his home). The extended Percival family also travelled widely in Europe, particularly in the Alps.

In 1925, plain but effective new laboratories were completed for the department (mainly for large practical classes for students of agriculture) above part of the Chemistry department at London Road. They continued to do admirable service for nearly fifty years.

The honours courses in Agricultural and Horticultural Botany

In 1925 there was the start of a new academic development of the greatest importance, made possible by the enlarged staff complement. In that year the first students were admitted to a four-year honours course of a new type, designed to combine a full academic training in botany with a complete professional specialisation in agricultural botany. The first year included those of the relevant basic sciences (Botany, Zoology, Chemistry, Physics and Geology) which students had not studied to a sufficient level at school. In the later years a sequence of courses in both the faculties of science and agriculture built up to a demanding final year. Taken as a whole, about two-thirds of the course was botanical. The first students graduated in 1929.

A parallel course in Horticultural Botany, managed, and I believe, initially largely taught by Brownie Erith, was introduced in 1950. It attracted a relatively small number of brilliant students. In one year, during the sixties, two of them were appointed to chairs – one in pure botany and the other in horticulture. Between them, these two honours courses produced many outstanding applied botanists, four of whom became Fellows of the Royal Society.

After 1956 the final years of these courses included all the branches of applied botany which the department felt it commanded sufficiently (anatomy, morphology

and taxonomy; genetics and plant breeding; environmental science and applied ecology; whole plant and crop physiology; and plant pathology). During the later sixties the introductory year was removed, and specialised options became necessary in the final year because biochemistry and molecular biology had to be added, and it was not possible to teach all seven of these branches to honours level in a three-year course.

These difficulties were reinforced, around 1970, by the marked decline in numbers, as well as in academic preparation, of prospective students. Indeed the course in horticultural botany had to be withdrawn in 1979 because by then there were too few applicants sufficiently well prepared as well as sufficiently bold, to cope with the demanding course. Moreover, during the seventies both academic managers and students began to insist on modular course structures. It seems evident to me that comprehensive professional courses of the kinds which we offered earlier may no longer be possible. Perhaps the success of the green movement has made formal botanical training superfluous – politically correct opinions on what is or is not ecologically sound seem nowadays to be amply sufficient.

RESEARCH IN AGRICULTURAL BOTANY, 1907–1932

This heading really means research by John Percival. In 1907, with the prospect of becoming free from wider academic responsibilities, Percival could for the first time begin to devote a substantial part of his time to personal investigations.

When he came to Reading he seems to have intended to study in detail the botany of all the more important economic plants of agriculture. One result of this was a collection of about 200 economic species which he maintained in the former Botanic Garden of the department at Shinfield, and which became widely, even internationally, regarded as a source of research material for botanists. But he soon found that the task he had envisaged was in fact too large for even his gargantuan botanical appetite.

Fortunately a good deal of the preliminary work was in fact done by J.M. Hector. His magisterial *Introduction to the Botany of Field Crops* (including many tropical and subtropical species) was published in South Africa in two volumes, in 1936. Twenty years later, it was still a valuable teaching resource.

Percival also established a fine herbarium of British plants and a collection, mounted on microscope slides, of their seeds. The former is incorporated in the herbarium of the Botany Department, and the latter is still used in teaching in the School.

Wheat breeding

Percival began to select and breed wheats around 1907. In 1909–10 the College Review reports the marked success of breeding from selected ears of exceptional quality. In 1910–11 he is reported to have completed work on the rivet variety Blue Cone ("the first College wheat"), which yielded so much more than other varieties that it compensated, in his view, for its less attractive baking quality. The dispute about quality versus tonnage rumbled on for years. Echoes of it are evident in the final paragraphs of Biffen's review of Percival's greatest work, "The Wheat Plant" (1921) (to which we shall return), in which he regrets the absence of a relevant discussion.

In 1913–14, 23 acres of Lane End Farm were occupied by Percival's wheats, several of which were reported to have given very promising yields in spite of adverse conditions. Selection of pure strains of high-yielding wheats continued in the Agricultural Botany department. There were encouraging reports over the years up to Percival's retirement in 1932. Among the named varieties were Partridge, Fox and Starling in addition to Blue Cone. In this work Percival seems to have been encouraged by the response of growers, and to have established a mutually satisfying relationship with Dunn's Farm Seeds of Salisbury.

Other participants in this symposium are better qualified than I am to assess the achievements of this long-sustained endeavour, but the programme encountered severe difficulties with wheat rust, and apparently with adaptation to different soils. G.D.H. Bell, in his book on *Cultivated Plants of the Farm* (1948) did not refer to any of Percival's varieties.

The Reading wheat collection

Percival's most widely acclaimed contribution to botanical studies of wheat arose from his general interest (reflected, for example, in the Wensleydale flora) in what it would nowadays be fashionable, politically correct, and perhaps even financially rewarding in terms of research grants, to call biodiversity. In this interest he was certainly ecumenical – one of his descendants, after a visit, refers to a collection of spiders, said to be the largest in Europe.

Between 1907 and 1930 he vigorously extended the collection of European wheats which he had brought from Wye in 1902 to cover more than 40 countries in all parts of the world. This was done with the aid of the Board (later the Ministry) of Agriculture and the United Kingdom Foreign Office. British embassies and consular posts in wheat-growing countries were asked to obtain samples of ears and seeds representing the kinds of wheat grown in them. The samples suggested were 4–5 spikes and an ounce of seed.

All this seems to have been done by correspondence. The choice of the kinds to be sent seems to have been left to the people on the spot. Though Percival enjoyed vacations in the wilder parts of Europe, the records do not suggest that he made field collections or surveys himself in any of the countries. He might have done, since for example in a letter to Vavilov (below) he writes authoritatively about the wheats of Egypt and other countries of North Africa and Western Asia, but on the whole he seems to have left the choices to locally- based people, who might be more likely than any transient visitor to know what kinds were significant for growers.

By 1911–12 the collection included 700 "lines", described as "pure". By 1915–16 there were 2000. In 1918–19 Percival felt sufficiently confident in his classification of the material to lay out the collection in systematic order – a defining, and indeed very satisfying stage in any such work, as I know well. To see one's intellectual endeavours summarised in order, on the ground, is extraordinarily rewarding.

He also felt, at this stage, that he had assembled samples of all the races of wheat in the world. Whether or not this was true (and by 1932, as a letter to Vavilov suggests, he clearly had some doubts) is far less important than what was actually done. In *The Wheat Plant* (1921) he offers partly original accounts of the anatomy and morphology

of *Triticum*, as a basis for a classification of the botanical diversity among the accessions. This remarkable work was the first of its kind on any group of crop plants.

Although we have some classified lists (by Percival and Erith) of the material in the collection, we do not have an accessions register for the European, world or the (later) British collections, and we have no more than a small part of the correspondence about them, but it does not seem that much detail was obtained on the natural, agronomic, or social environments in which the sampled crops had been grown, and to which they might be adapted. How far the accessions represented the full range of diversity among the kinds of wheat recognised, maintained and developed by growers in the countries, and how far they represented the more recent endeavours and interests of professional breeders and agronomists, is also seldom clear.

Very little is recorded about costs or quarantine in this considerable venture. Even less is recorded about local participation, indigenous knowledge, farmers' rights and intellectual property, which would hedge around any such effort today, if they did not actually stifle it altogether.

In 1927–8 Percival began, in addition, a "new study of the wheats of the British Isles". By 1930–1 he had assembled 100 different kinds, from growers and seed merchants, on which he based *Wheat in Great Britain* (1934, 2nd edition 1948).

National and international recognition

The Wheat Plant was widely acclaimed in Britain and in the world. Even before it appeared, the correspondence through which the collection had been assembled had done much to secure for Percival, and also for Reading, a substantial international reputation. The archives contain several congratulatory reviews and letters from Biffen at Cambridge, Beaven (curator of the National Barley collection) at Warminster, and others in Britain. W.B. Brierley regarded it as the finest monograph in the world's agricultural literature. It helped to gain for Percival a Cambridge Sc.D. in about 1922. (The external assessors were Biffen and the agrostologist Stapf). As I have already noted, Percival was a vice-President of the Linnean Society in 1926–7, and seems to have represented the Society at the International Genetics Conference in Berlin in 1927.

N.I. Vavilov, whom many senior plantsmen still regard ("centres of origin" notwithstanding) as the greatest agricultural botanist of our time, described the appearance of *The Wheat Plant* as "the greatest event in all applied botany – a great achievement – the best book on wheat from the existence (*sic*) of this world" (letter of 23 November 1921). In 1927, on the reverse of a photograph from his visit to Abyssinia, he addresses Percival as "The Wheat King". Vavilov visited Reading at least twice, in 1914 and 1921. We have his signature in the visitors' book of our former botanic garden, and a number of letters from him to Percival in the library archive. These letters, and the converse letters from Percival to Vavilov, will be brought together by Professor J. Hawkes and published separately.

In 1927 Percival was elected a member of the Scientific Council of the International Institute of Agriculture, in Rome, a forerunner of the Food and Agricultural Organization. Its main work in those days was to assemble statistical data about

agriculture throughout the world. This has continued to the present day in the remarkable statistical service of FAO.

The collection in later years

By the mid-1930s the accessions numbered about 2500. During 1934–7 they were grown out so that Percival and Brierley could record the incidences of rust, mildew, and insect damage – a vast endeavour. A particularly severe rust attack in 1938 made it desirable to repeat the study, but before this could be undertaken the land was turned over to war-time food production and the annual sowing of the collection seems to have been suspended.

In the annual sowings in earlier years, in autumn, 15–20 grains from a single ear of each accession were sown in a 6-inch square of ground separated from other accessions by about 15 inches in a row of such squares, separated from adjacent rows of squares by 20 inches. The ears were not bagged. "As self-fertilisation is the rule in wheat, each variety in the collection is a 'single' or pedigree line" (from an undated note by Percival or Erith). At harvest, 12 ripe ears of each variety were harvested and stored in tin biscuit boxes, $16 \times 4 \times 4$ inches, which (like the main fund which supported the work), came from the firm of Huntley and Palmer.

"The constancy of the pedigree line from year to year, its variation, the occurrence and splitting of crosses, and errors in sowing and harvesting can be checked by comparison of the produce of succeeding seasons" (but no comment on the results). It may be relevant here that a report in 1920–21 refers to an investigation on rogue plants found among crops of pedigree wheats – though no results of the investigation were reported in later years.

All the field work, and much of the harvesting, labelling, cleaning and storing, seems to have been done by a single gardener, Middleton, who had worked devotedly with Percival for many years and seems to have had sole effective charge of the wheats after 1949. In the later years part only of the collection was sown out each year, presumably for lack of money, time, labour and land.

John Cooper, who wished to interest himself in the collection in the later 1940s, felt that the accessions he saw did not consistently correspond with their descriptions in *The Wheat Plant*. John Jones, who joined the department in 1955, comments that only about 50 accessions were grown and that there were a great many tins.

In the same year my predecessor, David Goodall, decided that work on the collection should cease. What was left of it was transferred to the National Institute of Agricultural Botany at Cambridge (copies of the correspondence are held in the herbarium library at Reading) – where there is no trace of it today, perhaps because it was incorporated in the NIAB collections. The most important relics are the sets of cards which Percival prepared, bearing examples of the ears of the different races of wheat, which were sold for £100 the set, and the herbarium collection of the different sorts of wheat.

Not for the first and certainly not for the last time, a great living plant collection, to which substantial and devoted effort had been applied, seems to have withered away for lack of a presiding genius and changes in priorities for funding. Though Percival's

work on it surely added to our general knowledge of *Triticum* and its relatives, it is less easy to identify any direct practical benefit for breeders, producers or consumers. He seems to have found himself in the same position as many another dedicated collector: he had assembled, described and classified the collection (his initial purposes) but had no thoughts about what to do next except to screen it for potentially useful attributes – which is a substantial, specialised and costly task, even if it is linked to a purposeful breeding programme.

In part, his difficulty may have come from the poverty of his information about the specific adaptations of the accessions. Even today, few people ask themselves why the treasured biodiversity is there in the first place, and how the diverse forms are adapted to the diverse conditions of the human and natural environments in which they succeed. Neither Percival nor Vavilov really asked questions of these kinds either – though Darwin had at least implied them many years before.

The collection of *Aegilops*

Around 1928, Percival received from P. Zhukovsky, a trusted colleague of Vavilov who was publicly humiliated by Lysenko after Vavilov's death, a seemingly complete collection of the species of the genus *Aegilops*, which has an important place in the history of the domestication of *Triticum*. In subsequent years he devoted much attention to the morphology and genetics of crosses between species of the two genera.

During the second world war, the collections of Vavilov's Institute of Plant Industry were dispersed for safety from Petrograd (then Leningrad) to different places in the former USSR. In 1957 a visiting Russian botanist, V.I. Sokolov, who had been in charge of the dispersal, told us that during the war the *Aegilops* collection had been lost. Fortunately the Reading collection had survived, perhaps because of Percival's long-continued interest in it. It was a great satisfaction to us that John Jones was able to send a complete set to Petrograd and so repay Zhukovsky's kindness of thirty years earlier. This was the start of a two-way traffic in seed materials, by way of our Department, between Petrograd and many parts of the world, which continued until the USSR had rebuilt its own direct associations with co-operating institutions in different countries.

Archaeological wheats

From around 1927 onwards Percival received many samples of wheat and other cereal grains, dry or carbonised, which had been found in tombs and other archaeological situations in Egypt and West Asia. His identifications, strengthened by those of the late Dr Hans Helbaek, helped to develop our interests in archaeobotany at Reading. We saw this as a part of the general study of the evolution of plants under domestication and the movements of economic plants around the globe. This led us to perceive agricultural botany as a significant bridging field, linking plant science to humane studies, and an essential component of the study of the cultural history of mankind.

In later years these interests were developed by several of our students. Gordon Hillman, along with Mark Nesbitt, has done much to maintain the European and West Asian links in this field, following his introduction to the specialised techniques with

Maria Hopf in Mainz, and his work with the British Institute in Ankara and in the
Institute of Archaeology in London.

Our links with archaeobotany and the evolution of cultivated plants in the New
World were established and have been maintained (along with much other demanding
work), in a series of original, substantial, and always rigorously professional,
contributions, by Barbara Pickersgill.

PERCIVAL'S LAST YEARS

Percival's last years were spent partly at Shinfield, where he continued with
investigations on cereals, including studies of germination in the wheat collection and
other aspects of seed physiology. Towards the end of the nineteen forties the house
there, "Leighton", was sold, and John and Suzanne moved to Alan's house at Mortimer,
"Cottesmore". John Percival died there on January 26th 1949, and Suzanne followed
him on 8 October of the same year. Their remains were cremated and the ashes were
interred in the grave in Aysgarth churchyard which had already received Edward and
Elizabeth Chapman and the two brothers (James and William) who had died young.
The gravestone consequently bears both the Chapman and the Percival surnames.

"No Ordinary Man"

We now come to my final task, which is to consider John Percival the man. Many
others have done this in different ways. Most have been concerned with the botanist, the
agricultural scientist, the academic developer. Of these assessors, the most moving and
authoritative was Dr. W.M. Childs, who was Principal of University College, Reading
from 1902–3 and the founding vice- Chancellor of the University of Reading from
1926. When Percival retired in 1932 they had worked alongside each other for thirty
years.

On this occasion Childs wrote that by the retirement of Professor John Percival,

> "The University will lose not only a man of science of world-wide
> distinction, and a mind of diversified resource and activity, but also a
> personality arresting and compelling. No-one could be ten minutes in
> John Percival's company, or see him at work or at play, without feeling
> that he was in the presence of no ordinary man.

> "Those who have had the good fortune to be taught by him do not need
> reminding of his vehement and tireless energy, his ardour in investigation,
> his wonderful acuteness in observation, and his gift of lucidity in
> exposition. I once heard him give a lecture on spiders: it was, I think, the
> best lecture I have ever heard; and I have thought differently about spiders
> ever since. What keen pupil of his could fail to respond to that infectious
> and warming eagerness in pursuit of knowledge which none but the born
> teacher possesses? How many times has a chance question, in a casual
> talk, revealed mines of unsuspected knowledge? People in all parts of the
> world have sent their conundrums to John Percival, conundrums relating
> to a diversity of things besides agricultural botany, in the confident and
> well-founded belief that his extraordinary memory and range of

information would supply a helpful answer. Percival's "Wheat Plant" and his "Agricultural Botany" have gone into all lands, but John Percival is more than a distinguished specialist.

"Why do I say this? I find it difficult to express as I should wish the feelings born of thirty years of comradeship and friendship. How can I explain how I came to understand, what others have understood also, that in this man there was something more than academic attainments, that there was in him a rare quality of spirit, simple, almost boyish in kind but unusual in intensity, and powerful to evoke response from those who in any degree had sympathies like his own? Here was a man who with all his quick energy and exuberance kept a certain aloofness from the common world. He might possibly have been a more successful man, in the common sense, if that aloofness had been less. Along with his devotion to his science went a love of wild things and wild and lonely places. He once said to me "I cannot be happy unless once a year I set my foot upon a crag". It was this passion for the wilderness that took him in his youth on adventurous and lonely journeys in remote Scandinavia, and in later years to the llyns and streams of the Welsh mountains, often rod in hand. I do not forget that it was Percival who taught me how to cast a fly.

"For thirty years, John Percival has been a great teacher here. He has brought fame to his department and to the University. He has been a friend and inspiration to many generations of students. For myself I am proud to think that the vicissitudes of so long a period have strengthened and deepened our friendship" (Childs, 1932).

To this deeply-felt tribute the other friends who wrote about him could add little. Sir Daniel Hall (1939), with whom he worked at Cambridge and Wye, and who knew him for more than fifty years, described him as a "heaven-born teacher and an incomparable field naturalist". Sir E. John Russell (1966) who also knew him at Wye, writes that "he was wiry, active, keen, with piercing eyes and bursting with energy" – and adds that he was a keen bird-watcher, even though he sometimes used his gun to protect the wheat collection against feathered predators. Evidently he was not his father's son for nothing. "He built up the subject of agricultural botany as he went along. He was an inspiring teacher, active in practical classes, and he prepared keys, initially for his students, to grasses, weeds and trees".

Percival's successor, W.B. Brierley, whose Linnean Society obituary of Percival (1949) seems to be based in part on Childs' note, describes him as of world stature, the leading agricultural botanist of his day, although some might assign that distinction to N.I. Vavilov. He goes on to describe him as a gifted teacher, lucid in exposition, with encyclopaedic knowledge of agriculture and botany. He was versatile in his knowledge of books and languages, and he was an artist and a musician, a most competent photographer and a skilled fly-fisherman. But he could be brusque, and he certainly seems to have been a firm disciplinarian who did not gladly suffer fools or trivialities.

An unsigned article in *The Agricultural Economist* of April 1907 refers to Percival's "free, cheery manner, not dry as dust, yet a strict and firm disciplinarian".

Many friends and relatives – especially Alan's American descendants – speak of his kindness, generosity and benevolence.

There is more to be said about Percival, some of which may in part explain the space around him, the aloofness, which Childs sensed.

His essential nature was inevitably that of a Dalesman, built up of the elements described by Arthur Raistrick (1985) – including integrity, almost aggressive self-sufficiency and self-reliance, independence coupled to lasting but unspoken comradeship, ready generosity without fuss, a habit of understatement, wry humour and resilience, constant effort against the hardships of a harsh environment, unspoken love and loyalty to his dale and its unique environment.

With these inherent attributes he seems to me to have combined a determination to advance from the potentially difficult social circumstances of his early youth, to which some of his descendants say he continued sensitive throughout his life. He seems to me to have been driven by a strong ambition to advance himself professionally and socially. As time went by, and his intelligence, memory, imagination and indefatigable industry continued to help him to achieve the successes and recognitions that were clearly his due, he may have had to confront significant personal difficulties. His wife Suzanne seems to have aged more rapidly than he did.

Alan, whose formal education ended early and abruptly, left home in about 1917 to enter military service, and later to follow business interests in the United States. In these years John Percival was working especially hard to prepare and publish "The Wheat Plant". He was also managing an important and growing department in which he did a great deal of the teaching himself. Of course, he had devoted help from his small staff, and especially from Brownie Erith, who joined the family at this time, but much of what had to be done to develop the department into one worthy of University status inevitably fell on him, including the evolution of the new honours courses already mentioned.

When the University was established in 1926 much of this had been achieved. He was 63 years old. Instead of looking forward, as some might have done, to the imminent end of his service, he continued at full pace until he retired in 1932 at the age of 69. This seems to have meant no more than that he stopped teaching. He continued, during the remainder of the decade, and apparently during the war years, and in spite of osteo-arthritis and other inevitable physical consequences of the passage of time, to work on the wheat collection and his other research interests, and to read, think and write.

It is evident that, as Childs noted, John Percival was no ordinary man, but I go further. I have concluded that in continuing throughout a long and active life to develop his professional outputs and competences, and to preserve his industry, his humanity, his generosity, and his personal courage, against seemingly increasing difficulties, he was a man of the hardest steel, proof against whatever blows the passage of time could deliver.

ACKNOWLEDGEMENTS

REFERENCES

Bell GDH. 1948. *Cultivated Plants of the Farm.* Cambridge: Cambridge University Press.

Brierley WB. 1949. John Percival. *Proceedings of the Linnean Society session* **161:** 248–251.

Childs WH. 1931–2. John Percival. *Tamesis* **30 (3):** 101.

Dufresne L. 1820. *Taxidermy, or the art of collecting, preparing and mounting objects of natural history, for the use of museums and travellers.* English Translation by (Mrs.) S. Bowdich. London: Longman, Hurst, Rees, Orme and Brown.

Frost C. 1987. *A history of British taxidermy.* Long Melford: published by the author.

Hall A.D. 1939. The South Eastern Agricultural College, Wye, Kent. *Agricultural Progress,* **16:** 1–7.

Millward D. 1988. *A flora of Wensleydale: a centennial review of the plants of the dale.* Location not stated: The Yoredale Natural History Society.

Percival J. 1888. The Flora of Wensleydale, Northwest Yorkshire. *The Naturalist* **13:** 125–143.

Percival J. 1900. *Agricultural Botany, theoretical and practical* (first edition; 4th impression of eighth edition 1945). London: Duckworth.

Percival J. 1910. *Agricultural Bacteriology: theoretical and practical* (first edition; 2nd edition 1920). London: Duckworth.

Percival J. 1921. *The Wheat Plant: A Monograph.* London: Duckworth (photographic reprint, 1974).

Percival J. 1934. *Wheat in Great Britain.* 1st edition. Shinfield: the author, 2nd. edition 1948. London: Duckworth.

Percival J, Luxmoore J. 1906. *Report on the soils of Dorset and suggestions on manuring, cultivation etc.* Reading: Agriculture Department, University College, and Dorset, County Council.

Prantl K, Vines SH. 1881. *An elementary textbook of botany* (2nd edition). London: W. Swan Sonnenschein and Allen.

Raistrick A. 1985. In: Forder J & E, Raistrick A. *Open fell, hidden dale.* Kendal, Cumbria: Frank Peters Publishing Ltd.

Russell EJ. 1966. *A history of agricultural science in Great Britain, 1620–1954.* London: Allen and Unwin.

Speight H. 1897. *Romantic Richmondshire.* Huddersfield: Yorkshire Naturalists Union.

Ville G. 1909. *Artificial manures: their chemical selection and scientific application to agriculture* (English translation). New edition, revised by Sir William Crookes, FRS and John Percival. London: Longmans.

Archeobotany

Archaeology, Percival, and the problems of identifying wheat remains

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Abstract

In Britain Percival had already established the study of crop remains from archaeological sites by the early 1920s. However, the archaeobotanical record of the wheats continues to be problematic, with identifications often being based on poorly-researched criteria. Agricultural botanists should therefore treat archaeological evidence with caution. Examples are cited of problems in identifying charred remains of the free-threshing wheats and approaches that have been explored in their resolution. Particular emphasis is given to the potential of chemical fingerprinting based on infrared spectroscopy for both supplementing and testing the use of morphological criteria. Morphological criteria for distinguishing hexaploid and tetraploid wheats are summarised in an appendix.

PERCIVAL'S CONTRIBUTION TO ARCHAEOBOTANY

In Britain, it was Percival who initiated the study of plant remains from archaeological sites, and his interests in archaeobotany have been maintained in Reading's Department of Agricultural Botany ever since. Hugh Bunting, for example, fought (unsuccessfully) to recruit Hans Helbaek, Europe's pre-eminent pioneer of archaeobotany, to the Department's research staff, and ensured that his teaching staff

included others active in archaeobotany such as Barbara Pickersgill. He also personally tutored his students in the role of archaeobotany in agricultural botany, as did Barbara Pickersgill in teaching crop evolution. Indeed, the involvement of Mark Nesbitt and myself in the subject was a direct result of this policy. Thereafter, under Peter Caligari, the Department has continued to support archaeobotanical studies in the hands of key researchers such as John Letts.

Percival did not himself publish many of his analyses of plant remains from archaeological sites. Notable exceptions include his 1936 paper on "Cereals of Ancient Egypt and Mesopotamia" and a chapter on "ancient British wheat" in his book *Wheat in Great Britain* published in 1934. However, it is clear from Wendy Carruthers' catalogue of Percival's Reading-based archives of archaeological plant remains (Carruthers, 1992) that he completed analyses of ancient remains of cereals from a vast array of sites in countries including India, Egypt, the then Palestine, Syria, Iraq, Turkey and Switzerland, and from over 40 sites scattered across the British Isles. We correspondingly find his identifications cited in the reports of excavators such as Mallowan, Caton-Thompson, Carter, Wheeler, Childe, and Pitt-Rivers.

In identifying ancient remains of cereals, Percival had the clear advantage of a comprehensive familiarity with the living wheats. Furthermore, the range of primitive forms available to him then was significantly greater than anything we can find in genebanks today. This became particularly apparent when Terry Miller and I explored his own set of the Percival wheat collection for dense- eared, short-grained *dicoccums* and *durums* of a sort that we find archaeo- logically, but which neither of us had encountered in living populations, whether under traditional cultivation or in genebanks. We quickly discovered that Percival had indeed collected several forms of both, albeit under names that inevitably pre-dated a modern understanding of wheat's genomic constitution.

WHEAT IDENTIFICATION IN ARCHAEOBOTANY TODAY:
A WARNING

There is a tendency among agricultural botanists to accord greater credibility to archaeological evidence than it deserves. This is particularly true in studies of ancient wheats, a point appropriately inferred by Miller (1992). The uncomfort- able reality is that (a) archaeobotanical evidence is often paltry, (b) progress in identifying archaeological remains of wheats has often been limited by Percival's archaeobotanical successors lacking his close familiarity with the morphology of modern wheats, and (c) there is disarray on the nomenclature appropriate for those remains of ancient wheats that have no exact modern counterparts.

On most archaeological sites wheats survive only as charred grains, as charred fragments of the densest bits of chaff, as impressions in pottery or adobe, or as phytoliths (opaline silica-bodies from the epidermis). Clearly, John Letts' remains of smoke-blackened thatch represent a remarkable exception here. Each of these classes of remains can present significant problems of identification. The problems have been further compounded by the reluctance of most archaeobotanists to commit sufficient time to examining a broad spectrum of populations of living wheats and their over-readiness to accept the identifications appended by seed stations to modern

reference specimens. This, in turn, has resulted in identifications of ancient specimens that are based on poorly-researched criteria. The net effect has been the publication of many dubious identifications and occasionally the publication of remains as "new species" when they represent no more than minor variants of modern taxa.

This might sound bleak, but in fact not all remains are so problematic, and even in the difficult groups secure identifications are often possible if we undertake appropriate studies of modern equivalents. An example of some of these problems and of approaches to their resolution comes from attempts to distinguish rachis remains of free-threshing tetraploids and hexaploids.

AN EXAMPLE FROM THE FREE-THRESHING WHEATS

From the late 1960s the use of flotation to extract charred remains of plants from archaeological deposits allowed the recovery of crop-processing waste, particularly cereal chaff. This had seldom been present in the grain caches and pottery imprints available to Percival and Helbaek. These chaff remains sometimes included wheat rachises. While the morphology of grains had often proved to be of limited value in distinguishing free-threshing tetraploids and hexaploids (Rothmaler, 1955; Schiemann, 1948; van Zeist, 1976; but see Kosina, 1984), the more intricate morphology of rachis remains offered grounds for greater hope.

Predictably, perhaps, the rachis features initially proposed by archaeo-botanists for distinguishing free-threshing tetraploids and hexaploids were based on rather paltry studies of living material, and they not only offered little diagnostic potential, but also spawned many misidentifications. The first more systematic study of rachises to be published was that undertaken by Willem van Zeist (1976). After examining a range of accessions from seed banks, he concluded there was complete overlap between the two ploidies in respect of each of the potentially diagnostic criteria that he examined. However, it was clear from his illustrations of the modern specimens he had used that several of them had been misidentified or mis-labelled by the source seed stations. This problem is familiar to many of us working in this field. For example, in a consignment of cereals that I received from one European seed station, 60% of them were mis-labelled at even the level of ploidy, a fact confirmed from chromosome counts in root-tip squashes.

However, more extensive studies of rachis morphology which were started in 1970 had already indicated that certain features were diagnostic of ploidy level after all. The rationale that I adopted in this study was an obvious one, and was a mirror image of the taxonomic analysis used by Sarkar & Stebbins (1956) in the hunt for the B genome donor. I took a range of populations of the D genome donor, *Aegilops squarrosa*; examined them for features that could be traced in hexaploid wheats but which were absent in free-threshing tetraploida; tested the usefulness of these features in distinguishing the rachises of living free- threshing hexaploids from those of a wide array of equivalent tetraploids; and then used the most reliable of them to identify ancient rachis remains. From the outset of the work, the identity of all the living specimens was established using independent (non-rachis) criteria.

After examination of some hundreds of specimens, it became apparent that at least five different features of rachis morphology allowed clear separation of free-threshing tetraploids and hexaploids (Hillman, 1983). The one notable exception was *Triticum carthlicum* which, despite its tetraploid complement of $2n = 28$ chromosomes, manifested several features seemingly traceable to the D genome, as well as four minor features peculiar to itself. The distinctiveness of *T. carthlicum* would seem to accord with genetic evidence for hexaploid involvement in its evolution (Vavilov & Jakushina, 1925; Kuckuck, 1979), notwithstanding the suggestion of Muramatsu (1986) that the Q gene of *carthlicum* and *aestivum* is shared by tetraploids such as *durum* and *dicoccum*. More minor exceptions included a distinctive race of Turkish *durum* in which some of the principal tetraploid rachis features were poorly developed. (The principal differences distinguishing hexaploids from most of the tetraploids, excluding *carthlicum*, are summarised in an appendix to this paper.)

Identifications of free-threshing wheat rachises at the level of the other classical "species" within ploidy also proved to be possible in some cases. For example, rachis internode proportions can often distinguish the more extreme forms in what appears from rachis morphology as a cline of variation represented by the classic *turgidums*, *durums* and *turanicums*, although sub-basal rachis fragments of the pyramidal *durums* inevitably overlap with medial rachis segments of the *turgidums*. In distinguishing these last taxa, therefore, rachis criteria would appear to be less specific than the morphological criteria used by Anna Filatenko (pers. comm., 1999) and Dorofeev & Migushova (1979), which indicate *turgidum* to be a discrete entity entirely distinct from *durum*.

Following the isolation of these rachis criteria in the early 1970s, and their presentation at the International Workgroup for Palaeoethnobotany in 1983, they have provided a means of identifying the ploidy level of charred rachis remains of free-threshing wheats from sites in both SW Asia (e.g. Hillman, in French, 1972; Hillman, 1978; Nesbitt, 1993, 1995; Moulins, 1997) and in Europe (Jacomet, 1987; Near, 1992; Maier, 1996; Schlumbaum & Jacomet, 1998; Letts, 1999). In SW Asia this new possibility of accurate identification to ploidy level has allowed a reappraisal of the evolution of hexaploid wheats generally (Nesbitt, this vol.), and in Europe they have allowed archaeobotanists to overturn the long-held assumption that all the early remains of free-threshing wheats were hexaploids (Maier, 1996; Nesbitt, this vol.).

So far, all of these remains of free-threshing wheats appear to represent species that are still extant, albeit with some different infra-specific variants. It is therefore disconcerting to see the erection of a "new species", *T. parvicoccum* Kislev (Kislev, 1980, 1981) on the basis of charred remains of rachis that appear to represent merely a short-grained form of dense-eared types of *durum* or *turgidum*. Although Percival (1921) described an Egyptian form of one such wheat as *T. pyramidale* Pers., and had incorporated related forms into his wheat collection under other names, all such forms were thereafter recognised as no more than "ear-types" within either *durum* or *turgidum* (Vavilov, 1931; Zhukovskiĭ, 1923/1951; Flaksburger, 1935; Gökgöl, 1939; Schiemann, 1948). Indeed, Kuckuck & Peters (1964) more recently produced just such forms as induced mutants from *dicoccum*. (Following Vavilov's observation that these dense-eared tetraploids appeared to parallel the variation found in the hexaploid

compactums, Schiemann (1948) designated them as forms within subspecies under the headings Ährentyp *duro-compactum* and Ährentyp *turgido- compactum*).

THE GLUME WHEATS

It is also often possible to distinguish some of the glume wheats reliably, so long as we have the remains of the grains and the spikelet forks (= glume bases + rachis nodes) that occur in abundance on many archaeological sites. For example, we can generally (but not always) distinguish between the glume wheats of different ploidies (Hillman *et al.*, 1996; Jacomet, 1987). *Within* a single ploidy level, however, disentangling domestic forms from their wild progenitors can be more problematic than is often assumed, not only when we use grain morphology, but also when we use features linked with rachis fragility (Hillman & Davies, 1990, 1992; Kislev, 1992; Zohary, 1992). In our attempts to detect the start of cultivation and unravel the processes of domestication, these problems clearly represent a serious impediment. Again within ploidy, in trying to separate AAGG from AABB tetraploids, we often face considerable difficulties in distinguishing charred spikelet forks and grains of *timopheevii* from those of the *dicoccum* range, and we have made no progress at all in distinguishing charred remains of *araraticum* from *dicoccoides*. Within the diploids, criteria for distinguishing equivalent remains of *boeoticum* and *uratu* also continue to elude us.

As for distinguishing remains of glume wheats from free-threshing wheats within the same ploidy level, it is often very difficult from charred remains of grains, but is generally feasible from remains of chaff. Nevertheless, we still sometimes face problems with chaff remains of a) speltiform *aestivums* of the sort described by Kuckuck (1964) and collected by us in eastern Turkey, and b) semi-brittle-eared *durums* of the sort that we have also found growing in Turkey. Examples of identifications of charred remains based on morphological criteria are discussed in the paper by Mark Nesbitt.

CHEMICAL CRITERIA

Several of the problems of identification based on morphological criteria are now beginning to be resolved by the use of chemical finger-printing. Several approaches have been explored using thin-layer chromatography, infrared spectroscopy (including fourier-transform infrared spectroscopy), pyrolysis mass-spectrometry, and gas-chromatography mass-spectrometry. By far the most useful so far has involved the use of infrared spectroscopy, particularly the results from Frances McLaren (McLaren, Evans & Hillman, 1989; McLaren, 1999; Hillman *et* al., 1994; Cave, 1999; Letts *et al.*, 1994). Seven years of analyses have enabled McLaren to assemble a substantial library of IR spectra of modern wheats of known identity, and these are providing a basis for identifying ancient specimens using equivalent spectra derived from extracts from charred grains or chaff fragments. The technique allows the separation not only of ploidies, but also of species such as *urartu* from *boeoticum,* and *timopheevi* from *dicoccum*. Indeed, it can even distinguish domestic forms from their wild ancestors, and other closely related forms such as *turgidum* from *durum*. In addition, comparisons of identifications based on chemical and morphological criteria applied independently

to the same specimens have allowed us to test the reliability of some of the morphological criteria.

Studies of DNA sequences recovered from charred remains of wheat grain also now offer the possibility of distinguishing ploidies, albeit at considerable expense (Brown. 1999; Brown *et al.*, 1998). Eventually, such techniques will doubtless allow more precise identifications.

OTHER FORMS OF PRESERVATION

In marked contrast to the problems posed by charred remains, when archaeobotanists such as John Letts have wheat remains in the form of whole plants as in his smoke-blackened thatch, then identification is possible at an altogether more sophisticated level, allowing the resolution of an entirely different set of questions of the sort explored in his paper (Letts, 1999).

In summary, after uncertain beginnings, the reliability of archaeobotanical data is slowly improving and is allowing us to address new questions concerning wheat evolution and the origins of agriculture of relevance to both agricultural botany and archaeology. Some of these questions form the subject of the following paper by Mark Nesbitt.

REFERENCES

Brown TA. 1999. How ancient DNA may help in understanding the origin and spread of agriculture. *Philosophical Transactions of the Royal Society, London, Series B* **354**: 89–98.

Brown TA, Allaby RG, Selares R, Jones GEM. 1998. Ancient DNA in charred wheats: taxonomic identification of mixed and single grains. *Ancient Biomolecules* **2**: 185–193.

Carruthers WJ. 1992. Percival and Helbaek's archive of plant remains. *Circaea, The Journal of the Association for Environmental Archaeology* **8**: 65–70.

Cave M. 1999. The use of chemical markers and chemometrics in the identification of charred remains of grasses from Epipalaeolithic sites in SW Asia. PhD dissertation, Institute of Archaeology, University College, London.

Dorofeev VF, Migushova EF. 1979. *Flora of cultivated plants. 1: Wheat.* Leningrad: Kolos. [in Russian].

Flaksburger CA. 1935. *Flora of cultivated plants.* Leningrad: Academy of Sciences.

French DH. 1972. *Excavations at Can Hassan III, 1969–1970.*

Gökgöl M. 1939. *Türkiye buğdayları* II. (= Turkey's wheats). İstanbul: Çelikcilt Matbaası. [in Turkish].

Hillman GC. 1978. On the origins of domestic rye – *Secale cereale*: the finds from aceramic Can Hasan III in Turkey. *Anatolian Studies* **28**: 157–174.

Hillman GC. 1983. Criteria for identifying the rachis remains of free-threshing wheats. *Sixth Symposium of the International Workshop for Palaeoethnobotany, Plants and ancient Man: Studies in palaeoethnobotany.* Groningen, 30 May – 3 June, 1983.

Hillman GC, Davies MS. 1990. Domestication rates in wild wheats and barley under primitive cultivation. *Biological Journal of the Linnean Society* **39**: 39–78.

Hillman GC, Davies MS. 1992. Domestication rates in wild wheats and barley under primitive cultivation: preliminary results and archaeological implications of field measurements of selection coefficient. In: Anderson PC (ed.). *Préhistoire de l'agricultre: nouvelles approches expérimentales et ethnographiques.* Paris: Éditions du CNRS, 113–158.

Hillman GC, Mason SLR, de Moulins MD, Nesbitt RM. 1996. Identification of archaeological remains of wheat: the 1992 London Workshop. *Circaea, The Journal of the Association for Environmental Archaeology* 12: 195–209.

Hillman GC, Wales S, McLaren FS, Evans J, Butler AE. 1993. Identifying problematic remains of ancient plant foods: a comparison of the role of chemical, histological and morphological criteria. *World Archaeology* 25: 94–121.

Jacomet S. 1987. *Prähistorische Getreidefunde: eine Einleitung zur Bestimmung prähistorische Gersten- und Weizen-Funde.* Basel: Botanisches Institute der Universität. Abteilung Pflanzensystematik und Geobotanik.

Kislev ME. 1980. *Triticum parvicoccum* sp. nov., the oldest naked wheat. *Israel Journal of Botany* 28: 95–107.

Kislev ME. 1981. The history of the naked wheats. *Zeitschrift für Archäologie* 15: 57–64.

Kislev ME. 1992. Agriculture in the Near East in the VIIth millennium BC. In: Anderson PC (ed.). *Préhistoire de l'agriculutre: nouvelles approches expérimentales et ethnographiques.* Paris: Éditions du CNRS, 87–93.

Kosina R. 1984. Morphology of the crease of wheat caryopses and its usability for the identification of some species: a numerical approach. In: van Zeist W, Casparie WA (eds). *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam: Balkema, 177–191.

Kuckuck H. 1964. Experimentelle Untersuchung zur Entstehung der Kulturweizen. I: die Variation des iranischen Speltweizens und seine genetischen Beziehungen zu *Triticum aestivum* ssp. *vulgare* (Vill., Host) Mac Key, ssp. *spelta* (L.) Thell. und ssp. *macha* (Dek. Et Men.) Mac Key, mit einem Beitrag zur Genetik des Spelta-Komplexes. *Zeitschroft für Pflanzenzuchtung* 51: 7–140.

Letts JG. 1999. Smoke blackened thatch: a unique source of late medieval plant remains from Southern England. Reading: English Heritage and the Department of Agricultural Botany and Rural History Centre, University of Reading.

Letts JG, Evans J, Fung M, Hillman GC. 1994. A chemical method of identifying charred plant remains using infra-red spectroscopy. In: Hastorf CA, Johannson C (eds). *Corn and culture in the prehistoric New World.* Boulder, California: Westview Press (University of Minnesota Publications in Anthropology No. 5), 67–80.

Maier U. 1996. Morphological studies of free-threshing wheat ears from a Neolithic site in southwest Germany, and the history of naked wheats. *Vegetation History and Archaeobotany* 5: 39–55.

McLaren FS. 1999. The role of chemical criteria in the identification of ancient Old World cereals. PhD dissertation, Institute of Archaeology, University College, London.

McLaren FS, Evans J, Hillman GC. 1990. Identification of charred seeds from Epipalaeolithic sites in SW Asia from chemical criteria. In: *Archaeometry '90: Proceedings of the 15th International Archaeometry Symposium, Heidelberg, 1990.* Basel: Birchauser, 797–806.

Miller, TE. 1992. A cautionary note on the use of morphological characters for recognising taxa of wheat (genus *Triticum*). In: Anderson PC (ed.). *Préhistoire de l'agriculutre: nouvelles approches expérimentales et ethnographiques.* Paris: Éditions du CNRS, 249–254.

Moulins DM. de 1997. *Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium B.C.* Oxford: British Archaeological Reports, International Series 683.

Muramatsu M. 1986. The *vulgare* super-gene Q: its universality in durum wheat and its phenotypic effects in tetraploid and hexaploid wheats. *Canadian Journal of Genetics and Cytology* 28: 30–41.

Near JK. 1992. Archaeological remains from Halai: a Neolithic settlement in central Greece. MSc thesis, Department of Human Environment, Institute of Archaeology, University College, London.

Nesbitt RMN. 1993. Ancient crop husbandry at Keman-Kalehöyük: 1991 archaeobotanical report. I. Mikasa T (ed.). *Essays on Anatolian Archaeology. Bulletin of the Middle Eastern Culture Center of Japan* 7: 75–97.

Nesbitt RMN. 1995. Plants and people in ancient Anatolia. *Biblical Archaeology* 58: 68–81.

Nesbitt RMN. Wheat evolution: integrating archaeological and biological evidence. (This volume).

Percival J. 1921. *The Wheat Plant: A Monograph.* London: Duckworth.

Percival J. 1934. *Wheat in Great Britain*. London: Duckworth.

Percival J. 1936. Cereals of Ancient Egypt and Mesopotamia. *Nature* **138:** 270–273.

Rothmaler W. 1955. Zur Fruchtmorphologie der Weizen-Arten (*Triticum* L.). *Feddes Repertorium* **57:** 209–216.

Schiemann E. 1948. *Weizen, Roggen, Gerste. Systematik, Geschichte und Verwendung*. Jena: Fischer.

Sarkar P, Stebbins GL. 1956. Morphological evidence concerning the origin of the B genome in wheat. *American Journal of Botany* **43:** 297–304.

Schlumbaum A, Jacomet S. 1998. Co-existence of tetraploid and hexaploid naked wheat in a Neolithic lake dwelling of Central Europe: evidence from morphology and ancient DNA. *Journal of Archaeological Science* **25:** 1111–1118.

Vavilov NI. 1931. The wheats of Abyssinia, and their place in the general system of wheats. *Bulletin of Applied Botany, Supplement* **51.** [In Russian with English resumé]

Vavilov NI, Jakushkina O. 1925. Contribution to the phylogenesis of wheat and the inter-species hybridisation in wheats (a hybridological analysis of the species *T. persicum* Vav.). [In Russian with English resumé]. *Bulletin of Applied Botany* **15:** 3–159.

Zeist W van. 1976. On macroscopic traces of food plants in southwestern Asia (with some reference to pollen data). *Philosophical Transactions of the Royal Society, Series B* **275:** 27–41.

Zhukovskiï PM. 1951. *Türkiyenin ziraî bünyesi* (= Turkey's agricultural constitution). Ankara: Türkiye Şeker Fabrikaları A.Ş. [Turkish translation of the 1923 Russian original: Земледельческыя Туцыя. Leningrad: Academy of Sciences.]

Zohary D. 1992. Domestication of the Neolithic Near East crop assemblage. In: Anderson PC (ed.). *Préhistoire de l'agriculutre: nouvelles approches expérimentales et ethnographiques*. Paris: Éditions du CNRS, 81–86.

APPENDIX

Summary of rachis criteria for distinguishing 4x and 6x wheats

The criteria for distinguishing rachis remains of hexaploid and tetraploid wheats (excluding *T. carthlicum*), as presented at the International Workgroup for Palaeoethnobotany in Groningen (Hillman, 1983) are summarised below. The criteria are intended primarily for distinguishing free-threshing members of either ploidy, but criteria numbers 2, 3, 4c and 5 can also be used to help distinguish their glume-wheat eqivalents.

T. DURUM GROUP (including *T. turgidum, T. turanicum* and *T.polonicum*	*T. AESTIVUM* GROUP (including *T. compactum*) + *T. sphaerococcum*
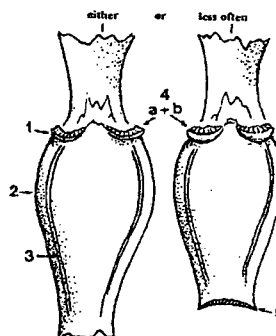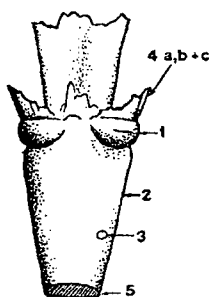
1. shape of rachis node immediately below point of glume insertion

Node often with a conspicuous rounded lump beneath each glume-insertion, with or without a thin fissure across the hump. (This feature is poorly developed in some small-eared pyramidal central Anatolian *durums*.)

Node with either (a) no lumps at all, and merely a narrow ridge below glume insert; or (b) weakly developed lower halves of lumps, in which the upper halves give the impression of having collapsed.

2. Shape of rachis internode – in lax-eared forms only. (In dense-eared forms of either ploidy, there is insufficient room for internode shape to be properly expressed.)

Rachis internodes forming ± straight-sided trapeziums, with only a slight incurved narrowing immediately below the node, even in extremely lax-eared tetraploids such as *turanicum* and *polonicum*.

Rachis internodes conspicuously shield-shaped, with a strongly curved widening of the upper third of the internode, and a more steeply curved narrowing just below the node.

3. Presence/absence of longitudinal lines near the outer edge of the convex (abaxial) race of rachis internodes.
(This feature has so far proved the most reliable of all those listed here.)

No trace of lines, except those resulting from occasional wrinkles due to shrinkage if the ears were cut while still green.

Clear longitudinal lines present, often bearing hairs. The lines often have the following form in T.S.

Ridge often with hairs (The lines are just as conspicuous in compact/ dense-eared forms.)

4. Glume-based morphology. Three linked features can be used here:

(a) Pieces of glume-based tissue commonly survive attached to rachis node. Such fragments then clearly exhibit features 4b and 4c.

(a) Glume-based deciduous, except for an extremely narrow crescentic band of inwards-sloping crumpled tissue attached to the rachis node. (This represents the lowest part of the fold of glume-base tissue described under 4b.)

(b) Glume-base never crumpled across primary nerve/keel. At most, has a very weak fold, and this only in spiklets with 3 or more fertile florets.

(b) Glume-base with crumpled fold across base of glume, with the fold extending right across the primary nerve + adjacent tertiary nerves. (Described by Schiemann, 1948, as "faltig eingezogen".)

(c) Acute angle on any surviving glume-base tissue (when viewed from above), with a keel often clearly discernible.

(c) Generally an obtuse angle on glume-base scar (viewed from above) and with no trace of a keel.

5. Roundness of rachis edge in transverse section.

Rachis edge in T.S. generally rounded.   Rachis edge in T.S. generally attenuated.
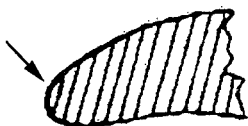
Wheat evolution: integrating archaeological and biological evidence

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Abstract

Understanding of wheat evolution has benefited from improvements in identification techniques for archaeological wheat remains, and from the development of genetic characterisation of current-day wheats, most recently using DNA variability. Archaeological and botanical evidence agree well in locating the domestication of einkorn (*Triticum monococcum*) and emmer (*Triticum dicoccum*) in the fertile crescent of the Near East at about 7500 years BC (uncalibrated). DNA characterisation offers excellent potential for narrowing the area of origin, and tracing the spread of crops to Europe. The origin of spelt (*T. spelta*) is more complex. Biological and archaeological evidence agree that spelt first results from the hybridisation of a cultivated tetraploid wheat and *Aegilops tauschii* near the Caspian Sea or in Transcaucasia. However archaeobotanical evidence for spelt in this region or on its putative routes to Europe is still scanty and is based on doubtful identifications. The sudden appearance of spelt in Early Bronze Age central Europe may be the result of a local hybridisation of free-threshing hexaploid wheat (*T. aestivum*) and emmer wheat. The time and place of the origins of European spelt await resolution.

INTRODUCTION

The size of the literature on the history and evolution of the wheats reflects two factors: firstly, their central role in agricultural economies and human culture over the last ten millennia, and secondly, the rich and fascinating variety of forms of wheat and their complex genetic basis. John Percival made significant contributions in both areas – to the history of human use of wheat through his archaeobotanical analyses of ancient wheat remains from archaeological excavations (Carruthers, 1992), and to the history

of wheat evolution through his morphological and agronomic studies. My aim in this paper is to survey progress in the use of archaeological evidence to understand wheat evolution since Percival's *The Wheat Plant* (Percival, 1921), and in particular to investigate the degree of correlation between archaeological evidence, primarily in the form of plant remains, and biological evidence such as genetics and biogeography. Rather than attempt a comprehensive survey (cf. Harlan, 1981; Bell, 1987; for hulled wheats: Nesbitt & Samuel, 1996) I focus on two issues: the domestication of the earliest cultivated wheats, einkorn and emmer, and the origin of spelt and bread wheat.

Note on wheat nomenclature

The confused state of current-day wheat nomenclature reflects the diverse approaches of wheat scientists (Morrison, this volume). In this paper I have chosen to follow the traditional classification of Dorofeev & Migushova (1979), as conveniently summarised by Morrison (1994), as it is simple to use and is similar to the classification used by most agronomists and archaeobotanists (Table 1).[1]

Note on radiocarbon dating

Radiocarbon dating has been used since the 1950s to date archaeological material including, since the 1980s, single charred seeds (Legge, 1986). However, radiocarbon dating systematically underestimates the age of objects, by 1000 to 1500 years during the Neolithic of the Near East. Until recently, calibration has not been possible for radiocarbon dates prior to 6000 uncal BC. A recent calibration (Stuiver *et al.*, 1998) allows radiocarbon dates from before this period to be converted to calendar year dates, and these new dates are likely to be widely adopted by the archaeological community. However, as an interim measure in this paper, I have used uncalibrated dates (indicated as uncal BC) for these early periods (Table 2), and calibrated dates (cal BC) for discussion of later European prehistory.

TABLE 2.   Dating of the main archaeological periods during which wheat domestication occurred in the Near East. Calibrated dates follow Stuiver *et al.* (1998). All dates are approximate and vary regionally.

	Uncalibrated yrs BC	Calibrated yrs BC
Epipalaeolithic		
Kebaran	18,000 – 10,800	21,700 – 13,400
Natufian	10,800 – 8,500	13,400 – 10,600
Neolithic		
Pre-Pottery Neolithic A	8,500 – 7,500	10,600 – 8,700
Pre-Pottery Neolithic B	7,500 – 5,500	8,700 – 6,300
Pottery Neolithic	5,500 – 4,200	6,300 – 5,200

1   Current wheat taxonomies are conveniently summarised at the GrainTax website:
    http://wheat.pw.usda.gov/ggpages/GrainTax/

TABLE 1. The main wheat species arranged according to genome and domestication status. Nomenclature follows Dorofejev & Migushova (1979)

Domestication status	Hulled/ free-threshing	Diploid group *Geonome*: A	Tetraploid group A^uB	Transcaucasian tetraploid group A^bG	Hexaploid group A^uBD
Wild	Hulled, fully brittle rachis	*T. boeoticum* Boiss. (A^b) **Wild einkorn** *T. urartu* Tum. ex Gandil. (A^u)	*T. dicoccoides* (Körn. Ex Aschers. & Graebn.) Schweinf. **Wild emmer**	*T. araraticum* Jakubz.	None
Domesticated	Hulled, semi-tough rachis	*T. monococcum* L. (A^b) **Einkorn**	*T. dicoccum* Schrank ex Schübl. **Emmer** *T. ispahanicum* Heslot *T. paleocolchicum* Men.	*T. timopheevii* (Zhuk.) Zhuk.	*T. spelta* L. **Spelt** *T. macha* Dekapr. & Menabde *T. vavilovii* (Tum.) Jakubz.
Domesticated	Free-threshing, fully tough rachis	*T. sinskajae* Filat. & Kurk. (A^b) - rare mutant in Turkish einkorn fields	*T. durum* Desf. **Macaroni wheat** *T. turgidum* L. **Rivet wheat** *T. turanicum* Jakubz. **Khorasan wheat** *T. polonicum* L. **Polish wheat** *T. aethiopicum* Jakubz. *T. carthlicum* Nevski in Kom. **Persian wheat**		*T. aestivum* L. **Bread wheat** *T. compactum* Host **Compact wheat** *T. Sphaerococcum* Percival

IDENTIFICATION OF ANCIENT WHEATS

Introduction

The basis of the identification of archaeological wheat remains is their comparison with living material of known identity. The major problem that faces archaeobotanists is incomplete preservation. Faced with a modern ear of wheat, the taxonomist can use a range of relatively well-documented morphological and genetical characters to determine identification to species. In contrast, archaeological material is usually the fragmented debris of crop-processing, preserved in very arid areas by desiccation or by special conditions such as thatch (Letts, 1999), but in most regions by charring.

Denied access to intact spikes, archaeobotanists have developed novel identification criteria based on careful examination of those parts of the ear that do survive, primarily the rachis segments and the grain. There is general agreement that reliable, repeatable identification criteria do exist for rachis remains, allowing hulled wheats to be separated from free-threshing ("naked") wheats, and determination of the ploidy level (Hillman *et al.*, 1996, Hillman, this volume). In contrast, grain identification is far more problematic, in part because the effects of charring on the endosperm usually lead to swelling and changes in shape and size, and in part because grain shape is largely a function of glume shape and texture, which may be quite similar in wheats of different ploidy levels such as emmer and spelt, or macaroni and bread wheat (cf. Millet, 1986). Grain shape and size is also significantly affected by number of grains developing in the spikelet (Maier, 1996).

Identifying domestication

Domestication is the process by which humans take reproductive control of plants or animals, modifying them for their own purposes. Selection pressures applied – consciously or unconsciously – in cultivation and harvesting have resulted in significant adaptations of crops to human needs. In wheat, these include the tough rachis (ensuring that grain is not lost during harvest), larger grains (ensuring better germination), higher ratio of starch to bran, and a range of physiological changes linked to higher yields (Evans, 1993). Of these characteristics, the first two are most easily detected in archaeological material. In wheat, unlike in barley, there are significant changes in size and shape of grain at domestication, although their detection is complicated by effects of charring. Identification of grains of wild einkorn is complicated by their close resemblance to wild rye grains and, without chaff, identification to genus is difficult. Identification of chaff is similarly complicated by the presence in the fertile crescent of morphologically similar, but reproductively isolated, species that are sibling to the wild wheats (Johnson & Dhaliwal, 1976). The morphological characters that separate *T. urartu* from *T. boeoticum* and *T. araraticum* from *T. dicoccoides* do not allow separation of archaeobotanical material.

The spike of wild cereals breaks up at maturity, allowing the grain-containing spikelets to be distributed. In domesticated wheat the rachis is tough, and disarticulation of the spike is done by humans after harvest. The spikelets of wild wheat break apart at the base of each rachis segment, leaving a neat, smooth abscission scar, in contrast to the ragged, torn scar of broken domesticated spikes (Hillman & Davies, 1990; Willcox, 1992). However, small numbers of torn rachis scars may result from

threshing of the lower spikelets which usually remain attached to the culm, even in mature ears (Hillman & Davies, 1992; Kislev, 1992). At established agricultural sites we do indeed find that most of the spikelets have torn scars, but the interpretation of very small numbers of torn scars at hunter-gatherer sites is problematic (Kislev, 1997).

There are also problems in dating early material. For example, the charred plant remains from the Pre-Pottery Neolithic A levels at Jericho consist of a few fragments of grain of uncertain status. The best evidence for domestication is a single clay imprint of two spikelets of an intact (and, therefore, domesticated) einkorn spike from level X, dating to the very latest part of the PPNA (c. 7600–7400 uncal BC). However, this is one of just three einkorn imprints still dated to the PPNA; a further 19 were redated from PPNA to Pottery Neolithic (Hopf, 1983: 609–10). In view of uncertainties about PPNA stratigraphy at the site, the remaining PPNA imprints are not secure evidence for domestication. The only other PPNA find of einkorn in the southern Levant is at Iraq ed-Dubb, where spikelet forks of domesticated einkorn or emmer were recovered from both Natufian and PPNA levels, and may be intrusive from later occupation of the Iron Age (Colledge, 1994). Without accelerator dating of individual spikelet forks, the significance of this material remains uncertain. The presence of domesticated emmer at PPNA Aswad (Phase Ia) is based on *Triticum* spikelet forks of unknown status and the presence of a small number of *T. dicoccum* grains that have not been directly dated (van Zeist & Bakker-Heeres, 1982: 184–5). Overall, evidence for domestication in the Pre-Pottery Neolithic A (PPNA, 8300–7600 uncal BC) is either lacking, as in the very abundant and well-preserved plant remains from Netiv Hagdud (Kislev, 1997), or based on small quantities of ambiguous material.

Free-threshing wheats

Both the wild wheats and their domesticated derivatives are hulled. The glumes are thickened and tough, while the mature rachis is brittle in wild wheats, and semi-tough in domesticates. In either case, on threshing the spike will break up into spikelets in which the grain is surrounded by the tough glumes (Nesbitt & Samuel, 1996). In the free-threshing ("naked") wheats the glumes are thin and easily broken off, while the rachis is fully tough. Threshing will separate the chaff from the grain. Both the grain and chaff of free-threshing wheats are very distinctive, the rachis segments lacking the prominent glume bases typical of hulled wheats, and the grains lacking the longitudinal creases impressed by tough glumes. However, further identification of free-threshing wheats has proved controversial since the earliest days of archaeobotany.

In 1853 falling lake levels in Switzerland led to the discovery of numerous lakeside dwellings. Abundant, well-preserved plant remains, including intact charred ears of wheat, were collected during excavations and were studied by the palaeobotanist Oswald Heer (Heer, 1865). He identified the hulled wheats einkorn, emmer and spelt, and three free-threshing wheats, dominated by hexa- ploid *Triticum vulgare antiquorum*. Subsequent archaeobotanists followed Heer's lead for the next century in ascribing remains of free-threshing wheats in Europe and elsewhere to hexaploid "bread wheat" (*T. aestivum* or *T. compactum*), on the basis of their short, wide grains and short rachis segments.

The 1970s saw a resurgence in excavations of Swiss lake villages, in connection with a major road-building programme. Archaeobotanists applied the new, rigorous rachis

criteria for free-threshing wheats (Hillman, this volume) to newly-excavated Swiss material dating from the Late Neolithic (Jungneolithikum, 4300–3500 cal BC) onwards and found that most rachis remains of free-threshing wheat were unmistakably tetraploid (Jacomet, Brombacher & Dick, 1989: 319–329; Jacomet & Schlichtherle, 1984). Further work on naked wheats from German Neolithic sites on Lake Constance has confirmed these results (Maier, 1996). Outside central Europe, relatively little systematic application of these identification criteria has been made, but archaeological records of tetraploid free-threshing wheats are known from medieval Britain and from the Neolithic period onwards in the Near East (Maier, 1996; Moffett, 1991). Clearly, the previous practice of blanket determination of free-threshing wheats as bread wheat was wrong; it appears to have been based on the belief that the short, compact grains typical of ancient charred free-threshing wheat could come only from bread wheat. However there is general agreement amongst archaeobotanists (Hillman *et al.*, 1996 for 1995; Jacomet *et al.*, 1989; Jones, 1998; Moffett, 1991) that grains of free-threshing wheat cannot be separated by morphology save in exceptional circumstances. Identifications that are not supported by explicit rachis criteria – that is, most identifications prior to the 1980s – can be accepted only as free- threshing wheat of unknown ploidy level.
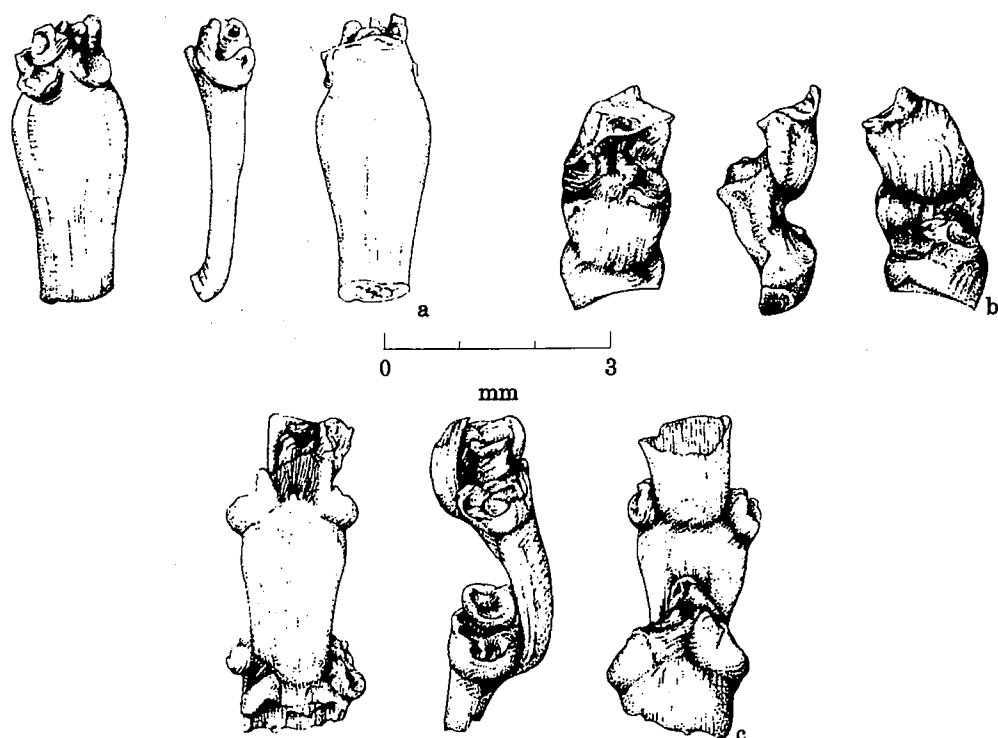
Figure 1. Charred free-threshing rachis segments from archaeological sites. **a.** Hexaploid (bread wheat, *Triticum aestivum*), Dilkaya Höyük, eastern Turkey; **b.** Hexaploid (compact type), Qaryat Medad, Syria; **c.** Tetraploid (macaroni wheat, *T. durum/turgidum*), Qaryat Medad, Syria. From Nesbitt & Goddard (1997).

A further controversial topic is the identification of ancient free-threshing wheat remains to specific taxa within their ploidy group, on the same lines as Heer's archaeological variant of bread wheat, *"Triticum vulgare antiquorum"*. For example, free-threshing wheat remains from the Indian sub-continent are often identified as *T. sphaerococcum* on the basis of their short, compact grains. In fact, most charred grains of naked wheat reported from Europe and the Near East have short grains (less than 5 mm long), regardless of whether they originate from tetraploid or hexaploid wheats. Identification as *T. sphaerococcum* would first require a much better understanding of the morphological traits of current-day populations, and second, demonstration that traits found in ancient material are sufficiently distinct to rule out other tetraploid and hexaploid wheats (Fuller, in press; Hillman *et al.*, 1996; Miller, 1992). Identification of compact-eared forms of wheat is complicated by the effects of charring, which can reduce grain length by 10% on average and rachis length by up to 25% (Hopf, 1955; Villaret-von Rochow, 1967). Some rachis segments are so short (Fig. 1) that they may genuinely represent a compact type. The very limited number of finds of free-threshing wheat that have been fully characterised by reliable rachis criteria, and our poor understanding of the effects of charring, makes premature attempts at definition of new species such as Kislev's ancient tetraploid free-threshing wheat, *T. parvicoccum* (Kislev, 1979/80).

DOMESTICATION OF EINKORN AND EMMER WHEAT

A brief history of research

The origins of agriculture have been a major focus of archaeological enquiry in the Near East for the last 50 years. The enhanced productivity of agriculture, compared to hunter-gatherer subsistence, underlies the rise of urban and literate civilisations in the ancient Near East, and their spread to Europe and, eventually, much of the globe (Diamond, 1997; Harris, 1996). By the Pre-Pottery Neolithic B period (PPNB, 7600–6000 uncal BC) a well-documented set of Neolithic "founder crops" is present at farming villages throughout the fertile crescent (Harris, 1998; Zohary & Hopf, 1993). These crops include two-row hulled barley, lentils, horsebean, chickpea, pea, and einkorn and emmer wheat (Zohary, 1996; Zohary & Hopf, 1993).

The combination of archaeobotany and botany has been successful in answering the broad "when" and "where" that led to plant domestication in the fertile crescent. Evidence from current-day distribution of wild cereals pointed to the fertile crescent, the "hilly flanks" surrounding the deserts and steppe of Syria, Iraq and Iran (Fig. 2), as the area in which domestication would have first occurred. Archaeological fieldwork has since confirmed that the earliest farming villages are indeed within or on the fringes of the fertile crescent, and date from about 7500 uncal BC (Table 3).

Archaeological evidence

If we are to explain the "why" of agricultural origins, we need a far more detailed understanding of the processes involved in the shift from foraging to farming. It is reasonably certain that most Epipalaeolithic people were hunter-gatherers, and that at least by the middle PPNB (7500–5500 uncal BC) most villagers in the Near East were farmers. The key question is what was happening in the PPNA (8300–7500 uncal BC), the earliest Neolithic period. As discussed above with reference to identification of

TABLE 3. Selected occurrences of wheat at Epipalaeolithic and Pre-Pottery Neolithic Near Eastern archaeological sites. Solid shading indicates identification on basis of chaff; grey shading is on basis of grain; ? indicates uncertain identification. EIN = einkorn, EM = emmer, NAK = free-threshing wheat, 4 or 6 refers to ploidy level based on reliable rachis criteria. Identifications of wild einkorn based on grain alone cannot usually be separated from Triticum urartu or wild rye (Secale). Identifications of wild emmer may refer to *T. dicoccoides* or *T. araraticum*. Bibliography for site reports is in Nesbitt & Samuel (1996).

Site (phase)	Country	Period	Date (uncal BC)	Economy	Wild			Domestic		
					EIN	EM	RYE	EIN	EM	NAK
Ohalo II	Israel	Epipalaeolithic (Kebaran)	17000	Foraging	▨	■				
Abu Hureyra (I)	Syria	Epipalaeolithic (Natufian)	9500–8000	Foraging	▨		▨		?	
Mureybit (I–III)	Syria	Epipalaeolithic & PPNA	8500–7600	Foraging	▨		■		?	
Qermez Dere	Iraq	PPNA	8200–7700	Foraging	▨					
Netiv Hagdud	Israel	PPNA	8000–7400	Foraging		■				
M'lefaat	Iraq	PPNA	7900–7700	Foraging	▨					
Jerf al Ahmar	Syria	PPNA	7800–7700	Foraging	■		■			
Dja'de	Syria	PPNB	7600–7000	Foraging	?					
Abu Hureyra (2A)	Syria	PPNB	7500–6000	Farming	▨				■	■
Beidha	Jordan	PPNB	7200–6600	Farming				■		
Cafer Höyük (XIII–IX)	Turkey	PPNB	7200–?7000	Farming	■	▨	?	■		
Jericho	Palestine	PPNB	7200–6800	Farming				▨		
Nahal Hemar (3–4)	Israel	PPNB	7100–6000	Farming					■	

Table 3 *continued*					EIN	EM	RYE	EIN	EM	NAK
Nevalı Çori	Turkey	PPNB	7200	Farming						
Çayönü (g–c)	Turkey	PPNB	7000–6700?	Farming		?				
Tell Aswad (II)	Syria	PPNB	6900–6500	Farming						
Aêıklı Höyük	Turkey	PPNB	6900–6500	Farming						
Wadi el-Jilat 7	Jordan	PPNB	6800–6400	Farming		?				
Ghoraife	Syria	PPNB	6800–6200	Farming						4 6
Halula	Syria	PPNB	6700–6600	Farming				?		
Can Hasan III	Turkey	PPNB	6600–5800	Farming						4 6
Cafer Höyük (III–IV)	Turkey	PPNB	?6500–6200	Farming			?			6
Abdul Hosein	Iran	PPNB	6500	Farming						
Ras Shamra (Vc)	Syria	PPNB	6500–6000	Farming						
Jarmo	Iran	PPN	6400?	Farming						
Ali Kosh (BM)	Iran	PPN	?6400–6000	Farming						
Tell Bouqras	Syria	PPN	6350–5850	Farming						
Tell Ramad (I)	Syria	PPNB (late)	6200–6100	Farming						
Wadi Fidan A	Jordan	PPNB (late)	6000	Farming						
Wadi el-Jilat 13	Jordan	Late Neolithic	5900–5800	Farming						
El Kowm II–Caracol	Syria	PPNB	5800–5700	Farming						4 6

domestication, the farming status of PPNA sites is much less certain than appeared a decade ago. Instead, efforts are concentrating on detecting changes in harvested species that might indicate cultivation of wild plants – an essential prelude to their domestication (Colledge, 1994, 1999). Experimental cultivation (Willcox, 1992) and modelling of wheat domestication (Hillman & Davies, 1990) suggest both that cultivation of wild cereals could occur indefinitely under harvesting conditions that do not apply selective pressure for domestication characters, but could occur very rapidly once the right set of circumstances – such as sickle harvest – came into place. It is therefore unlikely that we can track the process of domestication at any one archaeological site.

At the same time, more detailed questions are being asked from the biological record. The small number of excavated sites from this early period, and continuing uncertainties about their dating, mean that we cannot currently locate domestication of wild cereals to any given part of the fertile crescent. If biological evidence showed that domestications of the Neolithic crops were single events occurring in one area, this would require significantly different explanations to a shift to farming occurring over a large part of the fertile crescent.

Botany of the wild ancestors

How reliable is the 1960s consensus on the distribution of the wild ancestors as an indication of their distribution 10,000 years ago? There is good reason to believe that current distribution both under and over-estimates the early Holocene distribution. The distribution shown in Figure 2 is of wild einkorn and wild emmer growing today in primary habitats; that is, those relatively undisturbed by humans. Wild einkorn is abundant in secondary, anthropogenic habitats such as roadsides and field edges over a far wider area, stretching from Yugoslavia to Transcaucasia (Harlan & Zohary, 1966; Zohary & Hopf, 1993). Its sibling species *T. urartu*, and both wild emmers are largely restricted to primary habitats. Given that the habitats of wild einkorn outside the fertile crescent are linked so closely to human activity, it seems reasonable to assume this distribution is the result of wild einkorn spreading as a weed alongside the spread of agriculture. Although the presence of wild einkorn (and wild barley) in the Aegean and the Balkans has led some scholars to suggest that einkorn could have been domesticated independently of its fertile crescent domestication (Dennell, 1985), archaeobotanical evidence demonstrates very clearly that agriculture and the Neolithic founder crops arrived in southeast Europe from the fertile crescent (Hansen, 1992; Nesbitt & Samuel, 1996). Support for this comes from recent DNA finger-printing and morphological analysis of wild einkorn forms from Greece. These proved to be only partly brittle-rachised, to share other morphological characters with domesticated einkorn, and to be genetically so closely related that they are best interpreted as a feral derivative of domesticated einkorn rather than its ancestor (Heun *et al.*, 1997).

Changing distribution of the wild wheats

There is also evidence that modern distribution underestimates early Holocene distribution. In part this is because of inadequate records of distribution. My map of wild einkorn distribution takes into account primary – though relatively sparse – stands in northwest Syria and western Jordan found in recent intensive exploration by ICARDA scientists (Valkoun, Waines & Konopka, 1999; Valkoun, this volume). The
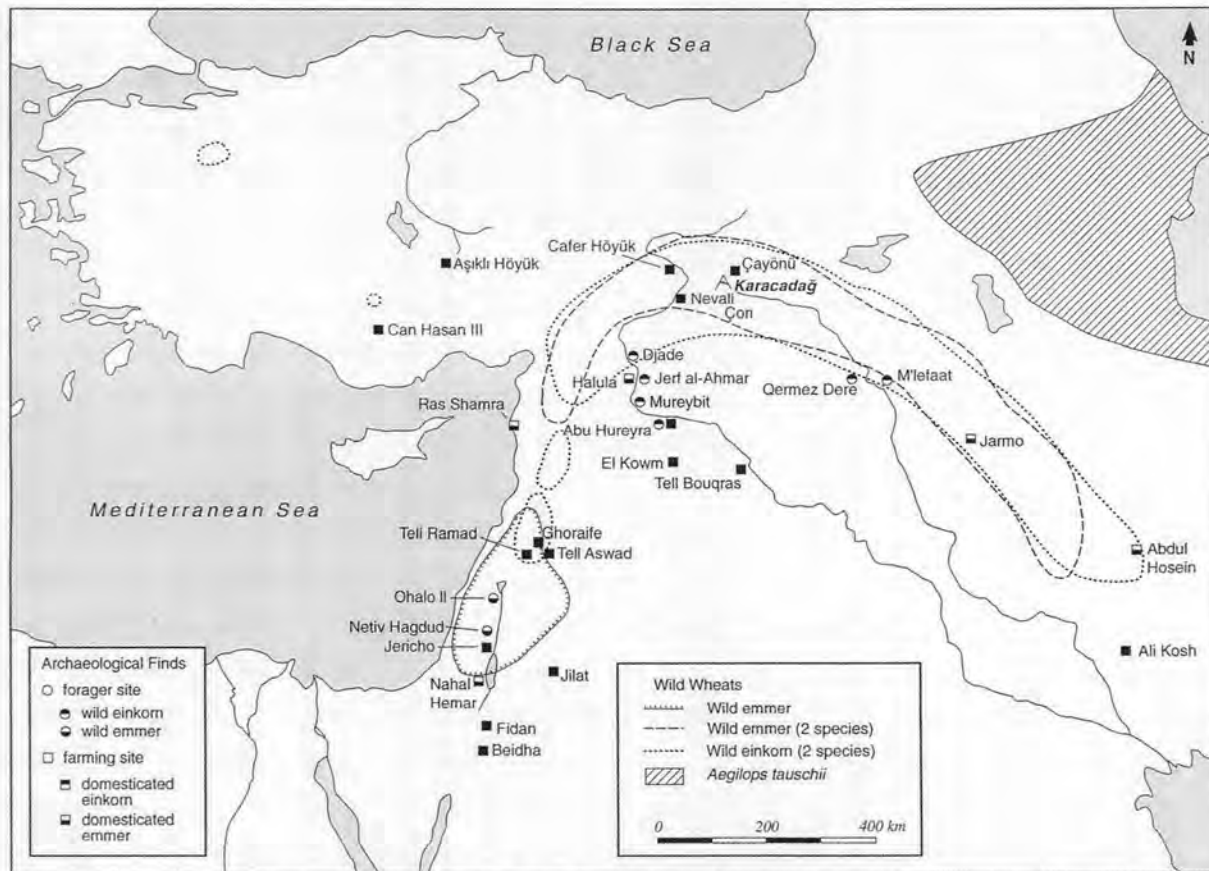
Figure 2. Distribution of early village sites in relation to wild ancestors of wheat. Southern zone of emmer is pure *T. dicoccoides*; northern zone also encompasses *T. araraticum*. Transcaucasian wild wheats are not shown. Wild einkorn distribution includes both *T. boeoticum* and *T. urartu*. The small einkorn zones in western Turkey represent primary stands in central Anatolia, where Gordon Hillman (in the 1970s) and I (in 1998) observed primary stands of wild einkorn on Karadağ mountain north of Can Hasan, and in northwest Turkey, where Zohary (pers. comm.) describes primary stands of wild einkorn west of Kutahya. Archaeological finds of wild einkorn may include wild rye.

relatively recent documentation of these stands is a reminder of just how incomplete our understanding is of the distribution and, especially, the ecology of wild wheats. Little is known of the climatic parameters that define distribution. Further evidence for changing distribution comes from archaeological finds of wild einkorn at pre-agrarian sites south of its current distribution, at Abu Hureyra, Mureybit and Jerf al-Ahmar (Table 3). These finds alone are not conclusive, as foodstuffs such as wild einkorn could have been imported from the north. However, the overall spectrum of plant species represented by the seeds and charcoal has led both Hillman (1996) and Willcox (1996) to argue convincingly that terebinth woodland and wild einkorn and rye extended as far south as Abu Hureyra and Jerf al-Ahmar in the past. Its current-day boundaries must be due in part to the impact of cultivation and grazing – particularly at these arid margins of growth – and in part to climatic change.

The overall picture is clear from pollen analysis of lake cores: at about 11,000 uncal BC wild cereals spread from their Ice Age refugia in the Levant (and perhaps elsewhere) into the fertile crescent. The presence of wild rye at the Euphrates sites suggests that the climate may even have been moister than today. The Younger Dryas climatic episode, in which temperatures and precipitation fell – to an unknown extent in southwest Asia – occurred between about 9000 and 8000 uncal BC (Helmer et al., 1998; Hillman, 1996). The impact of the Younger Dryas on distribution of wild cereals is controversial, beyond the likely retreat of wild einkorn from the north Syrian steppe (Moore & Hillman, 1992). Although Jones, Allaby & Brown (1998) and Hole (1998) have suggested that wild einkorn distribution could have changed in a highly unpredictable manner, there is archaeobotanical evidence that wheat distribution may have been relatively stable. First, there is an excellent match in the broad picture of archaeobotanical finds of wild wheat prior to the beginning of farming and current-day distribution, at least in the Levant and northern fertile crescent. At the two sites in the southern Levant wild emmer zone – Ohalo II and Netiv Hagdud, wild emmer is the only wheat. At the six forager sites in the wild einkorn zone of the northern fertile crescent, only wild einkorn or wild rye is present (Table 3, Fig. 2). While the sample of suitable hunter- gather sites is small, these results suggest that – as today – wild einkorn did not extend to the southern Levant, while wild emmer did not extend as far south as wild einkorn in the northern fertile crescent (Nesbitt & Samuel, 1998).

Where were einkorn and emmer domesticated?

Overall, both archaeological and botanical evidence suggests that current- day distribution of wild wheats is a reasonable guide to their distribution 10,000 years ago, with the proviso that the distribution of wild einkorn has shrunk. The next question is whether we can further localise wheat domestication within this area. T. boeoticum and T. dicoccoides are morphologically and genetically very close to their domesticated derivatives, and were identified as wild ancestors by some botanists relatively early – the 1880s for wild einkorn and the 1890s for wild emmer [see Feldman (1977) for the full story of the discovery of the wild ancestors]. However, populations of both wild species show not enough morphological variation to point to populations from any one area as more likely candidates as the wild ancestors. It has been suggested that as most domesticated einkorn has one-grained spikelets, it is more likely to derive from wild einkorns at the westerly end of its distribution (subspecies. aegilopoides), as these have

Figure 3. Distribution of endemic wheat species in Transcaucasia and Iran.

exclusively one-grained spikelets (van Zeist & Bakker-Heeres, 1982: 190–191; van Zeist & de Roller, 1991/1992). However, the spikes of wild einkorn from the eastern part (ssp. *thaoudar*) contain a mixture of one and two-grained spikelets. One-grained domesticated einkorn is always substantially larger than the grain of the two-grained form, so under strong selection pressure (e.g. for larger spikelets for sowing) it is likely that the one-grained form would have evolved very quickly from two-grained wild einkorn.

There is some evidence of morphological diversity in emmer. An exception- ally large-grained form of wild emmer, that closely resembles domesticated wheats in many other respects, grows in the upper Jordan valley (Poyarkova & Gerechter-Amitai, 1991). However, Blumler (1999) has argued convincingly that this similarity has resulted from introgression of *T. durum* into wild emmer in this region, and therefore

does not point to these populations as more probable wild ancestors. Differences have been noted between ancient European and Near Eastern domesticated emmers, for example in heavier glume venation on the latter (Hillman *et al.*, 1996; de Moulins, 1997: 36–37). Once the geo- graphical patterning of these differences is better known, they may throw light on patterns of spread of emmer wheat.

Genetics has proved more informative than morphology. Two lines of evidence have been explored. First is the non-domestication in the fertile crescent proper of the two sibling species, *T. urartu* and *T. araraticum*, even though these grow mixed with wild einkorn and emmer throughout most of their range. Although *T. araraticum* was to be domesticated as *T. timopheevi*, its narrow distribution restricted to western Georgia (Fig. 3), suggests it was domesticated later, outside the fertile crescent. Although it is only circumstantial evidence, the fact that only two* of the four species were domesticated suggests that one or few domestication events occurred (Zohary, 1996; Zohary, 1999). However this, like all arguments based on study of the current-day domesticates, cannot take account of the possible disappearance of other domesticated populations. It is possible that multiple domestications occurred, but that other domesticated populations have since been displaced by one dominant package of crops and are extinct. In the case of wild einkorn, however, more detailed genetic evidence does point to a single domestication. DNA finger-printing points conclusively to populations of wild einkorn on Karacadağ in southeast Turkey (Fig. 2, not to be confused with Karadağ in central Turkey) as by far the closest wild relative of einkorn, and thus its wild ancestor (Heun *et al.*, 1997, see also Nesbitt, 1998). In general, genetic evidence points to single or few domestication events for the Neolithic founder crops (Zohary, 1999). Assessment of evidence from DNA variation in domesticated emmer for two waves of emmer spreading into Europe – perhaps resulting from separate domestications – awaits characterisation of the wild ancestors (Allaby, Banerjee & Brown, 1999; Brown, 1999).

ORIGIN OF SPELT WHEAT AND BREAD WHEAT

Early research

Pioneering cytogenetical work in the years immediately before and after publication of Percival's monograph was to demonstrate that wheat was a polyploid series of, respectively, diploid, tetraploid and hexaploid wheats (Table 1). Percival's hypothesis that the spelt group was the result of hybridisation between the tetraploid group and one or more diploid *Aegilops* species was confirmed in the 1940s by experimental hybridisation of *T. dicoccum* and *Aegilops tauschii* (= *Ae. squarrosa*), resulting in a hybrid wheat with strong morphological similarities to *T. spelta* and which crossed easily with *T. spelta* and *T. aestivum* (Kihara, 1944; McFadden & Sears, 1946)[1]. Subsequent experiments have shown that all crosses of tetraploid wheats, whether or not free-threshing, with *Ae. tauschii* result in hulled spelt wheat (Kerber & Rowland, 1974).

Once the hybrid origin of the hexaploid wheats had been established by the 1920s, it was clear that hulled *T. spelta* was the more primitive form and that *T. aestivum* was

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1   Although the tetraploid parent was reported as *T. dicoccoides*, it has subsequently been re-identified as *T. dicoccum* (Sears, 1976).

derived from it. However, archaeobotanical evidence indicated that spelt wheat appeared in a geographically circumscribed region of central Europe well after the arrival of the original Neolithic founder crops, which included abundant hexaploid naked wheats (now recognised as including tetraploids – see above). Therefore, European spelt wheat could be understood best as originating from bread wheat, either by a simple mutation, or by introgression (hybridisation followed by back-crossing with *T. aestivum*) of *T. aestivum* and *T. dicoccum*. Experiments in artificial hybridisation of these two species produced progeny very similar in morphology to spelt wheat (Mac Key, 1966).

The origins of spelt wheat in Europe

Once accurate wheat identification criteria were developed in the 1980s, it became clear that naked wheat – some of it certainly hexaploid – is present in the earliest Neolithic (Bandkeramik) of central Europe (5400–4900 cal BC), although it is far less common than emmer. Although most free-threshing wheats in the Swiss lake settlements discussed above have been re-identified as tetraploid, hexaploid free-threshing wheats are abundant at Middle Neolithic sites (Rössen culture, 4700–4300 cal BC) outside the Swiss lake area (Maier, 1996: 50). Even in the lake settlements, ancient DNA gives evidence for the presence of hexaploid free-threshing wheat (Schlumbaum, Jacomet & Neuhaus, 1998).

Spelt appears in the Swiss lake district in the Early Bronze Age (2200–1500 cal BC) and during the same period elsewhere in Europe, at sites ranging from Germany to Greece. Re-examination of some finds has shown Early Bronze Age finds to be reliable but claimed Late Neolithic identifications to be unreliable (S. Jacomet, personal communication). Spelt is absent from the now very extensive range of Near Eastern archaeobotanical assemblages (Miller, 1991). Isolated occurrences are due to mis-identification of *Aegilops* chaff, abundant and morphologically somewhat similar, as at Yarym Tepe in northern Iraq (Bakhteyev & Yanushevich, 1980, illustrated in Bakhteev, Lisitsina & Yanushevich, 1992: 150) or to isolated finds as at Erbaba in Turkey (van Zeist, 1983) which perhaps represent mutant forms of *T. aestivum*.

Archaeobotanical evidence for the presence of hexaploid free-threshing wheat and emmer in Neolithic Europe shows that spelt *could* therefore have originated from a hybridisation event of a free-threshing hexaploid and a hulled tetraploid wheat in this region. However, this has been overshadowed by new archaeobotanical evidence for spelt in Transcaucasia and north of the Black Sea, suggesting an alternative route of travel to Europe that avoids the Near East, explaining why there are no Near Eastern finds of spelt. This archaeobotanical evidence forms the basis of the most widespread current interpretation (e.g. Andrews, 1964; van Zeist, 1976: 37; Zohary & Hopf, 1993: 52–53), that spelt originated once, in Transcaucasia or northwest Iran, and travelled westwards to Europe, arriving in Europe as a second-wave crop several millennia after the arrival of agriculture.

The origins of spelt and bread wheat in the Near East

The origin of bread wheat in the Near East remains as problematic as the origins of spelt in Europe. The hybridisation between a tetraploid wheat and *Aegilops tauschii* could take place only once agriculture with tetraploid wheats reached the distribution zone of *Aegilops tauschii*. This extends from northern China westwards to west and

southwest of the Caspian Sea, well northeast of the fertile crescent (Fig. 2). As agriculture did not reach the Caspian Sea until after 6000 uncal BC, the hybridisation could not have occurred until then (van Zeist, 1976). However, reliable rachis criteria (discussed above) have been used to identify hexaploid free-threshing wheats in 30 different samples from all the excavated phases at Can Hasan III, dating from 6400–5700 uncal BC (Hillman, 1978: 168), and at Cafer Höyük, in levels III and IV dating to about 7000–6200 uncal BC (de Moulins, 1993). There is thus a conflict between the archaeobotanical evidence for seventh millennium uncal BC domestication of hexaploid bread wheat, and archaeological and biological evidence that the hybridisation of its ancestor, *T. spelta*, could not have occurred until after 6000 uncal BC.

Archaeological work since the 1960s has confirmed van Zeist's dating of the earliest agricultural sites around the Caspian. Sites further to the south, in the Zagros mountains, such as Jarmo, Ali Kosh and Abdul Hosein have good evidence of farming (including emmer) by 6500–6400 uncal BC (Table 3). In contrast, intensive surface survey around Haji Firuz Tepe and Yanik Tepe, both in Iranian Azerbaijan southwest of the Caspian Sea, failed to uncover any evidence of occupation earlier than 5500 uncal BC (Hole, 1987: 44–45). The Zagros mountains appear to have acted as a barrier to the rapid spread of agriculture in this direction. Is it possible that the distribution of *Aegilops tauschii* in fact extended further west, allowing the hybridisation to occur much earlier?

Distribution of *Aegilops tauschii*

Today *Aegilops tauschii* grows abundantly in northern Iraq, eastern Turkey, Armenia and Azerbaijan, as well as in the southern fringes of the Caspian and to the east (van Slageren, 1994: 330; Zohary & Hopf 1993: 51). However many of the western occurrences are in secondary habitats (Zohary, Harlan & Vardi, 1969). In Figure 2 I have extended the possible primary distribution to include more of the relatively frequent records from Armenia and Azerbaijan. *Ae. tauschii* is divided into two subspecies, *tauschii* and *strangulata*. Evidence from isozymes (Jaaska, 1980; Nishikawa, 1983) points to *strangulata* as the most likely contributor of the D-genome. This is distributed in two separate regions, in Transcaucasia and southeast of the Caspian. More detailed studies using variation in DNA have shown that some accessions identified as *tauschii* on morphological grounds in fact share the genepool of *strangulata*, and that this genepool is more geographically widespread than first thought, stretching to north-central Iran and southwest Caspian (Dvořák et al., 1998). *T. aestivum* is most closely related to *strangulata* accessions from southwest Caspian and Transcaucasia (in particular Armenia). *Ae. tauschii* accessions from southeast Turkey and western Iran are subspecies *tauschii* and are therefore not closely related to bread wheat. It appears that the hybridisation event(s) must indeed have occurred in the Caspian or Transcaucasian regions.

Recent cultivation of spelt in Transcaucasia

If Transcaucasia did play any role in the origin of spelt or its spread to Europe, given the remarkable diversity of wheats in the region today, it seems likely that spelt could still be present. In the recent past spelt has been recorded in southeast Transcaucasia in Azerbaijan, cultivated with *T. aestivum* (Dorofejev, 1971), and in southeast Iran (Fig. 3) (Kuckuck, 1959; Kuckuck & Schiemann, 1957). Dorofejev suggests that both the Azerbaijan spelt and Kuckuck's Iranian spelt might be of secondary origin, while a rare

form of spelt with denser ears known as *T. macha* Dek. et Men. might be a remnant of the primary domestication of spelt. However, *T. macha* has a remarkably limited distribution, grown only on about 50 hectares of land in western Georgia (Fig. 3), mixed with a form of *T. dicoccum* known as *T. paleocolchicum* (Dekaprelevich & Menabde, 1932). Given that *T. macha* has a very limited distribution, is somewhat weedy with very brittle ears, and has a rachis disarticulation (wedge-type) different from that of spelt, it most probably has a late, secondary origin, perhaps by crossing of *T. dicoccum* and *T. aestivum*. Jakubziner suggests *T. macha* is derived from *T. paleocolchicum* (a form of *T. dicoccum*) which it closely resembles, presumably by introgression to *T. aestivum*. Investigations of alcohol dehydrogenase isoenzymes showed that *T. macha* does not share the same type of isoenzyme with *T. paleocolchicum*, but rather with other Transcaucasian emmer and spelt (Jaaska, 1978: 214). However, recent RFLP DNA analyses suggest that both *T. macha* and *T. paleocolchicum* derive from a cross between hexaploid wheat and wild emmer, confirming that *T. macha* is not an ancestral form of hexaploid wheat (Dvořák & Luo, this volume). All the hexaploid wheats, including *T. macha*, share a common D-genome genepool, and there is thus no evidence for separate hybridisation with *Ae. tauschii* leading to *T. macha* (Dvořák *et al.*, 1998).

Archaeological evidence for spelt in Transcaucasia

Given the problems in chronology with a Caspian origin of spelt, how does the alternative location, Transcaucasia, compare? A shadowy Aceramic Neolithic period, of unknown agricultural status, is followed by a widespread Neolithic, characterised by round-housed farming villages, in Georgia, Armenia and Azerbaijan. This is contemporary with sites such as Haji Firuz further to the south, beginning at about 5500 uncal BC (Chataigner, 1995: 37; Mellaart, 1975: 201–202). A Transcaucasian origin of spelt therefore does not resolve the dating problem.

Is spelt present at these Neolithic settlements? *T. spelta* is recorded from Arukhlo 1 in Georgia (5500 uncal BC and later) and the published drawings, although unclear, do seem to show a spikelet with barrel-type articulation and elliptical transverse section (Janushevich, 1984: 271). However, spelt is apparently absent from those Armenian and Azerbaijan sites for which we have published plant remains (Chataigner, 1995: 202). Without further documentation of the Arukhlo find, the sporadic nature and uncertain identification of spelt finds in Transcaucasia is insufficient evidence for their presence in prehistory. Then, as today, most wheat was free-threshing. Although a wide variety of identifications are made (e.g. *T. turgidum, T. durum, T. compactum, T. carthlicum, T. aestivum* and *T. compactum*) these are not documented by detailed morphological criteria (Lisitsina & Prishchepenko, 1977). In practice, the ploidy level of free-threshing archaeological material is unknown. Plant remains from a number of Georgian sites examined and comprehensively published by Schultze-Motel (1988a, b) are comparable to those found at Near Eastern sites, containing abundant free-threshing wheat and none of the unusual species recorded by other archaeobotanists. The wide range of wheat species identified in ancient material undoubtedly reflects knowledge of the current-day diversity of wheats in the region, and the desire to claim its pivotal role in wheat evolution (cf. Lisitsina,1978; Menabde, 1970).

Evidence of spelt on the northerly route around the Black Sea is also uncertain. Janushevitch has published a series of well-illustrated archaeobotanical reports on

material from Moldavia, Ukraine and the Crimea, through which spelt must have passed. All the spelt spikelets illustrated are narrow and rounded, with a thickened base (Janushevich, 1984: 268, 270; Janushevitch, 1986: 8). They strikingly resemble the spikelets of *Aegilops cylindrica*, a weedy species that is abundant in the Balkans and north of the Black Sea and Transcaucasia. In Transcaucasia *Ae. tauschii* is also a candidate species.

Summary

   Neither biological nor archaeobotanical evidence allow any definite statement on where and when current day populations of spelt had their origin. The experimental evidence of genetics demonstrates that a hybridisation of spelt must have occurred before the evolution of hexaploid free-threshing wheat. Evidence from DNA (Dvorák *et al.*, 1998, 1999) and from isozymes (Jaaska, 1980) points to a monophyletic origin of hexaploid wheat. Suggestions that *T. aestivum* originated independently in China (Yen, Luo & Yang, 1988) are not supported by DNA analyses. These show that Chinese *T. aestivum* shares the same rDNA genotype as *Ae. tauschii strangulata* in the Caspian and Transcaucasian regions, rather than the genotype present in *Ae. tauschii* in China (Lagudah, Appels & McNeil, 1991: 393). Isozyme evidence (Jaaska, 1978) however does show relatively consistent differences in alcohol dehydrogenase isoenzymes between Asian and European forms of spelt, suggesting that the European forms did not originate simply by migration from Asia. This is supported by RFLP DNA analyses that find European spelts to be most closely related to European bread wheats (in particular, Alpine club wheats) and only distantly related to Asian spelt (Dvorák *et al.*, 1999; Dvorák & Luo, this volume). This is consistent with origin of spelt in Europe by introgression of emmer into free-threshing hexaploid wheats.

   The lack of archaeological evidence for spelt in the Near East or Transcaucasus suggests that spelt was a brief transitory form prior to the emergence of bread wheat. If, for example, the hybridisation was of *T. durum* and *Ae. tauschii*, rather than *T. dicoccum*, the result would have been a hulled wheat in a free-threshing field. Because the crop-processing requirements of hulled wheats are different to those of free-threshing wheats, there would be a strong selection pressure for free-threshing characters, combined with a strong selection pressure in the upland areas for the more cold-resistant properties given by the D-genome to hexaploid wheats. This scenario would suggest that, as with domestication of wild wheats, the process may be so quick that the transitional stage (i.e. spelt) would not be visible in the archaeological record. Evidence from genetics is equivocal on the identity of the tetraploid ancestor. Reconstitution of the tetraploid component of bread wheat, by removal of the D genome, resulted in a free-threshing wheat (Kerber, 1964). Evidence of genes for waxiness points to emmer (Tsunewaki, 1966). Further genetical investigation of the nature of the tetraploid ancestor of hexaploid wheats would be valuable. In the meantime, neither archaeological nor genetical evidence resolve the problem of the origin of European spelt.

CONCLUSIONS

   My two case-studies offer different perspectives on progress since Percival's time. Our understanding of einkorn and emmer domestication has benefited enormously from

the far greater range of excavations in the Near East and improvements in dating and recovery of archaeological plant remains. While the differentiation between hunter-gatherer and early farming settlements is recognised as problematic, this has driven archaeobotanists to record plant remains more carefully – particularly for characters relating to rachis fragility – and to explore new techniques of detecting pre-domestication cultivation, especially during the PPNA period. Botanical evidence has benefited from the great increase in collection of wild and cultivated plants, particularly by Russian botanists in the 1920s, and Japanese and American botanists in the 1960s and 70s. Genetic characterisation of the wild wheats has been successful in showing their relationships to the domesticated wheats, and in the case of einkorn, in narrowing down the likely area of domestication. However, the ecology of the wild wheats is still insufficiently studied, and as a result key questions about its past distribution are difficult to answer. Overall, biological and archaeological evidence have meshed well in understanding the domestication of einkorn and emmer.

In the case of spelt wheat and bread wheat, re-examination of archaeo- botanical evidence suggests that the origins of spelt are as unresolved now as in the 1920s. Botanical and archaeological evidence make it absolutely clear that the initial hybridisation of spelt must have occurred in the Caspian or Transcaucasian region by 6500 uncal BC, but evidence of spelt itself remains highly elusive. Botanical evidence has in part confused issues by drawing attention to sporadic current-day occurrences of *T. spelta* and *T. macha* in Transcaucasia and Iran which might, like the European spelt, result from hybridisation of emmer and bread wheat. Older identifications of spelt need checking urgently. Improved characterisation of the D genome and the application of DNA analyses now suggest that older views (of Percival's day) are perhaps correct, that European spelt originated independently in Europe from hybridisation of tetraploid wheat and *T. aestivum*. Integration of biological and archaeobotanical work will continue to be essential in solving this problem.

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REFERENCES

Allaby RG, Banerjee M, Brown TA. 1999. Evolution of the high molecular weight glutenin loci of the A, B, D and G genomes of wheat. *Genome* **42**: 296–307.

Andrews AC. 1964. The genetic origin of spelt and related wheats. *Der Züchter* **34**: 17–22.

Bakhteev FK, Lisitsina GN, Yanushevich ZV. 1992. Fossil remains of cultivated plants from Yarym-tepe III in the northern Iraq. *Rossiyskaya Arkheologiya* **1992**: 148–155.

Bakhteyev FK, Yanushevich ZV. 1980. Discoveries of cultivated plants in the early farming settlements of Yarym-Tepe I and Yarym-Tepe II in northern Iraq. *Journal of Archaeological Science* **7**: 167–178.

Bell GDH. 1987. The history of wheat cultivation. In: Lupton FGH (ed.). *Wheat Breeding*. London, New York: Chapman and Hall, 31–49.

Blumler MA. 1999. Introgression of durum into wild emmer and the agricultural origin question. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origins of agriculture and crop domestication.* Aleppo: ICARDA, 252–268.

Brown TA. 1999. How ancient DNA may help in understanding the origin and spread of agriculture. *Philosophical Transactions of the Royal Society of London. Series B* **354 (1379):** 89–98.

Carruthers WJ. 1992. Percival and Helbaek's archive of plant remains. *Circaea* **8:** 65–70.

Chataigner C. 1995. *La Transcaucasie au Néolithique et au Chalcolithique.* Oxford: British Archaeological Reports, International Series 624.

Colledge S. 1994. Plant exploitation on Epipalaeolithic and early Neolithic sites in the Levant. Ph.D thesis, University of Sheffield.

Colledge S. 1999. Identifying pre-domestication cultivation using multivariate analysis. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origins of agriculture and the domestication of crop plants in the Near East.* Aleppo: ICARDA, 121–131.

Dekaprelevich LL, Menabde VL. 1932. Spelt wheats of Western Georgia (Western Transcaucasia). *Bulletin of Applied Botany, of Genetics and Plant-Breeding (Trudy po Prikladnoi Botanike, Genetike i Selektsii)* **Series V:** 3–46.

Dennell R. 1985. *European economic prehistory: a new approach.* London: Academic Press.

Diamond J. 1997. *Guns, germs and steel: the fates of human societies.* London: Jonathan Cape.

Dorofeev VF, Migushova EF. 1979. *Flora of cultivated plants. Vol. I. Wheat.* Leningrad: Kolos.

Dorofejev WF. 1971. Die Weizen Transkaukasiens und ihre Bedeutung in der Evolution der Gattung *Triticum* L. 3. Die Spelzweizen Transkaukasiens (*T. macha* Dek. et Men., *T. spelta* L. ssp. *spelta* Dorof., ssp. *kuckuckianum* Gökg. und ssp. *vavilovii* Sears). *Zeitschrift für Pflanzenzüchtung* **66:** 335–360.

Dvorák J, Luo M-C, Yang Z-L, Zhang H-B. 1998. The structure of the *Aegilops tauschii* genepool and the evolution of hexaploid wheat. *Theoretical and Applied Genetics* **97:** 657–670.

Dvorák J, Luo M-C, Yang Z-L. 1999. Genetic evidence on the origin of *Triticum aestivum* L. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origins of agriculture and crop domestication.* Aleppo: ICARDA, 235–251.

Evans LT. 1993. *Crop evolution, adaptation and yield.* Cambridge: Cambridge University Press.

Feldman M. 1977. Historical aspects and significance of the discovery of wild wheats. In: Kimber G, Redei GP (eds). *Stadler Symposium 9.* Columbia, Missouri: University of Missouri, 121–145.

Fuller DQ. In press. Fifty years of archaeobotanical studies in India: laying a solid foundation. In: Settar S, Korisettar R (eds). *Indian archaeology in retrospect. Volume III. Archaeology and interactive disciplines.* New Delhi: Oxford University Press and IBH.

Hansen J. 1992. Franchthi cave and the beginnings of agriculture in Greece and the Aegean. In: Anderson PC (ed.). *Préhistoire de l'agriculture.* Paris: Éditions du CNRS, 231–247.

Harlan JR. 1981. The early history of wheat: earliest traces to the sack of Rome. In: Evans LT, Peacock WJ (eds). *Wheat science – today and tomorrow.* Cambridge: Cambridge University Press, 1–19.

Harlan JR, Zohary D. 1966. Distribution of wild wheats and barley. *Science* **153:** 1074–1080.

Harris DR (ed.). 1996. *The origins and spread of agriculture and pastoralism in Eurasia.* London: UCL Press.

Harris DR. 1998. The origins of agriculture in southwest Asia. *The Review of Archaeology* **19:** 5–11.

Heer O. 1865. Die Pflanzen der Pfahlbauten. *Neujahrsblatt der Naturforschenden Gesellschaft in Zürich* **68:** 1–54.

Helmer D, Roitel V, Saña M, Willcox G. 1998. Interprétations environnmentales des données archéozoologiques et archéobotaniques en Syrie du Nord de 16000 BP à 7000 BP, et les débuts de la domestication des plantes et des animaux. In: Fortin M, Aurenche O (eds). *Espace naturel, espace habité. Actes du colloque tenu à l'Université Laval (Québec) du 5 au 7 mai 1997.* Lyon: Maison de l'Orient Méditerranéen, 9–33.

Heun M, Schäfer-Pregl R, Klawan D, Castagna R, Accerbi M, Borghi B, Salamini F. 1997. Site of einkorn wheat domestication identified by DNA fingerprinting. *Science* **278:** 1312–1314.

Hillman GC. 1978. On the origins of domestic rye – *Secale cereale*: the finds from Aceramic Can Hasan III in Turkey. *Anatolian Studies* **28**: 157–174.

Hillman GC. 1996. Late Pleistocene changes in wild plant-foods available to hunter-gatherers of the northern Fertile Crescent: possible preludes to cereal cultivation. In: Harris DR (ed.). *The origins and spread of agriculture and pastoralism in Eurasia.* London: UCL Press, 159–203.

Hillman GC, Davies MS. 1990. Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications. *Journal of World Prehistory* **4**: 157–222.

Hillman GC, Davies MS. 1992. Domestication rate in wild wheats and barley under primitive cultivation: preliminary results and archaeological implications of field measurements of selection coefficient. In: Anderson PC (ed.). *Préhistoire de l'agriculture: nouvelles approches expérimentales et ethnographiques.* Paris: Éditions du CNRS, 113–158.

Hillman GC, Mason S, de Moulins D, Nesbitt M. 1996. Identification of archaeological remains of wheat: the 1992 London workshop. *Circaea* **12**: 195–209.

Hole F. 1987. Archaeology of the Village Period. In: Hole F (ed.). *The archaeology of Western Iran.* Washington, DC: Smithsonian Institution Press, 29–78.

Hole F. 1998. Letters: Wheat domestication. *Science* **279**: 303.

Hopf M. 1955. Formveränderungen von Getreidekörnern beim Verkohlen. *Berichte der Deutschen Botanischen Gesellschaft* **68**: 191–193.

Hopf M. 1983. Appendix B. Jericho plant remains. In: Kenyon K, Holland TA (eds). *Jericho. Volume V. The pottery phases of the tell and other finds.* London: British School of Archaeology in Jerusalem, 576–621.

Jaaska V. 1978. NADP-dependent aromatic alcohol dehydrogenase in polyploid wheats and their diploid relatives. On the origin and phylogeny of polyploid wheats. *Theoretical and Applied Genetics* **53**: 209–217.

Jaaska V. 1980. Electrophoretic survey of seedling esterases in wheats in relation to their phylogeny. *Theoretical and Applied Genetics* **56**: 273–284.

Jacomet S, Brombacher C, Dick M. 1989. *Archäobotanik am Zürichsee. Berichte der Zürcher Denkmalpflege, Monographien 7.* Zürich: Orell Füssli.

Jacomet S, Schlichtherle H. 1984. Der kleine Pfahlbauweizen Oswald Heer's – Neue Untersuchungen zur Morphologie neolithischer Nacktweizen-Ähren. In: van Zeist W, Casparie WA (eds). *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam: A.A. Balkema, 153–176.

Janushevich ZV. 1984. The specific composition of wheat finds from ancient agricultural centres in the USSR. In: van Zeist W, Casparie WA (eds). *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam: A.A. Balkema, 267–276.

Janushevitch ZV. 1986. *Kulyturnye rasteniia severnogo prichernomoryia.* Kishinev: Shtiintsa.

Johnson BL, Dhaliwal HS. 1976. Reproductive isolation of *Triticum boeoticum* and *Triticum urartu* and the origin of the tetraploid wheats. *American Journal of Botany* **63**: 1088–1094.

Jones G. 1998. Wheat grain identification – why bother? *Environmental Archaeology* **2**: 29–34.

Jones MK, Allaby RG, Brown TA. 1998. Letters: Wheat domestication. *Science* **279**: 302–303.

Kerber ER. 1964. Wheat: reconstitution of the tetraploid component (AABB) of hexaploids. *Science* **143**: 253–256.

Kerber ER, Rowland GG. 1974. Origin of the free threshing character in hexaploid wheat. *Canadian Journal of Genetics and Cytology* **16**: 145–154.

Kihara H. 1944. Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare. Agriculture and Horticulture (Tokyo)* **19**: 13–14.

Kislev ME. 1979/80. *Triticum parvicoccum* sp. nov., the oldest naked wheat. *Israel Journal of Botany* **28**: 95–107.

Kislev ME. 1992. Agriculture in the Near East in the VIIth millennium BC. In: Anderson PC (ed.). *Préhistoire de l'agriculture.* Paris: Éditions du CNRS, 87–93.

Kislev ME. 1997. Early agriculture and paleoecology of Netiv Hagdud. In: Bar-Yosef O, Gopher A (eds). *An early Neolithic village in the Jordan valley.* Cambridge, MA: Peabody Museum of Archaeology and Ethnology, Harvard University, 209–236.

Kuckuck H. 1959. On the findings of *Triticum spelta* L. in Iran and on the arising of *Triticum aestivum*-types through crossing of different *spelta*-types. *Wheat Information Service* **9–10**: 1–2.

Kuckuck H, Schiemann E. 1957. Über das Vorkommen von Spelz und Emmer (*Triticum spelta* L. und *Tr. dicoccum* Scübl.) im Iran. *Zeitschrift für Pflanzenzüchtung* **38**: 383–396.

Lagudah ES, Appels R, McNeil D. 1991. The Nor-D3 locus of *Triticum tauschii*: natural variation and genetic linkage to markers in chromosome 5. *Genome* **34**: 387–395.

Legge AJ. 1986. Seeds of discontent: accelerator dates on some charred plant remains from the Kebaran and Natufian cultures. In: Gowlett JAJ, Hedges REM (eds). *Archaeological results from accelerator dating.* Oxford: Oxford University Committee for Archaeology, 13–21.

Letts JG. 1999. Smoke blackened thatch: a unique source of late medieval plant remains from Southern England. Reading: English Heritage and the Department of Agricultural Botany and Rural History Centre, University of Reading.

Lisitsina GN. 1978. Main types of ancient farming on the Caucasus – on the basis of palaeo-ethnobotanical research. *Berichte der Deutschen Botanischen Gesellschaft* **91**: 47–57.

Lisitsina GN, Prishchepenko LV. 1977. *Paleoetnobotanicheskie nakhodki kavkaza i blizhnego vostoka.* Moscow: Nauka.

Mac Key J. 1966. Species relationship in *Triticum*. In: *Proceedings of the Second International Wheat Genetics Symposium.* Lund: Hereditas, 237–276.

Maier U. 1996. Morphological studies of free-threshing wheat ears from a Neolithic site in southwest Germany, and the history of the naked wheats. *Vegetation History and Archaeobotany* **5**: 39–55.

McFadden ES, Sears ER. 1946. The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *Journal of Heredity* **37**: 81–89, 107–116.

Mellaart J. 1975. *The Neolithic of the Near East.* London: Thames and Hudson.

Menabde VL. 1970. To the history of wheat cultivation. In: *VIIe Congres International des Sciences Anthropologiques et Ethnologiques. Volume V.* Moscow: Nauka, 500–505.

Miller NF. 1991. The Near East. In: van Zeist W, Wasylikowa K, Behre K-E (eds). *Progress in old world palaeoethnobotany.* Rotterdam: A.A. Balkema, 133–160.

Miller TE. 1992. A cautionary note on the use of morphological characters for recognising taxa in wheat (genus *Triticum*). In: Anderson PC (ed.). *Préhistoire de l'agriculture: nouvelles approches expérimentales et ethnographiques.* Paris: Éditions du CNRS, 249–253.

Millet E. 1986. Relationships between grain weight and the size of floret cavity in the wheat spike. *Annals of Botany* **63**: 417–423.

Moffett L. 1991. The archaeobotanical evidence for free-threshing tetraploid wheat in Britain. In: Hajnalová E (ed.). *Palaeoethnobotany and archaeology. International Work-Group for Palaeoethnobotany 8th Symposium.* Nitra: Archaeological Institute of the Slovak Academy of Sciences, 233–243.

Moore AMT, Hillman GC. 1992. The Pleistocene to Holocene transition and human ecology in southwest Asia: the impact of the Younger Dryas. *American Antiquity* **57**: 482–494.

Morrison LA. 1994. Re-evaluation of systematic relationships in Triticum L. and Aegilops L. based on comparative morphological and anatomical investigations of dispersal mechanisms. Ph.D thesis, Oregon State University.

Moulins de D. 1993. Les restes de plantes carbonisées de Cafer Höyük. *Cahiers de l'Euphrate* **7**: 191–234.

Moulins de D. 1997. *Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium B.C.* Oxford: British Archaeological Reports, International Series 683.

Nesbitt M. 1998. Where was einkorn wheat domesticated? *Trends in Plant Science* **3**: 82–83.

Nesbitt M, Goddard J. 1997. Why draw seeds? Illustrating archaeobotany. *Graphic Archaeology* **1997**: 13–21.

Nesbitt M, Samuel D. 1996. From staple crop to extinction? The archaeology and history of the hulled wheats. In: Padulosi S, Hammer K, Heller J (eds). *Hulled wheats. Proceedings of the First International Workshop on Hulled Wheats.* Rome: International Plant Genetic Resources Institute, 41–100.

Nesbitt M, Samuel D. 1998. Letter. Wheat domestication: archaeobotanical evidence. *Science* **279:** 1432.

Nishikawa N. 1983. Species relationship of wheat and its putative ancestors as viewed from isozyme variation. In: *Proceedings of the 6th International Wheat Genetics Symposium.* Kyoto: 53–63.

Percival J. 1921. *The Wheat Plant: A Monograph.* London: Duckworth.

Poyarkova H, Gerechter-Amitai ZK. 1991. Two variants of wild emmer (*Triticum dicoccoides*) native to Israel: morphology and distribution. *Canadian Journal of Botany* **69:** 2772–2789.

Schlumbaum A, Jacomet S, Neuhaus J-M. 1998. Coexistence of tetraploid and hexaploid naked wheat in a Neolithic lake dwelling of central Europe: evidence from morphology and ancient DNA. *Journal of Archaeological Science* **25:** 1111–1118.

Schultze-Motel J. 1988a. Archäologische Kulturpflanzenreste aus der Georgischen SSR (Teil 1). *Kulturpflanze* **36:** 421–435.

Schultze-Motel J. 1988b. Archäologische Kulturpflanzenreste aus der Georgischen SSR (Teil 2). *Kulturpflanze* **37:** 415–426.

Sears ER. 1976. A synthetic hexaploid wheat with fragile rachis. *Wheat Information Service* **41–42:** 31–32.

van Slageren MW. 1994. *Wild wheats: a monograph of Aegilops L. and Amblopyrum (Jaub. & Spach) Eig (Poaceae).* Wageningen: Wageningen Agricultural University, Agricultural Papers; 94–7.

Stuiver M et al. 1998. INTCAL98 radiocarbon age calibration, 24,000-0 cal BP. *Radiocarbon* **40:** 1041–1083.

Tsunewaki K. 1966. Comparative gene analysis of common wheat and its ancestral species. II. Waxiness, growth habit and awnedness. *Japanese Journal of Botany* **19:** 175–229.

Valkoun J, Waines JG, Konopka J. 1999. Current geographical distribution and habitat of wild wheats and barley. In: Damania AB, Valkoun J, Willcox G, Qualset CO (ed.). *The origins of agriculture and crop domestication.* Aleppo: ICARDA, 293–299.

Villaret-von Rochow M. 1967. Frucht- und Samenreste aus der neolithischen Station Seeberg, Burgäschisee-Süd. *Acta Bernensia* **2:** 21–64, Tafel I–VIII.

Willcox G. 1996. Evidence for plant exploitation and vegetation history from three Early Neolithic pre-pottery sites on the Euphrates (Syria). *Vegetation History and Archaeobotany* **5:** 143–152.

Willcox GH. 1992. Archaeobotanical significance of growing Near Eastern progenitors of domestic plants at Jalès (France). In: Anderson PC (ed.). *Préhistoire de l'agriculture.* Paris: Éditions du CNRS, 159–177.

Yen C, Luo MC, Yang JL. 1988. The origin of the Tibetan weedrace of hexaploid wheat, Chinese Spring, Chengdu-guang-tou and other landraces of the White Wheat complex from China. In: Miller TE, Koebner RMD (eds). *Proceedings of the Seventh International Wheat Genetics Symposium. Volume 1.* Cambridge: Institute of Plant Science Research, 175–179.

Zeist W van. 1976. On macroscopic traces of food plants in southwestern Asia (with some reference to pollen data). *Philosophical Transactions of the Royal Society of London, Series B* **275:** 27–41.

Zeist W van. 1983. A palaeobotanical study of Neolithic Erbaba, Turkey. *Anatolica* **10:** 47–89.

Zeist W van, Bakker-Heeres JAH. 1982. Archaeobotanical studies in the Levant. 1. Neolithic sites in the Damascus basin: Aswad, Ghoraifé, Ramad. *Palaeohistoria* **24:** 165–256.

Zeist W van , de Roller GJ. 1991/1992. The plant husbandry of aceramic Çayönü, SE Turkey. *Palaeohistoria* **33/34:** 65–96.

Zohary D. 1996. The mode of domestication of the founder crops of Southwest Asian agriculture. In: Harris DR (ed.). *The origins and spread of agriculture and pastoralism in Eurasia.* London: UCL Press, 142–158.

Zohary D. 1999. Monophyletic vs. polyphyletic origin of crops on which agriculture was founded in the Near East. *Genetic Resources and Crop Evolution* **46:** 133–142.

Zohary D, Harlan JR, Vardi A. 1969. The wild diploid progenitors of wheat and their breeding value. *Euphytica* **18:** 58–65.

Zohary D, Hopf M. 1993. *Domestication of plants in the old world. The origin and spread of cultivated plants in West Asia, Europe, and the Nile Valley.* Second edition. Oxford: Clarendon Press.

Taxonomy and Distribution

Wheat taxonomy

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Abstract

With the new techniques of cytogenetics, genetics and molecular biology, wheat taxonomy has advanced dramatically since John Percival's time, but it is still chaotic at the lower levels with little consensus. Large reference collections, such as that made by Percival, have an important role in typifying and fixing the names of variants, as well as in identification.

The wheat taxonomist has a difficult job. The variation in *Triticum/Aegilops* is extraordinary and one has only to look through the enormous herbarium collection of wheat that John Percival amassed to see the diversity. Hybridization and polyploidy have occurred frequently and been assisted by man over a long period, complicating the systematics enormously. Most botanists recognise about 20 species of *Triticum* and a further 20 of *Aegilops* (Mabberley, 1997). The taxonomist is still at a loss to know how to deal with this variation, and despite a symposium dedicated to the Infraspecific Classification of Wild and Cultivated Plants, some years ago (Styles, 1986), we are practically no further forward, although we appear to appreciate the problems better. *The International Code of Botanical Nomenclature* (Greuter *et al.*, 1994) and *The International Code of Nomenclature for Cultivated Plants – 1995* (Trehane *et al.*, 1995) do not work well for large cultivated plant complexes. A worrying situation also seems to occur, as different accessions in different collections appear to bear the same name. There is no satisfactory system for typification and certain identification of agricultural variants and garden cultivars. The Royal Horticultural Society's Herbarium at Wisley has been developing and accumulating 'Standard Portfolios' in accordance with Principle 3 of the *International Code of Nomenclature for Cultivated Plants — 1995* (Miller, 1999), in an effort to overcome this problem as far as possible.

The molecular biologists are producing many new cladograms that are resulting in the publication of a large amount of nomenclatural changes to reflect phylogeny. In

some ways, the situation has become worse, with a divergence of opinion as to whether paraphyletic taxa are allowable. The study of wheat taxonomy has been very active with the production of a lot of data from isozyme work and modern molecular techniques that have raised considerable taxonomic and nomenclatural problems.

The advent of cladistics caused a sudden increase in the more critical examination and testing of character homology to good effect. The use of molecular biological techniques in more recent years, in a great many taxonomic research projects, has meant that the traditional characters from morphology, including S.E.M., are not initially studied to the degree that they were. If the molecular techniques work, there is often only then a more thorough examination of morphological characters to support cryptic molecular groups (Rudall, 2000). Nesbitt (this volume) has shown that there is a great need for special-purpose classification for archaeologists working with charred remains where most of the usual characters have been burnt away. The sort of data required will only ever be provided by the archaeologists themselves as they look at a great deal of fragmentary material especially critically, developing their own specialist character sets.

In the case of wheat, the plant breeders have further complicated the situation. Their work is not based on the characters used by the taxonomists, i.e. breeders' taxonomies are not those of taxonomists. Therefore, it is no surprise that Bunting (pers. comm.) reports that Percival had no great effect on contemporary British wheat breeding. It would be interesting to speculate on what Percival would think of the situation today.

Percival's work was based on the thousands of samples sent in from all over the world from his contacts (including Vavilov, as shown by letters recently rediscovered in The University of Reading and in archives of the Vavilov Institute of Plant Industry, St Petersburg) and by the efforts of our ambassadors and consuls. Percival did not undertake fieldwork, despite the necessity for ecological and field characters to be used in the taxonomy of such agronomic species. He would have to start his work all over again: not only because of extra, modern wheat cultivars, but because so much has changed or become extinct. Wheat has evolved. A visit to the Anti Atlas in Morocco in 1997 revealed cereal fields very different from the subsistence crops on an earlier journey in 1974. This presents a nightmare scenario to a taxonomist.

Percival had over 2000 wheat variants in cultivation in Reading. It is not true that wheat is always self-pollinated, although the frequency of cross-pollination is very low, in the order of a fraction of one per cent (Zohary, 1971). Evidence here showed that wheat harvested from the Reading collection did not always match well with old specimens collected years earlier and stored in the 'tins' (Bunting, pers. comm.). The National Institute of Agricultural Botany, Cambridge were sent material from Percival's living wheat collections to maintain it in better order. They do not seem to have succeeded, and I believe they no longer maintain it as such.

The Percival wheat herbarium contains the species and variants known to him, although many are in poor condition, having been ravaged by pests in the past. It is important in providing illustrations to his work, especially so to archaeobotanists because it is so large and puts together so many variants from around the world. It gives them a splendid reference collection from the Percival era. Indeed, it was surely used

for this by Percival. The University of Reading holds an important world-wide collection of Percival/Helbaek ancient cereals from numerous archaeological sites (Carruthers, 1992). These were in part samples sent to Percival for identification. But one must question just how useful this can be to the present-day taxonomist. Techniques will allow DNA to be extracted, but it will be degraded, and destructive sampling of limited historical material is always to be deprecated. This scenario will become more and more of a problem. Specimen treatments to prevent infestation also take their toll. For instance, some of Percival's collection was microwaved in the past to kill biscuit beetles. It is interesting to note that to my knowledge there has been only a single request to see it in the last 25 years, and that was from Laura Morrison. It is always assumed that collections made by botanists are likely to be deposited in their home institution, and although it must be said that our entry in *Index Herbariorum* (Holmgren, Holmgren & Barnett, 1990) does not actually mention Percival, I do not think this would have stopped inquiries. Whilst the value of the collection in supporting molecular studies may be limited, it does seem that it can be used to compare with collections of Percival still in cultivation in Britain, Germany, Russia and the United States. With the restrictions placed on the acquisition of plant specimens by the Convention on Biodiversity, these old collections have taken on a new importance.

REFERENCES

Carruthers WJ. 1992. Percival and Helbaek's archive of plant remains. *Circaea* 8: 65–70.

Greuter W, Barrie FR, Burdet HM, Chaloner WG, Demoulin V, Hawksworth DL, Jørgensen PM, Nicholson DH, Silva PC, Trehane P, McNeill J (eds). 1994. *International Code of Botanical Nomenclature.* Königstein: Koeltz Scientific Books.

Holmgren PK, Holmgren N, Barnett LC. 1990. *Index Herbariorum, Part 1: The Herbaria of the World.* Eighth edition. New York: New York Botanical Garden For the International Association for Plant Taxonomy.

Mabberley DJ. 1997. *The Plant Book.* Cambridge: Cambridge University Press.

Miller D. 1999. Raising Standards. *The Garden:* 282–283.

Rudall PJ. 2000. 'Cryptic' characters in monocotyledons: homology and coding. In: Scotland RW, Pennington RT (eds). *Homology and systematics.* London: Taylor & Francis, 114–123.

Styles B. (ed.) 1986. *Infraspecific Classification of Wild and Cultivated Plants.* London: Academic Press.

Trehane P, Brickell CD, Baum BR, Hetterscheid WLA, Leslie AC, McNeill J, Sponberg, SA, Vrugtman F (eds). 1995. *International Code of Nomenclature for Cultivated Plants.* Wimborne: Quarterjack Publishing.

Zohary D. 1971. Origin of South-west Asiatic Cereals: Wheats, Barley, Oats and Rye. In: Davis PH (ed.). *Plant Life of South-West Asia.* Edinburgh: Botanical Society of Edinburgh.

The Percival Herbarium and wheat taxonomy: yesterday, today, and tomorrow

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Abstract

The spike specimens that John Percival used to document his living wheat collection are contained in a boxed Herbarium set held by the University of Reading. Not housed in the University Herbarium facility, this significant collection of wheats, made during the early years of the 20th century, has been neglected due to misunderstanding of its historical heritage and scientific value. Its potential as a record of pre-modern wheat diversity as well as a source for DNA specimen material is as yet unrecognized. There is a connection between the handling of the Percival Herbarium and the chaos that now rules wheat taxonomy. Classification of the wheats has a long historical tradition with roots in the ancient herbalist lore of Greco-Roman times. Although most modern treatments of *Triticum* L. and *Aegilops* L. are founded in the biological species concept, they still operate under the influences of their early taxonomic history. From an evolutionary perspective, attempts of the genomic classification schools to present correct wheat taxonomies of phylogenetic relationships have not been successful. To ensure its future as a tool of communication and record-keeping, wheat researchers must separate taxonomy from phylogenetic reconstruction. Just as attention should now focus on preserving the heritage of the Percival collection, the research community should draw from the example of Percival's *The Wheat Plant* and support a multi-disciplinary monographic project to revise the taxonomy of the wheats.

INTRODUCTION

As the 19th century was coming to a close, the University of Reading's agricultural botanist John Percival set out to remedy, in his words, "the botanist's neglect of cultivated plants" (Percival, 1921: vii). He began with the wheats, embarking on a project that lasted more than 20 years. Had he been able to fulfill his dream, *The Wheat Plant* would have

been the first in a series of volumes, each dedicated to a major agricultural crop. We are fortunate that Percival selected wheat as his first monographic task. Except for the work produced under the leadership of Vavilov during the scientific heyday of the pre-Stalinist USSR, the scope and breadth of *The Wheat Plant* is unparalleled in the voluminous research literature on the wheats. After almost 80 years, this monograph still serves as a valuable reference. Although Percival's concept of genetics, evolutionary relationships, and plant breeding is long outdated, his extensive treatment of wheat taxonomy, morphology, anatomy, growth, and development is relevant today. As we face the beginning of the 21st century, it is appropriate to reflect upon Percival's scientific legacy and the inspiration which produced it.

THE PERCIVAL WHEAT COLLECTION

Living collection

During the preparation of *The Wheat Plant*, Percival amassed a living collection of wild and domesticated wheats which he described as "probably the most representative collection in existence, and derived from almost all wheat- growing regions of the world" (Percival, 1921: viii). Unfortunately, wars, politics, and changing agricultural practices have now irreparably altered the diversity from which this collection was made, preventing any modern-day duplication of what was possible in Percival's day. Once numbering over 2500 living accessions, the complete Reading Collection is now essentially lost, although some accessions have found their way to genebank collections in England, Germany, Russia, Japan, New Zealand, Canada, and the USA. The renewed interest which has been fostered by this symposium will do much to focus attention on what remains of this heritage.

Although protecting wheat biodiversity has now developed into an international issue, it was not a "cause célèbre" during and following Percival's professional career. Budgetary constraints, initially imposed by World War II and subsequently by University administrative priorities (see Bunting, this volume), are responsible for the events which led to the collection's demise. The University simply could not afford to regenerate the 2500 accessions regularly. According to official correspondence made available at the Symposium, by 1955 only 200 viable accessions remained and these were turned over to the National Institute of Agricultural Botany in Cambridge as a more fitting repository for their upkeep. There is no information at this writing as to their current status although staff members of the former Plant Breeding Institute, to which the IAB was connected, believe them to be lost. The Department of Agricultural Botany at Reading continued to maintain its own collection into the 1960s but it too was eventually lost to budgetary constraints and other research priorities.

Perhaps even more tragic within the historical context is the loss of Percival's books and papers which would have at least provided his personal record for the collection. No catalogue to the complete 2500-accession Reading Collection has yet been located. It is likely from the information which has been pieced together by Hugh Bunting's research into the Percival family history that upon his parents' deaths, Alan Percival, the only surviving child, sold anything of his father's that was of value and destroyed the rest. Thus, we are left with very little direct information about the Reading Collection and practically nothing of Percival's personal papers and correspondence.

The Percival Herbarium

To some extent, the Percival Herbarium that is still held by Reading University compensates for the loss of the living collection, but this preserved collection has also not fared well. During an August 1991 visit to Reading to view the Percival Herbarium collection, I was led not to the Herbarium but to a downstairs laboratory in the Plant Sciences Laboratories building. Stacked inside the cabinet beneath a fume hood and on the adjacent floor were 74 leather-bound wooden boxes containing hundreds of sheets of Percival's specimens, all showing some degree of damage by insects, water and mould. Quite a number of the boxes had to be pried from the floor, a very telling sign of the considerable passage of time since their last use. What lay forgotten in those boxes represents a significant scientific legacy that we would do well to rediscover.

Percival's Herbarium comprises three components. A 15-box demonstration set, created to accompany *The Wheat Plant*, contains spike specimens of the material displayed in the figures illustrating the monograph. Three other such demonstration sets are held by the Herbaria of the British Museum and The Royal Botanic Gardens, Kew and the research collection of the John Innes Centre in Norwich, England. The N.I. Vavilov Institute of Plant Industry (VIR) also holds 11 boxes of Percival wheat specimens, presumably a partial demonstration set. The other 59 boxes of the Percival Herbarium are unique to the Reading University's holdings. Of these, one component consists of 50 boxes containing specimens of wheat cultivars arranged by country or region (27 boxes), *T. dicoccoides* and cultivars of durum and bread wheats (15 boxes), synthetic hybrid material of *Aegilops* × *Triticum* (5 boxes) and wheat × rye crosses (1 box), and oats (2 boxes). The remaining nine boxes, smaller in size, each hold a single sheet of glume specimens which Percival used in his morphological studies and for illustrations in *The Wheat Plant*. In each of the 63 wheat specimen boxes are, on average, 20 cardboard herbarium sheets on which four to eight spike specimens are mounted and labelled with species and cultivar names, common name (where available), and country of origin. By a modest estimate, the 63 boxes of wheat spikes contain 5000 specimens. Given the careful botanist that Percival was, his Herbarium probably documents the whole of the original living Reading Collection. However, without a catalogue to the complete 2500-accession collection, it is not possible to verify the completeness of the Herbarium.

At some point following the close of his career, Percival's Herbarium ceased to have any recognizable value to the University except for an occasional use as teaching material. However foolish this may appear to us now, the neglect is understandable within the context of the time, for these years mark a period of dramatic changes in the practice of wheat taxonomy. The other more pervasive factor deciding the collection's fate is the low status generally given by the botanical sciences to domesticated plant taxonomy and its working specimen material. Although divisions are not always very clear between the basic research of the agricultural and botanical sciences, there are sharp lines which separate the systematics and taxonomy of wild versus domesticated plants. The practice of wheat taxonomy has largely fallen into the hands of geneticists who usually do not place a value on herbarium work or specimen documentation. On the other side, Herbaria do not typically value 20th century domesticated plant specimens produced by agricultural programs as priority herbarium material for which

they need to make space. On the basis of these attitudes and events, it is not difficult to understand the University's failure to incorporate the Percival Herbarium collection into its own Herbarium facility. Interestingly, the fate of the Percival Herbarium offers a fitting metaphor for launching a discussion of wheat taxonomy, which also has suffered from neglect and misunderstandings of historical heritage.

WHEAT TAXONOMY — YESTERDAY

Wheat taxonomy has developed under two influences – a long historical tradition dating to classical antiquity and, by contrast, the relatively short 80 years of wheat genetics whose beginning was marked in 1918 by the independent discoveries by Sax and Sakamura of the allopolyploid series in *Triticum*. Today's taxonomic controversies originate in arguments over generic circumscription and phylogenetic relationships. Usually omitted from this discussion is the influence of the earlier botanical tradition on the development of modern taxonomy. This tradition, particularly its treatment of the domesticated wheats, is worthy of examination. In the ensuing discussion, names and authority citations follow the classifications of Dorofeev *et al.* (1979) for *Triticum* and Hammer (1980) for *Aegilops*, unless otherwise indicated.

Historical origins

The names *Triticum* and *Aegilops* have their origins in the vernacular of ancient herbalists and folklore. According to the Roman scholar Varro (116–28 BCE), the name *Triticum* came from the Latin *tero* which translates: "I rub grains from the ear", i.e. "I thresh" (J & C Cotte, 1912; Jasny, 1944 citing the Latin scholar Varro). Thus, in its original usage, *Triticum* had a practical, descriptive meaning. The Romans applied the term loosely, usually in a narrow sense for the naked, free-threshing wheats (durum, rivet, and bread wheats) or otherwise more broadly for both naked and hulled wheats together (Jasny, 1944). Ancient names for hulled wheats (emmer and spelt) which have subsequently figured in the taxonomy and vernacular include *Zea, far,* and *spelta*. *Aegilops* has consistently been a term for wild grasses with awns, but the translation of the Greek from which it was derived has been variously interpreted (Slageren, 1994). According to Bor (1968), the meaning that is most likely to be true to the original derivation is "a grass similar to that liked by goats", an interpretation, which he notes, is verified by the avid appetite of goats for the long and profusely-awned wild wheats.

The structure of domesticated wheat taxonomy also has its roots in classical antiquity. Pre-Linnaean botanists adopted both the ancient vernacular and descriptive concepts of domesticated wheats. We can trace the beginnings of our current taxonomic concept of domesticated wheats to the Roman agricultural writer Columella (1st century CE) who classified the naked, tough-rachis wheats into *Triticum* and the hulled, semi-fragile rachis wheats into *Zea* (Percival, 1921). This concept consistently held and was given its formal botanical tradition by Caspar Bauhin in his printed Herbal *Pinax Theatri Botanici* (1623). Linnaeus developed his concept of *Triticum* under the influence of C. Bauhin, J. Bauhin and J.H. Cherler (1651), and Morison (1715). He employed the broad Roman meaning of *Triticum*, uniting the pre-Linnaean *Triticum* and *Zea* into his genus *Triticum* L.[1] In the *Species Plantarum* (1753), Linnaeus described five domesticated wheat species – *T. aestivum, T. hybernum, T. turgidum, T. spelta,* and *T. monococcum,* all forms known by the Romans. He later added *T.*

polonicum and *T. compositum* in 1762 and 1774, respectively. Only two of these Linnaean names have dropped into the synonymy – *T. hybernum* now a synonym for *T. aestivum* and *T. compositum* a synonym for *T. turgidum*. *Triticum spelta* as originally conceived by Linnaeus actually encompassed both emmer and spelt wheats, a practice also dating to the ancient Greco-Roman concept of hulled wheats. It was not until Schübler (1818) described *T. dicoccum* as a distinct species (Morrison, 1998) that the current concept of *T. spelta* L. began to develop.

In the century and a half from publication of the *Species Plantarum* to the beginning of the modern period of wheat taxonomy, *Triticum* saw many changes and additions. This brief review highlights only several of the more significant contributions. Schübler (1818) subdivided *Triticum* into two separate sections of naked and hulled wheats, thereby returning to the Columellan concept. Seringe (1841–1842) created three genera – *Triticum* for the naked wheats, *Spelta* for the hulled wheats emmer and spelt, and *Niveria* for the hulled einkorn wheat. Alefeld (1866) placed "polish" wheat in its own genus *Deina* (*D. polonicum*) and created one large species, *T. vulgare* under which all other domesticated wheats were ranked in nine varietal groups. Körnicke (1885) reduced *Triticum* to three large species, *T. vulgare, T. polonicum*, and *T. monococcum*. Grenier & Godron (1855), Hackel in Engler and Prantl (1887) and Ascherson & Graebner (1901) united *Aegilops* and *Triticum* together into one genus *Triticum*. Of note here are similarities in these early species concepts with those that have shaped the taxonomy of the 20th century.

Wild wheats and the domestication bias

Aegilops L. has always been a genus of wild species. As originally described by Linnaeus, it was not allied with *Triticum*. Slageren (1994) can be consulted for a historical review of *Aegilops* classification which in its development has been considerably less complex than is the case for *Triticum*. Concerning the four wild *Triticum* species, two of them were described in the 19th century. The diploid A[b]-genome wild wheat was described initially in 1834 as *Crithodium aegilopoides* by Link, in 1854 as *Triticum boeoticum* by Boissier, and in 1857 as *Triticum aegilopoides* by Balansa. Thirty years later, Kornicke (1885) designated Balansa's *Triticum aegilopoides* as the wild progenitor of *T. Monococcum*.

The tetraploid AB-genome wild wheat has a more complicated history (See Aaronsohn, 1910). First collected by Kotschy in 1855 on Mt. Hermon, it lay misidentified as a specimen of *Hordeum spontaneum* C. Koch until 1873 when Körnicke recognized its significance. Strangely, Körnicke did not announce his discovery until 1889. He declared this wild form to be the progenitor of cultivated wheat. In 1906 after several years of searching, Aaronsohn who was the Director of the Jewish Agricultural Experimental Station in Haifa, Palestine (modern-day Israel), and an active botanist, rediscovered populations of this wild wheat in the Upper Galilee and on Mount Hermon. Originally, *"dicoccoides"* was treated with an infraspecific ranking – named by Körnicke (1889) as *Triticum vulgare* var. *dicoccoides* and later by

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1   As circumscribed, *Triticum* L. had two sections, *Annua* and *Perennia*. The five species treated under
  ˙*Annua* form the Linnaean foundation for *Triticum sensu stricto*. Linnaeus classified two wild perennial
  grasses now treated in *Elymus* L. under the *Perennia* section; now treated in *Elymus* L. under the
  Perennia section.

Ascherson & Graebner (1901) as *Triticum sativum* subsp. *dicoccum* var. *dicoccoides*. It is an interesting footnote that Aaronsohn and his predecessors were looking for the wild prototype of naked wheats (durum and bread wheats), a search which in and of itself excluded the then known diploid wild wheat, *T. boeoticum*, from consideration as a progenitor species.

Handling of the wild *Triticum* species offers an important example of the historical bias which has framed the taxonomy of *Triticum* and which still exerts its unshakable influence today. Two other wild species were identified in this century; the tetraploid AG-genome wheat, *T. araraticum* (Jakubziner, 1947) and the diploid A^U-genome wheat, *T. urartu* which was first identified in 1937 by Thumanian but not validly published until 1972 by Gandilyan. Of the four wild *Triticum* species, three are associated with a domesticated form of equivalent ploidy level – *T. boeoticum* with *T. monococcum*; *T. dicoccoides* with *T. dicoccum*, and *T. araraticum* with *T. timopheevii*. When not given specific rank (as is the case in most current treatments), these wild species are treated as infraspecific taxa under their domesticated counterparts, never the other way around. *Triticum urartu*, now accepted as the A-genome progenitor of the durum and bread wheats, has no corresponding diploid domesticated form. It is not recognized by some geneticists and thus disappears when *T. monococcum* is designated the lead diploid species (e.g. Kimber & Sears, 1987). This subordination of the wild progenitors is an interesting anomaly in the otherwise evolutionary approach claimed by the practitioners of genomically based wheat taxonomy. The emphasis on the domesticated species and the structuring of *Triticum* around them has not changed since antiquity. Moreover, the historical and modern-day emphasis is generally focused on the naked wheats, particulary *T. aestivum,* such that our perspective on the evolution of *Triticum* is usually approached experimentally and otherwise from the vantage point of *T. aestivum*. This research bias, which frames the direction of current evolutionary studies, is very strongly rooted in the past.

WHEAT TAXONOMY – TODAY

Early modern classifications

The modern era of wheat taxonomy begins with the treatments of Schulz (1913), Thellung (1918), and Percival (1921). Schulz was innovative in establishing the three morphological groupings that later proved to match the ascending ploidy levels for *Triticum*. Thus his einkorn, emmer, and dinkel groups corresponded respectively to diploid, tetraploid, and hexaploid wheats. Thellung followed in the footsteps of Körnicke by reducing *Triticum* to three species – *T. monococcum, T. turgidum*, and *T. aestivum*. This reduced concept of *Triticum*, using the same species names, reappears in the genomic treatments that developed in the latter half of this century. Percival divided *Triticum* into two groups, each headed by one of the two wild species known at that time – *T. aegilopoides* (Link) Balansa ex Körn. (= *T. boeoticum*) for the diploid group and *T. dicoccoides* for the polyploid group. Under these, he placed the eleven domesticated wheats, designating them as races or cultivated species and keeping their specific status, e.g. *T. monococcum* under *T. aegilopoides*. Percival, as did Schulz before him, was unusual for placing these two wild species in a position as progenitor taxa to the

domesticated ones. This treatment concept which gives evolutionary status to the wild wheats is a unique development in the modern taxonomy.

In their subsequent monographic treatments of *Triticum*, Flaksberger (1935) and Dorofeev *et al.* (1979) followed Schulz's organization of *Triticum*. These two classifications are largely unknown outside Russia, a consequence of language barrier and politics. As traditionally structured morphological treatments, they have exerted little influence on our current handling of the genus. Criticism of the more recent Dorofeev *et al.* treatment is quite common and consistent. According to Mac Key (1981, 1988) and other geneticists who take an interest in wheat taxonomy, this treatment fails because it delineates domesticated species by morphological characters rather than by genealogical ones, giving species ranking to morphological variants which differ by only one to several major genes. This claim, equally voiced by other proponents of genomic classification that a species must be treated, and therefore circumscribed, as a discrete phylogenetic unit, is actually at odds with evolutionary history of the wheat complex as well as the practicalities of taxonomy, a point which I will explore below. First, I would like to review the developments which have led to what Mac Key (1988) has aptly described as the chaos of wheat taxonomy.

Genomic classification

In the decades following publication of *The Wheat Plant*, cytogeneticists began to define wheat species on the basis of genomic constitution and gene differences. While the taxonomic application of these genetic concepts has been evolving over a 50-year period, the underlying basis, in the form of genomic constitution, has remained relatively constant. Three conflicting taxonomic approaches have been taken, largely the work of five cytogeneticists. Hitoshi Kihara (Japan) and James Mac Key (Sweden) maintained *Triticum* and *Aegilops* as separate genera composed of species following different evolutionary paths; Wray Bowden (Canada) and Ernest R. Sears (USA) dealt with the wheat complex as one large unit subdivided into diploid and allopolyploid groups; Áskel Löve (USA) treated genome constitution as a generic unit, thus dividing *Triticum* into three genera and *Aegilops* into 13.

Kihara introduced the genome analyser-method which uses meiotic studies of diploid × polyploid hybrids to determine genome identity. Pairing homology between the diploid analyser genomes (now designated C, D, M, N, S, S^b, S^l T, and U) and corresponding genomes in the polyploids serves as the indicator of genetic relationship (Lilienfeld, 1951) and thereby, taxonomic status. Kihara's genomic treatment of *Aegilops* (1954, 1963) varied little from the morphological treatments of the early monographers of *Aegilops*, Zhukovsky (1928) and Eig (1929a). The two recent *Aegilops* monographs of Hammer (1980) and Slageren (1994) essentially adopt Kihara's genomic treatment. It is Kihara's genome analyser-method which has so significantly influenced modern wheat taxonomy. Dvořák (1988), Seberg (1989), Waines & Barnhardt (1992), and Seberg & Petersen (1999) have been among the few who have critically evaluated the weaknesses and limitations of this typological method, particularly for assessing phylogenetic relationship.

Mac Key (1988) has given a good deal of attention to the issues of domesticated plant taxonomy, particularly the conflict presented by the need for more flexibility in wheat taxonomy balanced against the requirements for exactness and nomenclatural stability.

Similar to Kihara's handling of *Aegilops*, his treatment of *Triticum* (Mac Key, 1966, 1988) did not diverge very far from the traditional, morphologically-based taxonomy. However, it is fundamentally different because the underlying genetic framework defines species as unique genomic units under which infraspecific taxa sharing the same genome formula are ranked. Thus, Mac Key's *Triticum* classification has only 6 species and 20 infraspecific taxa versus the 26 species and 1039 infraspecific taxa of the Dorofeev *et al.* classification[2]. Slageren's (1994) proposed treatment of *Triticum* follows Mac Key with only minor nomenclatural changes.

The taxonomic treatment of an enlarged genus *Triticum* by Bowden (1959) was an attempt to provide geneticists with the correct scientific names for the wild and domesticated wheats and their interspecific hybrids. Bowden dealt with the wheats of *Triticum* as hybrid species whose progenitors included members of *Aegilops*, a situation which in his mind necessitated an all-inclusive genus *Triticum*. As a supporting rationale for this "nomenclaturally correct" taxonomy, Bowden invoked the *International Code of Botanical Nomenclature* (Lanjouw, 1956), an interpretation giving legitimacy and credibility to his treatment. Suffice it to say that Bowden erred in his application of the *Code,* which is a set of rules governing nomenclature not classification structure, a point that I have discussed elsewhere (Morrison, 1992, 1994; see also Gupta & Baum, 1986; Mac Key, 1966, 1981, 1988). Bowden's taxonomic concept of an enlarged *Triticum* was further built and refined by Sears and his associates (hereafter, the Sears school: Morris & Sears, 1967; Kimber & Sears, 1987; Kimber & Feldman, 1987). Their *Triticum* is a large genus of genomically defined species loosely organized into diploid (1 *Triticum* species; 10 or 11 *Aegilops* species) and allopolyploid (4 *Triticum* species; 11 or 13 *Aegilops* species) groupings. The inconsistency between the current treatments of Kimber & Sears (1987) and Kimber & Feldman (1987) in the ranking of three species – *T. sharonense* (Eig) Feldman & Sears, *T. peregrinum* Hackel in J. Fraser, and *T. rectum* (Zhuk.) Bowden – is responsible for their variable number of species. Although Bowden can be faulted for his misinterpretations of the *Code*, his attempt to employ proper taxonomic procedure was admirable. However, those in the Sears school have not been so careful. According to the *Code,* seven of the names in their treatments are unusable because they are illegitimate, invalid, or ambiguous. At the opposite end of the taxonomic spectrum is the genomic treatment of Löve (1984) with 16 genera, each defined by a differentiated chromosome set. Comparatively speaking, Löve took a radical approach by designating genome constitution as a generic taxonomic unit. In reality, he is a splitter who has divided the diploid and allopolyploid clusters of *Triticum* and *Aegilops* into their component parts. Löve's treatment is cumbersome but its generic organization is relatively consistent with traditional handling of the wheats at the sectional level.

Lesser-known classifications

Chennaveeraiah (1960) produced a lesser-known genomic treatment which moved the diploid S-genome species of *Aegilops* into *Triticum* on the basis of shared similarities of morphology (glume keel) and cytology (submedian centromeres). He also moved the diploid *Ae. mutica* into its own genus *Amblyopyrum*, a move originated

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2   The Dorofeev *et al.* treatment actually classifies 27 species, a number which includes a synthetic, AGD- genome amphidiploid to which the name *T. kiharae* has been given.

by Eig (1929b) and followed by Tan (1985) in the *Flora of Turkey*, an important taxonomic contribution to wheat classification, and later by Slageren (1994). Dissension within the ranks of the genomic classification schools has not been restricted to Mac Key. Chennaveeraiah (1960) also criticized Bowden's enlargement of *Triticum*, commenting that it did not solve the problems in wheat taxonomy but created new ones. Other lesser-known classifications of note include Nevski (1934), Schiemann (1948), Mansfeld (1953), and Gandilyan (1980). These treatments, together with the others reviewed above, do not include all the modern classifications of *Triticum* and *Aegilops*. They do offer an idea of the unusually large number crowding the taxonomy and thereby provide an insight into how confusing the situation has become for taxonomists and users alike.

Re-evaluating the biological species concept

As a body of genetic work, the genomic classifications represent a significant contribution to the understanding of evolutionary relationships in the wheat complex. They developed under the influence of the biological species concept (see Mayr, 1963) which in the context of its time offered a modern system by which to show species relationships via the taxonomy. However, systematists are now re-evaluating the limitations of the biological species concept (e.g. Templeton, 1989; Judd, *et al.*, 1999). Similarly, the typological genome characterizations, on which genomic classification is based, are under revision (see Dvořák, 1998 and references cited therein). The plant systematic community is actively exploring and debating the correct handling of species as evolutionary and/or taxonomic units (cp. Steussy, 1990; Bachman, 1999 and references cited therein; Judd *et al.*, 1999; discussions in volumes 46–48 of *Taxon*). This debate illustrates the difficulty in reaching any kind of consensus on whether our human concept of species as evolutionary entities is real or artificial. This dilemma is particularly difficult with the wheats because they are in an actively-evolving group that often defies taxonomic categorization. To bring wheat taxonomy into the future, we must deal with the realities and practicalities of what it must do to serve the research community best, rather than become engaged in endless philosophic debates.

Where genomic classifications fail

From a practical perspective, the genomic classifications of the wheats are cumbersome to use outside their purely genetic context. It is impossible for genebank managers to know how to interpret a request for material delivered as simply "5 accessions of *Triticum turgidum*". Is the request for the wild form "*dicoccoides*" or for one of the 10 recognized domesticated tetraploid forms; "*dicoccum*", "*durum*", "*turgidum*", "*polonicum*", "*turanicum*", "*aethiopicum*", "*carthlicum*", "*karamyschevii*", "*jakubzineri*", "*ispahanicum*"? This problem of what exactly a taxonomic name does or does not encompass becomes more troubling in the literature, particularly because authors of research articles typically fail to clarify which taxonomic treatment they are following. The problem becomes even more complex due to careless nomenclatural errors that pervade the genomic treatments and to the differences in names for *Aegilops* species when treated in *Triticum sensu lato*. A frequently-encountered example is offered by the D-genome species. Is it *Ae. squarrosa* or *Ae. tauschii*; *T. tauschii* or *T. aegilops*? For newcomers to the wheat

research community who are not familiar with the historical development of the
taxonomy, the confusion can be overwhelming.

WHEAT TAXONOMY – TOMORROW

The problems of wheat taxonomy have been recognized for some time (See Miller,
1987; Mac Key, 1988; Morrison, 1993, 1994) but usually they garner little attention
beyond informal conversations and symposium presentations. How well these
problems catch the attention of the wheat genetic community will determine whether
the current situation of competing classifications and inconsistent uses of names and
species concepts will continue unabated into the future. One curative measure, which
will remedy at least some of the more pressing problems of communication, is already
under way in the *GrainTax* Synonymy Tables Project. Initiated on the
recommendations of the Taxonomy Workshop held in August 1998 at the 9th
International Wheat Genetics Symposium in Saskatoon, Canada, this project is
developing an internet compilation of wheat classifications which will provide an
authoritative source for checking current and historical treatments of *Triticum* and
Aegilops (Morrison & Raupp, 1999). Accessible directly on http://www.ksu.edu/wgrc/
Germplasm/Taxonomy or by link from http://wheat.pw.usda.gov/ggpages// GrainTax,
the interactive database of tables will be set up to link names to their respective
classifications as well as to their synonyms. The *GrainTax* tables are a good first step,
but they will aid researchers only in dealing with the confusing chaos of the
nomenclature. To confront the underlying causes for so many conflicting taxonomic
concepts, each claiming to be the *correct* one for expressing phylogenetic
relationships, requires an examination of our expectations about taxonomy.

To begin, it will be necessary to step away from the back and forth debate over which
taxonomic approach is the correct one, recognizing that this goal is just as elusive today
as it was in 1959 when Bowden claimed to have produced a "nomenclaturally correct"
classification. For most of this century, wheat geneticists have attempted to dictate an
ideal of the biological species, an entity that does two things – as a genetic, evolutionary
unit, it denotes phylogenetic relationship; as a taxonomic unit, it delimits a discretely
defined category for classification. This ideal has not been met. Obviously, from the
many different wheat classifications now in use, there is no agreement on a universal
genetic/taxonomic unit. The problem lies not with the discipline of taxonomy but with
our expectations of what taxonomy can and should do.

Diverse evolutionary histories

Systematists are now recognizing that the unique evolutionary histories of plant
species cannot be handled by the broad generalizations embodied in the biological
species concept (Judd *et al.*, 1999). Genomic classifications of the wheats, which
purport to be phylogenetic treatments, have failed to serve as functional taxonomies
because they ignore the diverse evolutionary histories characterizing the wheat
complex. Wheat species have evolved by different mechanisms of hybrid speciation
and continually undergo change by gene flow and introgression. As the following
examples will show, there is no uniform mode of speciation by which a wheat species
can be defined, be it wild or domesticated.

Typically, the wheat complex is cited as a group that has evolved by allopolyploïdy. However, there are variations on this mechanistic theme which have led to different evolutionary histories. While it has been useful to describe the wheat complex as an assortment of polyploid clusters, each organized around a lead diploid species whose pivotal genome is held in common, this characterization by Zohary & Feldman (1961) is an over-simplification. Clusters definitely do exist in the group, but they are not limited to polyploids and they do not all share the same routes of development. Multiple hybridization events among the same or different combinations of diploid, and in some cases polyploid, parents has produced what may be more appropriately described as reticulated species arrays – UM-genome array (*Ae. geniculata, Ae. biuncialis, Ae. columnaris, Ae. neglecta*), US-genome array (*Ae. kotschyi, Ae. peregrina*), and the DM-genome array (*Ae. crassa, Ae. ventricosa, Ae. vavilovii*). The genus *Triticum* has traditionally been dealt with as a genus with two different evolutionary lines – AB/ABD – and AG/AAG-genome lines. Recent evidence, which establishes *T. urartu* as the A-genome progenitor and *Ae. speltoides* as the most probable B/G-genome progenitor (Dvořák & Zhang, 1990; Dvořák *et al.*, 1992), supports treating *T. dicoccoides* and *T. araraticum* as related components of a species array. Likewise, the ABD-genome domesticated wheats constitute an array. Their diversity is explained by multiple hybridization events at different times and locations, albeit from the same D-genome genepool (Dvořák, Luo & Yang, 1998; Dvořák *et al.*, 1998; Dvořák & Luo, this volume; Nesbitt, this volume). The diploid S-genome taxa also form a species array which is defined by variation in their common genome and by the parallel dimorphic inflorescence forms which form two homologous series – *Ae. speltoides, Ae. longissima*, and *Ae. searsii* versus *Ae. speltoides* ssp. *ligustica, Ae. longissima* ssp. *sharonensis*, and *Ae. bicornis*. Additionally, homoploid speciation is the likely mechanism by which *Ae. searsii* evolved.

Introgression and gene flow further contribute to messy species borders. The AB-genome domesticated wheats *T. carthlicum* and *T. turgidum sensu stricto* have probable origins as hybrids that evolved from natural crosses between *T. aestivum* and a tetraploid wheat (Schiemann, 1948, citing Vavilov; Kuckuck, 1982). Blumler's recent interpretation of evidence characterizing populations of *T. dicoccoides* in the Upper Jordan Valley of modern-day Israel (1998) suggests that introgression between the wild emmer and cultivated durum wheats has played a significant role in the evolution of these wild populations. Recent documentation of viable hybrids between *Ae. cylindrica* and cultivars of *Tr. aestivum* in the Pacific Northwest wheat-growing region of the USA (Mallory-Smith, Hansen & Zemetra, 1996) suggests that hybrid speciation in the domesticated setting is an ongoing evolutionary process.

The limits by which wheat species are defined are complicated further by intergrading variation. In the genome arrays mentioned above, species borders are not always clear-cut. Polyploid species are noted for their overlapping variation and intermediate forms (Zohary & Feldman, 1962). Collectors of wild wheats have noted the difficulties of differentiating among wild wheat taxa and have considered the possibilities of interbreeding species mixtures (M Feldman, pers. comm.; RJ Metzger, pers. comm.). A similar problem exists at the infra- specific level. For the diploid *Ae. comosa*, intergrading variation hinders a consistent taxonomic separation between its infraspecific forms, ssp. *comosa* and ssp. *heldreichii*. The dimorphic, infraspecific forms of *Ae. speltoides*, "*speltoides*" and

"*ligustica*", grow naturally in mixed populations; joining these two distinct morphological forms is a continuum of rachis and awn variation which cannot be easily handled taxonomically (Morrison, pers. obs.).

A practical taxonomy

Variation in domesticated forms is largely the result of the human role in wheat evolution. Unfortunately, domesticated wheats are treated differently from their wild relatives by the fact that their development via evolutionary processes is ignored. While few genetic differences separate the wild species from their domesticated counterparts or separate one domesticated form from another, that fact alone does not justify overlooking their variation, and thus their biodiversity. It is foolish to dismiss minor wild or domesticated genetic variants as insignificant entities; they are the consequences or harbingers of evolutionary change whether by human intervention or via natural events. If we continue to construct genomic/phylogenetic classifications which do not treat such geographic races as the domesticated tetraploid "*ispahanicum*", we will not only lose the name but along with it, we will also lose the diversity.

In the larger systematic debate, Bachman (1998) has suggested handling the "species" dilemma by separating traditional taxonomy and its nomenclatural system from phylogenetic reconstruction. If such a scheme were adopted as a remedy to the current chaos of wheat taxonomy, it would require a paradigm shift, a challenge for geneticists and taxonomists alike. But for a workable solution to bring wheat taxonomy into the future, such a dramatic change in our thinking is essential. Genomic classification, which has become synonymous with phylogenetic classification, is obviously at odds both with the practical purpose that taxonomy must serve and the diverse evolutionary histories of the wheats. It makes sense to apply taxonomy to the task of creating a practical system by which we assign workable classification categories, albeit often arbitrarily defined, to ensure a means of uniform communication. Phylogenetic reconstruction should not be forced upon our ability to name and categorize identifiable entities of taxonomic classification. The reliability of a structured taxonomic system that could serve as a uniform means of communication will become essential for dealing with fast-moving developments of our evolutionary concepts. Changing phylogenetic concepts can form their own "alternate taxonomies" (Bachman, 1998) as the need arises. They should be seen as serving a separate and different function from the taxonomy that classifies species and infraspecific taxa into well-defined categories which enable communication and germplasm maintenance.

CONCLUSION

Returning again to the Percival Herbarium, we can see that there are parallels in its neglect and the current situation of wheat taxonomy. Just as we have overlooked the historical tradition of taxonomy, we have failed to value the working material that supports it. There are only three other early 20th century collections that can rival that of Percival. Watkins, the English plant breeder, gathered wheats from across the British Empire via the British Consuls (See Miller, Ambrose & Reader, this volume). Gökgöl monographed the rich diversity of wild and domesticated wheats native to Turkey (Gökgöl, 1935, 1939, 1955), carefully documenting her work with living and herbarium collections both of which have been lost. Russian specialists of the VIR

began collections in 1894 under the leadership of its first director Batalin and by 1931 had built a worldwide collection of 28,000 living wheat accessions (Flaksberger & Jakubziner, 1931; Udaczin & Merezhko, 1994). The living material and preserved specimens from these collections that do survive are priceless scientific treasures that offer a record of landrace diversity as it existed relatively untouched since the beginnings of Asian and European agriculture. Despite the ravages of time, insects, and the elements of a laboratory fume hood, the Percival Herbarium is still a historical legacy with considerable value. If only to honour Percival and his scientific tradition, the University has an obligation to restore and preserve the Herbarium, but there is a far more compelling reason for bringing those weathered boxes out of oblivion. In them is a storehouse of DNA available for sampling with the tools of molecular biology for handling Herbarium and archeobotanical specimens (See Brown *et al.,* 1994; Savolainen *et al.,* 1995; Schlumbaum, Neuhaus & Jacomet, 1998). The future for the Percival Herbarium for documenting pre-modern era wheat diversity and contributing to biotechnological advances in wheat breeding could be quite promising if only recognized.

As for the future of wheat taxonomy, it also offers an as yet unrecognized potential. To tap that potential will require a challenging reassessment of our expectations of taxonomy versus phylogenetic reconstruction. As long as wheat geneticists and taxonomists continue to follow their separate courses, this cannot be accomplished. Taxonomy needs to be viewed as a means of communication, not only in the literature and for purposes of defining germplasm requests, but also as a language for databases and record-keeping of the myriad of genetic stocks developing from molecular genetics. Should it continue on its current path, there will only be increasingly larger obstacles to interfere with communication among (and within) the specialties of wheat research. Percival, the consummate agricultural botanist, very much in the Darwinian tradition, offers an example for finding a solution. *The Wheat Plant* is the culmination of an exacting multidisciplinary study. While not possible by one individual working alone today, such a monographic project involving representative specialists from the disciplines of taxonomy, systematics, genetics, plant breeding, germplasm maintenance, and archeobotany is what is needed to resolve the problems of wheat taxonomy. Such a project will require the full philosophic and monetary support of the wheat research community. If there is to be a future for wheat taxonomy and likewise for stable communication among the specialties, it is time to renew the Percival tradition and undertake a modern revision of *The Wheat Plant.*

REFERENCES

Aaronsohn A. 1910. *Agricultural and botanical explorations in Palestine.* USDA, Bureau of Plant Industry, Bulletin No. 180. 64 pp.

Alefeld F. 1886. *Landwirtschaftliche Flora.* Berlin: Wiegandt & Hempel.

Ascherson PFA, Graebner KORPP. 1901. *Synopsis der mitteleuropäischen Flora* 2(6): 640–720.

Bachmann K. 1998. Species as units of diversity: an outdated concept. *Theory in Biosciences* 117: 213–230.

Balansa, B. 1857. *Plantae d'Orient exsiccate.*

Bauhin C. 1623. *Pinax theatri botanici.* Basel.

Bauhin J, Cherler JH. 1651. *Historia Plantarum Universalis,* 2. Yverdon.

Blumler, MA. 1998. Introgression of durum into wild emmer and the agricultural origin question. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The Origins of Agriculture and Crop Domestication: The Harlan Symposium*. Aleppo: ICARDA; 252–272.

Boissier PE. 1854. Diagnoses plantarum orientalium novarum, series 1. *Como* **2(13)**: 69.

Bor NL. 1968. Gramineae, 28. *Aegilops* L. In: Townsend CC, Guest E, Al-Rawi A (eds). *Flora of Iraq* **9**: 173–194.

Bowden WM. 1959. The taxonomy and nomenclature of the wheats, barleys, and ryes and their wild relatives. *Canadian Journal of Botany* **37**: 657–684.

Brown TA, Allaby RG, Brown KA, O'Donoghue K, Sallares R. 1995. DNA in wheat seeds from European archaeological sites. *Experientia* **50**: 571–575.

Chennaveeraiah MS. 1960. Karyomorphologic and cytotaxonomic studies in *Aegilops*. *Acta Horti Gotoburgensis* **23**: 85–178.

Cotte J & C. 1912. *Étude sur les blés de l'antiquité classique*. Paris: J.B. Baillière & Fils.

Dorofeev VF, Filatenko AA, Migushova EF, Udaczin RA, Jakubziner MM. 1979. Wheat. In: Dorofeev VF, Korovina ON (eds). *Flora of cultivated plants. Vol. 1.* Leningrad (St Petersburg): Kolos.

Dvořák J. 1988. Cytogenetical and molecular inferences about the evolution of wheat. In: Miller TE, Koebner RMD (eds). *Proceedings of the 7th International Wheat Genetics Symposium* **1**: 187–192.

Dvořák J. 1998. Genome analysis in the *Triticum-Aegilops* alliance. *Proceedings of the 9th International Wheat Genetics Symposium, Saskatoon, Canada* **1**: 8–11.

Dvořák J, Zhang H-B. 1990. Variation in repeated nucleotide sequences sheds light on the phylogeny of the wheat B and G genomes. *Proceedings of the National Academy of Sciences* **87**: 9640–9644.

Dvořák J, diTerlizzi P, Zhang H-B, Resta, P. 1990. The evolution of polyploid wheats: identification of the A genome donor species. *Genome* **36**: 21–31.

Dvořák J, Luo MC, Yang ZL. 1998. Genetic evidence on the origin of *Triticum aestivum* L. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The Origins of Agriculture and Crop Domestication: The Harlan Symposium*. Aleppo: ICARDA 235–251.

Dvořák J., Luo MC, Yang ZL, Zhang H-B. 1998. The structure of the *Aegilops tauschii* genepool and the evolution of hexaploid wheat. *Theoretical and Applied Genetics* **97**: 657–670.

Eig A. 1929a. Monographisch-kritische Übersicht der Gattung *Aegilops*. *Feddes Repertorium Specierum novarum regni vegetabilis*; Beiheifte **55**: 1–228.

Eig A. 1929b. *Amblyopyrum* Eig. A new genus separated from the genus *Aegilops*. *PZE Institute of Agriculture and Natural History, Tel Aviv, Agricultural Record* **2**: 199–204.

Flaksberger CA, Jakubziner MM. 1931. New ways of wheat breeding in USSR. *Tehnika sots Zenledelija* **6**: 6–9.

Flaksberger CA. 1935. Cereals: Wheat. In: Wulff EV (ed.). *Flora of cultivated plants*. Lenin Academy of Agricultural Sciences, Institute of Plant Protection. Vol. 1. Moscow: State Agricultural Publishing Company [in Russian].

Gandilyan PA. 1972. On the wild-growing species of *Triticum* of the Armenian SSR. *Botanicheskii Zhurnal* **57**: 173–181.

Gandilyan PA. 1980. Key to wheat, *Aegilops*, rye and barley. *Academy of Science, Armenian SSR, Erevan*, 190.

Gökgöl M. 1935. *Türkiye Buğdaylan (Die Türkischen Weizen)*. Volume 1. Tohum Yeğritim Enstitüsü Yayını 7. Tarim Bakanlığı, Istanbul.

Gökgöl M. 1939. *Türkiye Buğdaylan (Die Türkischen Weizen)*. Volume II. Yeşilköy Tohum Islah Enstitüsü Yayın 14. Tan Matbaasi, Istanbul.

Gökgöl M. 1955. *Buğaylann Tasnif Anahtari [Wheat Identification Key]*. Nesriyet ve Haberlesme Müdürlüğü 716 Ziraat Vekâleti, Istanbul.

Grenier M, Godron M. 1855. *Flore de France*. Paris: J-B Baillière, **3**: 598–603.

Gupta PK, Baum BR. 1986. Nomenclature and related taxonomic issues in wheats, triticales and some of their wild relatives. *Taxon* **35:** 144–149.

Hackel E. 1887. Gramineae. In: Engler A, Prantl K (eds). *Die natürlichen Pflanzenfamilien. Leipzig:* Verlag von Wilhelm Engelmann, 80–86.

Hammer K. 1980. Vorarbeiten zur monographischen Darstellung von Wildpflanzensortimenten: *Aegilops L. Kulturpflanze* **28:** 33–180.

Jakubziner MM. 1947. On names on varieties and species of hard wheat. *Selektsii i Semenovodstvo* **163:** 40–46.

Jakubziner MM. 1958. New wheat species. *Proceedings of the 1st International Wheat Genetics Symposium.* Winnipeg: Public Press Ltd. 207–220.

Jasny N. 1944. *The wheat of classical antiquity.* Baltimore: Johns Hopkins Press.

Judd, WS, Campbell, CS, Kellogg, EA, Stevens, PF. 1999. *Plant Systematics: A Phylogenetic Approach.* Sunderland: Sinauer Associates, Inc.

Kihara H. 1954. Considerations on the evolution and distribution of *Aegilops* species based on the analyser-method. *Cytologia* **19:** 336–357.

Kihara H. 1963. Interspecific relationship in *Triticum* and *Aegilops. Seiken Zihô* **15:** 1–12.

Kimber G, Feldman M. 1987. *Wild wheat: an introduction.* Special Report. 353. Columbia: College of Agriculture, University of Missouri.

Kimber G, Sears ER. 1987. Evolution in the genus *Triticum* and the origin of cultivated wheat. In: Heyne EG (ed.). *Wheat and wheat improvement.* 2nd edition. Madison: American Society of Agronomy, 154–164.

Körnicke F. 1885. Die Arten und Varietäten des Getreides. In: Körnicke, F, Werner H (eds). *Handbuch des Getreidebaues.*

Körnicke F. 1889. *Verhandlungen des naturhistorisches Vereines der preussischen Rheinlande, Westfalens und des Reg.-Bezirks Osnabrück.* **46:** 21.

Kuckuck H. 1982. Beiträge zur Evolution und Systematik der Kulturweizen. *Biologisches Zentralblatt* **101:** 349–63.

Link HFr. 1834. Symbolae ad floram graecam. *Linnaea* **9:** 132.

Lanjouw J (Chairman, Editorial Committee). 1956. International code of botanical nomenclature. *Regnum Vegetabile.* Utrecht: International Association of Plant Taxonomists.

Lilienfeld FA. 1951. H. Kihara: genome-analysis in *Triticum* and *Aegilops.* X. Concluding review. *Cytologia* **16:** 101–122.

Linnaeus C. 1753. *Species plantarum.* Stockholm.

Linnaeus C. 1762. *Species plantarum* (2nd edition), Stockholm

Linnaeus C. 1774. *Systema vegetabilium* (13th edition), Murray JA (ed.). Wein.

Löve Á. 1984. Conspectus of the Triticeae. *Feddes Repertorium* **95:** 425–521.

Mac Key, J. 1966. Species relationships in *Triticum.* Proceedings of the 2nd International Wheat Genetics Symposium. *Hereditas Suppl.* **2:** 237–276.

Mac Key, J. 1981. Comments on the basic principles of crop taxonomy. *Kulturpflanze* **29:** 199–107.

Mac Key, J. 1988. A plant breeder's aspect on taxonomy of cultivated plants. *Biologisches Zentralblatt* **107:** 369–379.

Mallory-Smith CA, Hansen J, Zemetra RS. 1996. Gene transfer between wheat and *Aegilops cylindrica. Second International Weed Control Congress* 441–445.

Mansfeld R. 1953. Zur allgemeinen Systematik der Kulturpflanzen I. *Kulturpflanze* **1:** 138–155.

Mayr E. 1963. *Animal Species and Evolution.* Cambridge, MA: Harvard University Press.

Miller TE. 1987. Systematics and evolution. In: Lupton FGH (ed.). *Wheat Breeding: Its Scientific Basis.* London: Chapman & Hall, 1–30.

Morris R, Sears ER. 1967. The cytogenetics of wheat and its relatives. In: Quisenberry KS, Reitz LP (eds). *Wheat and wheat improvement.* Madison: American Society Agronomy, 19–87.

Morison R. 1715. *Plantarum Historiae Universalis Oxoniensis,* 3. Oxford.

Morrison LA. 1993. *Triticum-Aegilops* systematics: taking an integrative approach. In: Damania AB (ed.). *Biodiversity and wheat improvement*. Chichester: John Wiley & Sons, 59–66.

Morrison LA. 1995. Taxonomy of the wheats: a commentary. In: Li ZS, Xin ZY (eds). *Proceedings of the 8th International Wheat Genetics Symposium*. Beijing: Agricultural Scientech Press **1**: 65–72.

Morrison LA. 1998. Lectotypification of *Triticum turgidum* and *T. spelta* (Poaceae). *Taxon* **47**: 705–710.

Morrison LA, WJ Raupp. 1999. *GrainTax* synonymy tables project: June 1999 progress report. *Wheat Information Service* **88**: 52–56.

Nevski, S. 1934. Wheat: *Triticum* L. In: Roshevitz RJ, Shishkin BK (eds). *Flora of the USSR*. Leningrad (St. Petersburg): Botanical Institute of the Academy of Sciences, USSR, 675–688.

Percival J. 1921. *The Wheat Plant; A Monograph*. London: Duckworth.

Sakamura T. 1918. Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. *Botanical Magazine, Tokyo* **32**: 151–154.

Savolainen V, Cuénoud P, Spichiger R, Martinez MDP, Crèvecoeur M, Manen J-F. 1995. The use of herbarium specimens in DNA phylogenetics: evaluation and improvement. *Plant Systematics and Evolution* **197**: 87–98.

Sax K. 1918. The behaviour of the chromosomes in fertilisation. *Genetics* **3**: 309–327.

Schiemann E. 1948. *Weizen, Roggen und Gerste: Systematik, Geschichte und Verwendung*. Jena: Gustav Fischer.

Schübler G. 1818. *Dissertatio inauguralis botanica sistens characteristicen et descriptiones cerealium*. Tübingen.

Schulz A. 1913. *Die Geschichte der kultivierten Getreide*. Halle: Verlag Louis Neberts.

Schlumbaum A, Neuhaus J-M, Jacomet S. 1998. Coexistence of tetraploid and hexaploid naked wheat in a Neolithic lake dwelling of Central Europe: evidence from morphology and ancient DNA. *Journal of Archaeological Science* **25**: 1111–1118.

Seberg O. 1989. Genome analysis, phylogeny, and classification. *Plant Systematics and Evolution* **166**: 159–171.

Seberg O, Petersen G. 1999. A critical review of concepts and methods used in classical genome analysis. *Botanical Review*: in press.

Seringe NC. 1841–2. Descriptions et figures des céréales européenes. *Annales des Sciences Physiques et Naturelles, d'Agriculture et de l'Industrie, Lyon* **4**: 373; **5**: 111–114.

Slageren M van. 1994. Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig. *Wageningen Agricultural University Papers* 1994(7).

Steussy TF. 1990. *Plant Taxonomy: The Systematic Evaluation of Comparative Data*. New York: University of Columbia Press.

Tan K. 1985. 14. *Triticum* L. In: Davis PH (ed.). *Flora of Turkey and the East Aegean Islands*. 9: 245–255. Edinburgh: Edinburgh University Press.

Templeton, AR. 1989. The meaning of species and speciation: A genetic perspective. In: Otte D, Endler JA (eds). *Speciation and its consequences*. Sunderland: Sinauer Associates, 3–27.

Thellung A. 1918. Neuere Wege und Ziele der botanischen Systematik, erläutet am Beispiele unserer Getreidearten. *Naturwissenschaftliche Wochenschrift*. Neue Folge **17**: 465–474.

Tumanian, MG. 1937. Noverij vid dikoj psjenizjeri, *Tr. Urartu* Thuman. *Trudy Armjanskogo filiala Akad. Nauk. SSSR, Ser. Biol.* **5**: 210–215.

Udaczin RA, Merezhko AF. 1994. World wheat VIR collection. *Selectsija i Semenovodstvo*. **3**: 2–12.

Waines JG, Barnhardt D. 1992. Biosystematic research in *Aegilops* and *Triticum*. *Hereditas* **116**: 207–212.

Zhukovsky PM. 1928. A critical systematic survey of the species of the genus *Aegilops* L. *Bulletin of Applied Botany Genetics and Plant Breeding* **18**: 417–609.

Zohary D, Feldman M. 1962. Hybridization between amphidiploids and the evolution of polyploids in the wheat (*Aegilops-Triticum*) group. *Evolution* **16**: 44–61.

The geographical distribution of wild wheats in their historical setting and current context

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Abstract

Geographical distribution of wild wheats, i.e. wild species of the *Triticum – Aegilops – Amblyopyrum* complex, is discussed in a broader context of the species evolution, taxonomy, conservation and utilization in wheat breeding. The paper includes a brief historical account the exploration of wild wheats and research relevant to the species' geography. The current geographical distribution data were obtained from the 'Global database of wild wheat relatives' maintained at the International Center for the Agricultural Research in the Dry Areas (ICARDA), Aleppo, Syria. The data are presented in a concise form in a table and charts based on the basic statistics for latitude, longitude and altitude in the case of 21 *Aegilops*, four wild *Triticum* and one *Amblyopyrum* spp. and their 8878 and 6527 natural population sites for latitude/ longitude and altitude, respectively. The geographical distribution is discussed in relation to the species evolution, genomic constitution and ecological adaptation. Geographical aspects of the intra-specific diversity and new challenges relating to wild wheat geography are also considered.

INTRODUCTION

The most valuable part of the diversity of plants is that which supplies the world's food. Wheat alone provides energy in food to one third of the human population (Harlan, 1992). Interestingly, most of the major food crops, including wheat, originated in dry lands with distinct climate seasonality. Their centres of primary diversity, which include the wild progenitors and relatives, are located in dry temperate zones or subtropics (Hawkes, 1983).

One of the three nuclear centres of agricultural origin, as defined by Hawkes, is the Near East arc, a relatively small area of semi-arid dry lands in the Near East. The particular climate of the region favoured the evolution of large- seeded, annual species. The nutrient-rich seeds enable vigorous plant establish- ment and growth in the cool and relatively humid winter season. The plants have to complete their vegetative cycle and scatter the seeds on the ground with the onset of the long, hot summer period of no rainfall.

The early plant gatherers found these plants a convenient source of concentrated energy and protein, which could be carried and stored easily. Archeological evidence documents that wheat was probably domesticated in the western part of the Near East arc some 10,000 years ago (Harris, 1998) and is, along with barley and lentil, the oldest cultivated crop of the Near East nuclear centre of agricultural origin. It played an essential role in the rise of the great Near East civilizations and was a basic component of the Neolithic Revolution package, which spread to other parts of the world (Zohary & Hopf, 1993).

The Near East region and the adjacent Mediterranean and West Asia are not only the primary centres of cultivated wheat origin and diversity but they are also the homeland of other annual species of the tribe Triticeae, including wild wheats.

THE HISTORICAL SETTING

Our interest in wild wheats, i.e. wild species of the *Triticum–Aegilops– Amblyopyrum* complex, is primarily based on their potential value for wheat breeding, since they belong to the primary and partly to the secondary gene pool of cultivated bread and durum wheat, as defined by Harlan & de Wet (1971). Consequently, useful genes can be transferred from these wild relatives to cultivated wheat by wide hybridization. As wheat is one of the world's two most important crops, it is understandable that more effort has been spent on wheat breeding and research than on any other crop. Generations of botanists, taxonomists, plant explorers, plant scientists, agronomists, breeders, archaeologists and, recently, molecular biologists have accumulated a considerable amount of knowledge and evidence on wild wheat phylogeny, taxonomy, cytogenetical relationships, and on their useful traits/genes for wheat breeding.

The advances in wheat taxonomy and cytology in 19th century resulted in the first attempts at crossing cultivated wheat with its primitive forms and wild relatives. Nevertheless, at the beginning of the 20th century, the knowledge of the geographical distribution of wild wheats was still rather limited. For example, only one wild *Triticum* species, wild einkorn (*T. baeoticum*), was known in its natural habitat, while wild emmer (*T. dicoccoides*) existed only as a herbarium specimen in Vienna (Aarohnson, 1910). The discovery of wild emmer plants near Rashaya, in what is now Lebanon, in 1906 by Aarohnson (Aarohnson, 1910) raised a new interest of botanists and plant explorers in the Near East region. A rich diversity of annual Triticeae forms was collected in the West and Central Asia and Caucasus region, as well as in the Mediterranean region of North Africa and Europe. Plant taxonomists, cytologists, breeders and scientists in other disciplines of applied plant science studied the collected plant material extensively and this concerted effort resulted in better understanding of

the relationships between cultivated wheats, particularly bread wheat, and wheat primitive forms and wild relatives.

John Percival was among the most prominent scientists of the first half of the 20th century, together with Vavilov, Kihara, Eig, Zhukovskyi and Sears, who provided the scientific background to wild wheat collection and to the use of wild relatives in wheat breeding. Excerpts from his unfinished *Aegilops* monograph written in the period of 1912–1932 (a copy of which was kindly provided to the author by Professor P.D.S. Caligari) provide a thorough species description, including chromosome number, plant morphology and traits of agronomic value (disease resistance). The detailed account of the species geographical distribution indicates his interest in exploration of wild wheat and its ecology.

The first exploration missions seeking wild Triticum and Aegilops revealed that the Near East region, and the Near East arc in particular, are rich in wild wheat taxa and forms. Together with the results of the intensive archeological research in the region, they demonstrated that the Near East was a centre of wheat's origin, domestication and primary diversity. The Russian botanist N.I. Vavilov soon recognized the global significance of the region and was among the first plant collectors to explore the rich diversity of the indigenous cultivated cereals and their wild relatives. In his mission to Syria and Palestine in 1926, he was amazed at the variation of wild emmer, T. dicoccoides, forms that he found (Vavilov, 1997).

The numerous exploration and collection missions gradually established the pattern of the geographical distribution and ecology of wild wheats. The distribution maps of wild wheats by Harlan & Zohary (1966) and Zohary & Hopf (1988) have been the most comprehensive and frequently-cited sources of information. However, as two wild *Triticum* spp., namely *T. araraticum* and *T. urartu* were described rather recently, in 1948 and 1972, respectively, and accepted by the scientific community even later, they were not treated separately in Harlan and Zohary's paper, while *T. urartu* is missing from Zohary and Hopf's book.

Johnson (1975) was probably the first to provide maps of geographical distribution for all four wild *Triticum* species. Recently, van Slageren (1994) published geographical distribution maps of all *Aegilops* spp. and *Amblyo- pyrum muticum* in his monograph. His maps are based on an extensive study of herbarium specimens and on collection site data from numerous explorations which he conducted in West Asia and North Africa during his stay at the International Center for Agricultural Research in the Dry Areas (ICARDA) in 1988–1994. Probably the most recent maps of geographical distribution of wild *Triticum* spp. and *Ae. speltoides*, *Ae. searsii* and *Ae. tauschii* were published by Valkoun, Waines & Konopka (1998). They are based on the geographical information obtained from the genetic resources databases held at ICARDA.

THE CURRENT CONTEXT OF THE GEOGRAPHICAL DISTRIBUTION OF WILD WHEATS.

Material and methods

In this paper, scientific names of wild *Triticum*, *Aegilops* and *Amblyopyrum* spp. follow the nomenclature of van Slageren's monograph (van Slageren, 1994), but the

wild *Triticum* sub-species are elevated to species level for *araraticum*, *baeoticum*, and *dicoccoides* (see Table 1). The map (Fig. 3), geographical variable and altitude means and standard deviations (Table 1) and all the geographical variable mean charts (Figs 1, 2, 4, 5) are based on the information held in the 'Global database of wheat wild relatives'. The database was originally developed by the International Plant Genetic Resources Institute (IPGRI, formerly IBPGR) in 1990; later it was upgraded, maintained, and regularly updated by the Genetic Resources Unit of ICARDA.

The database was compiled from information provided by 52 genebanks on 18,000 entries of wild *Triticum*, *Aegilops* and *Amblyopyrum*, including 13,300 entries with collection site geographical co-ordinates, which represent nearly 9,000 natural populations. ICARDA, being the major source of the information with 3,300 database entries, contributed data gathered during 50 collection missions conducted in collaboration with the national programs of Syria, Jordan, Lebanon, Iraq, Iran, Turkey,
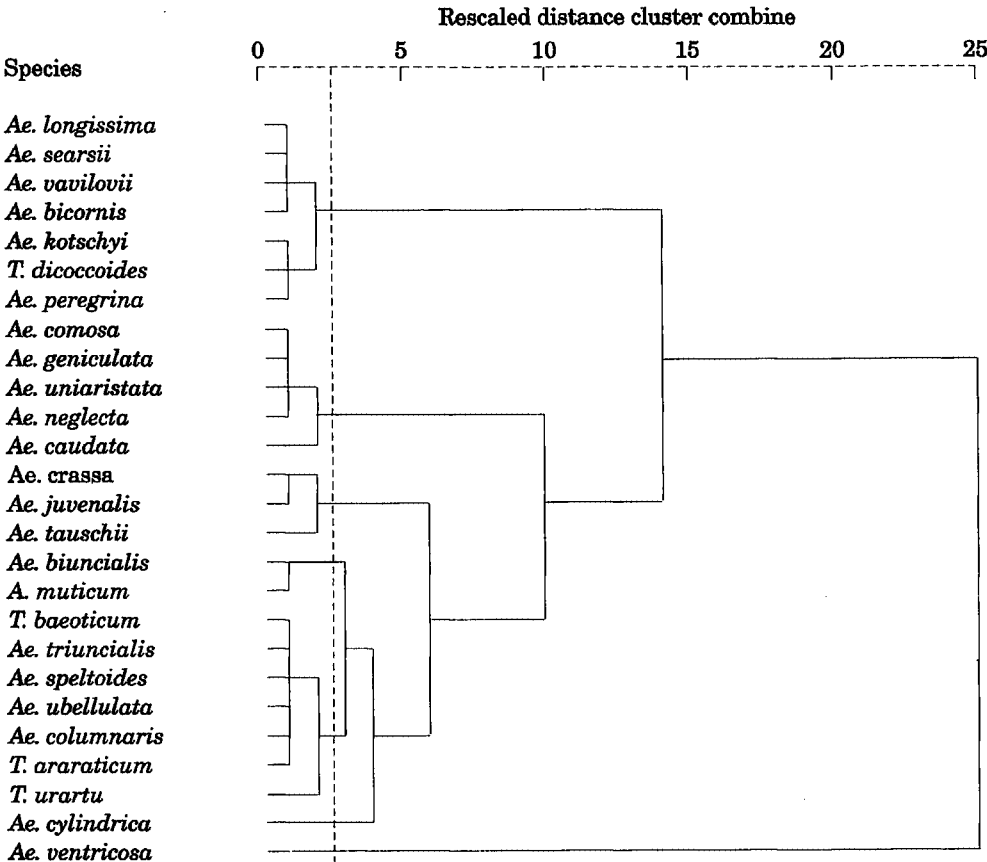
Figure 1. Dendrogram for 26 wild wheat species based on latitude and longitude means (in decimal degrees and transformed to Z-scores) using the between-group linkage method and squared Euclidean distance as a measure. The dashed line in an arbitrary distance separates five species clusters and two single species.
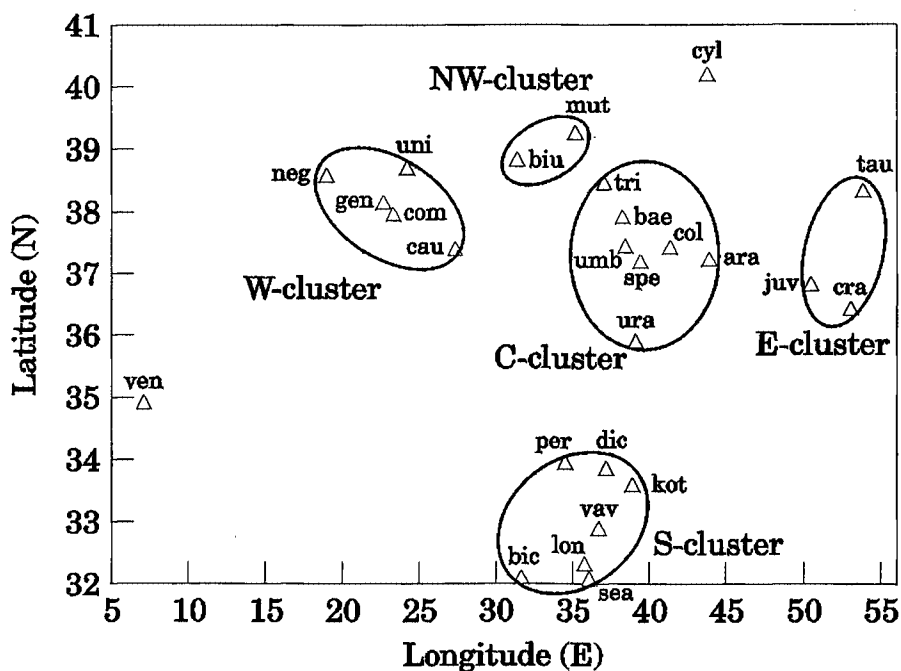
Figure 2. Plot of latitude and longitude means for 26 wild wheat species. See the text for cluster description.

Armenia, Cyprus, Egypt, Libya, Tunisia, Algeria, Morocco, Bulgaria, Russia, Turkmenistan, Uzbekistan, Pakistan and Tajikistan. Data for collection sites in Palestine were mostly not available.

The map in Figure 3 was produced by Mapmaker; geographical variable statistics and their plots were derived from the original dbase files using SPSS 9.0 (Windows) and Microsoft PowerPoint software packages. Correlation coefficients of rainfall with geographical coordinates were computed from the ICARDA wild wheat database with data for 1130 populations. The geographical distribution and altitude data for *Triticum, Aegilops* and *Amblyopyrum* spp. are presented in a concise form as basic statistics, i.e. variable means and standard deviations. Latitude and longitude values were converted into decimal degrees to facilitate computation and statistical analysis.

An additional parameter 'area' was calculated by multiplication of the latitude and longitude standard deviation. While the mean indicates the central tendency of the species' geographical distribution, standard deviation gives an idea about the dispersion of natural population sites around the variable means. The 'area' is a rectangle, in which the sides are represented by latitude and longitude standard deviations. This parameter indicates the relative sizes of the species' geographical areas.

The geographical distribution of wild wheat species

The scientific names, genomic composition, the basic statistics for latitude, longitude and altitude in the case of 21 *Aegilops,* 4 *Triticum* and 1 *Amblyopyrum* spp. are presented in Table 1. The latitude and longitude total means, 37.95°N and 35.84°E, respectively, are similar to the values given by Kimber and Feldman (1987; 80) for the centre of the geographical distribution. The data in the global database show that the 26 species of the *Aegilops–Triticum– Amblyopyrum* complex occupy an area extending from 10°W in Morocco to 111°E in Henan province, China, and from 28°N in Iran to 56° N in Russia.

The number of population sites (count in Table 1) varies greatly from species to species. *Ae. longissima, Ae. uniaristata, Ae. bicornis* and *Ae. juvenalis* are very poorly represented in the global database, and probably in the *ex situ* global collections as well. Regarding *Ae. longissima* and *Ae. bicornis,* this may partly be due to missing data for Palestine. On the other hand, the most frequent species, *Ae. triuncialis,* accounts for 21% of the total with its 1907 population sites. Diploid *Aegilops* spp. (see the single-genome species in Table 1) usually have much smaller standard deviations for both latitude and longitude than the polyploids, with the exception of *Ae. tauschii* and *Ae. umbellulata.* Tetraploid species (two-genome species in Table 1) display the highest 'area' values, except for *Ae. peregrina* and wild *Triticum* spp. This indicates that the combination of two genomes is optimal in the genus *Aegilops* for providing adaptation to a wide range of environments.

Hierarchical cluster analysis revealed the relationships among the species geographical position (Fig. 1). The dendrogram is based on standardized mean values (Z-scores) of the geographical co-ordinates. A line drawn at an arbitrary distance of 2.5 on the relative distance scale separates five species clusters and two single species, *Ae. cylindrica* and *Ae. ventricosa,* the latter being far away from the other species. A two-dimensional plot of the latitude and longitude means in Fig. 2 shows the geographical position of the dendrogram clusters.

The distribution of the diploid species and their characteristics corroborate the evolutionary theory which suggests that the process of the annual Triticeae speciation probably started in the northern part of the Near East arc, in today's southeastern Turkey and northern Syria (West, McIntyre & Appels, 1988). The region is globally richest in *Aegilops*, with 17 species (van Slageren, 1994), as well as in wild *Triticum*, with all four species present. The speciation within the *Triticum–Aegilops– Amblyopyrum* complex started at the diploid level from a common ancestor, which migrated to the northern part of the Near East arc from steppes north of the Caucasus (Hammer, 1980). According to Hammer, diploid species with more primitive traits are located close to this centre of origin, while the species with advanced characters were evolving at the periphery of the geographic distribution of the genus.

The map of geographical distribution of five *Aegilops* diploid species (Fig. 3) and the plot of geographical coordinate means (Fig. 2) show that *Ae. speltoides,* a species with primitive traits, such as out-crossing and having an ambivalent mode of spike shattering, is located in the centre of the diploid species' distribution. The central cluster (C-cluster) in Fig. 2 also includes *Ae. umbellulata* (Section Aegilops) and wild *Triticum* diploids.
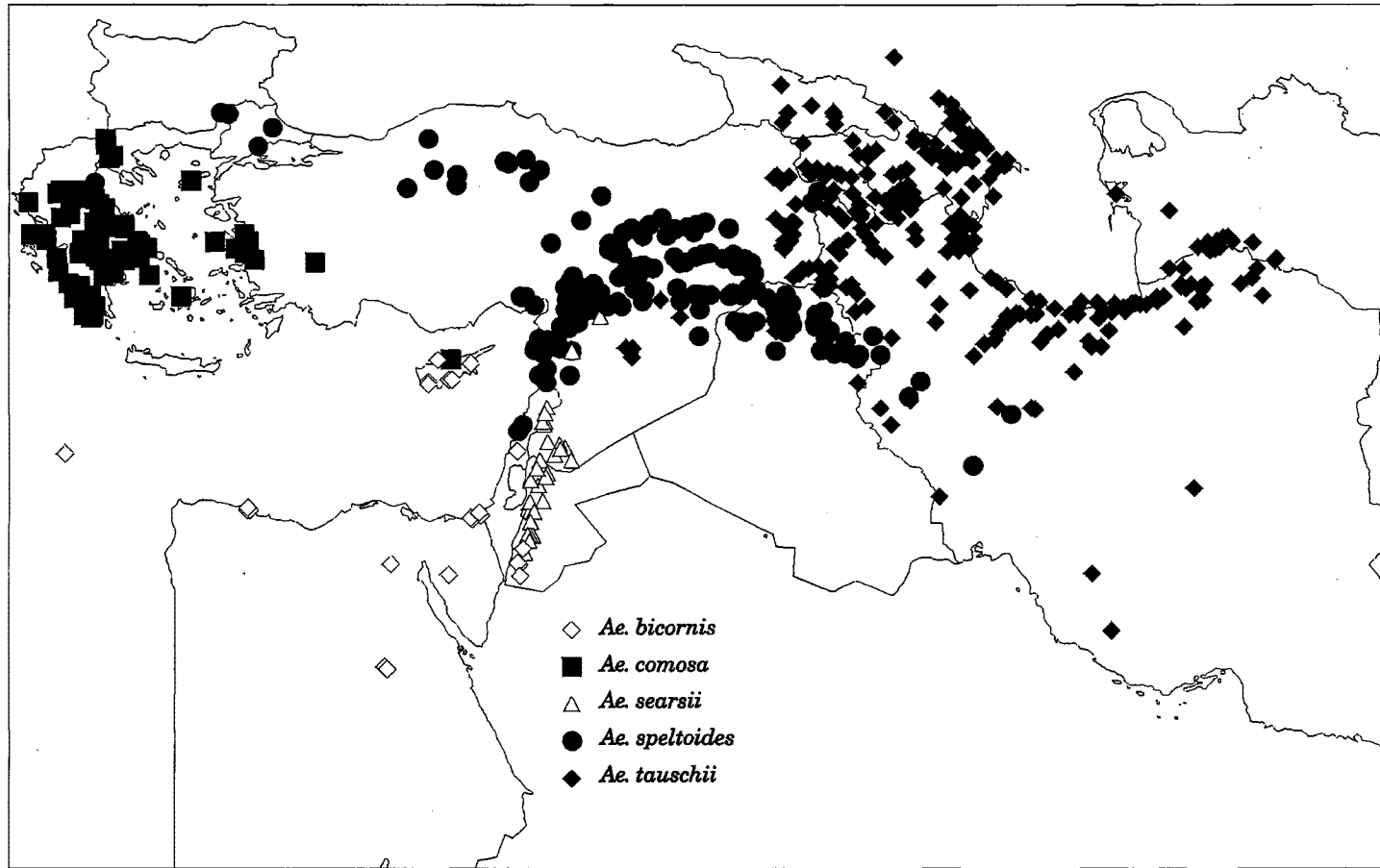
Figure 3. Map of collection sites (populations) distribution for five *Aegilops* diploid species. Only West Asia and Caucasus region sites are shown for *Ae. tauschii.*

Legend:
◇ *Ae. bicornis*
■ *Ae. comosa*
△ *Ae. searsii*
● *Ae. speltoides*
◆ *Ae. tauschii*

TABLE 1. Scientific names, genomic formula, ecological variable means, standard deviations and counts, 'area' and name abbreviations for *Aegilops* (*Ae.*), *Amblyopyrum* (*A.*) and wild *Triticum* (*T.*) species.

Species	Genome[*]	Latitude (N)[***]			Longitude (E)[***]			Altitude (m asl)			Area[**]	Abbrev.
		Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N		
Ae .bicornis (Forssk.) Jaub. & Spach	S[b]	32.10	1.95	19	31.57	3.87	19	265	372	14	7.55	bic
Ae. biuncialis Vis.	U<u>M</u>	38.80	3.32	1006	31.42	9.60	1006	451	385	723	31.87	biu
Ae. caudata L.	C	37.36	1.78	328	27.35	5.15	328	348	348	228	9.17	cau
Ae. columnaris Zhuk.	U<u>M</u>	37.43	2.23	127	41.18	5.96	127	1106	519	110	13.29	col
Ae. comosa Sm. in Sibth. & Sm.	M	37.94	1.10	154	23.25	2.37	154	460	337	83	2.61	com
Ae. crassa Boiss.	<u>D</u>M/<u>DD</u>M	36.40	2.64	223	52.97	10.94	223	852	498	147	28.88	cra
Ae. cylindrica Host	<u>DC</u>	40.22	2.66	857	43.64	11.27	857	982	559	586	29.95	cyl
Ae. geniculata Roth	<u>MU</u>	38.15	3.37	727	22.62	11.56	727	411	383	533	38.96	gen
Ae. juvenalis (Thell.) Eig	<u>D</u>MU	38.80	1.25	15	50.37	9.58	15	691	447	14	11.98	juv
Ae. kotschyi Boiss	<u>S</u>U	33.56	2.95	129	38.73	9.08	129	628	501	102	26.79	kot
Ae. longissima Schweinf. & Muschl.	S[l]	32.32	0.55	9	35.63	0.83	9	537	118	3	0.44	lon
Ae. neglecta Req. ex Bertol.	U<u>M</u>/U<u>MN</u>	38.60	2.51	649	18.94	18.59	649	551	418	508	46.66	neg
Ae. peregrina (Hack. in J. Fraser) Maire & Weiller	<u>S</u>U	33.93	1.68	181	34.45	3.30	181	473	434	157	5.54	per
Ae. searsii Feldman & Kislev ex Hammer	S[s]	32.09	1.00	47	35.97	0.35	47	964	295	46	0.35	sea
Ae. speltoides Tausch	S	37.19	1.41	296	39.37	4.09	296	612	310	220	5.77	spe
Ae. tauschii Coss.	D	38.34	2.83	770	53.85	10.22	770	949	552	519	28.92	tau
Ae. triuncialis L.	U<u>C</u>/<u>C</u>U	38.43	2.57	1907	36.99	16.90	1907	772	534	1407	43.44	tri
Ae. umbellulata Zhuk.	U	37.43	2.26	233	38.32	7.14	233	763	578	163	16.14	umb
Ae. uniaristata Vis.	N	38.68	1.90	15	24.13	3.55	15	623	378	10	6.75	uni
Ae. vavilovii (Zhuk.) Chennav.	<u>D</u>MS	32.86	1.97	68	36.53	1.92	68	911	386	65	3.78	vav
Ae. ventricosa Tausch.	<u>D</u>N	34.93	2.77	67	7.09	11.48	67	835	373	56	31.80	ven
A. muticum (Boiss.) Eig	T	39.25	0.88	42	35.19	4.37	42	879	359	25	3.85	mut
T. araraticum Jakubz.	GA	37.22	1.65	86	43.76	2.70	86	911	264	60	4.46	ara
T. baeoticum Boiss. emend E. Schiem.	A	37.89	2.05	527	38.20	6.85	527	845	407	408	14.04	bae
T. dicoccoides (Körn. ex Asch. & Graebn.) Thell.	BA	33.85	2.08	257	37.12	2.22	257	1045	311	228	4.62	dic
T. urartu Tumanian ex Gandilyan	A	35.85	2.37	139	38.91	3.74	139	950	402	113	8.86	ura
Total		37.95	3.05	8878	35.84	15.34	8878	717	51	6527	46.79	

[*] : Genomic formula according to Waines & Barnhart (1992). Underlining in polyploids indicates modification from the original diploid species genome.

[**] : A rectangular 'Area' has been calculated as multiplication of the latitude and longitude standard deviation for each species

[***] : in decimal degrees
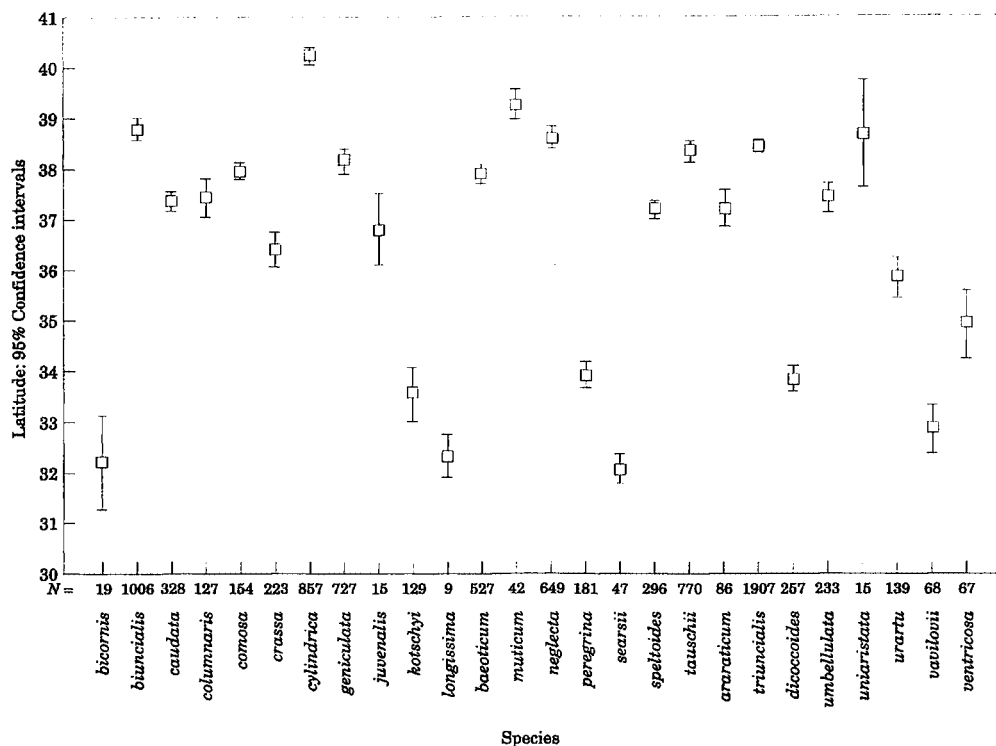
Figure 4. Plot of latitude means and 95% confidence intervals
based on data for 26 wild wheat species and 8878 populations.

Another old species, *A. muticum*, is found in the proximity in the northwestern cluster (NW-cluster). Diploid species of the Section Comopyrum (Jaub. & Spach) Zhuk., *Ae. comosa* and *Ae. uniaristata*, are located westwards, while *Ae. caudata* of the Section Cylindropyrum (Jaub. & Spach) Zhuk. is associated with them in the western cluster (W-cluster), being positioned somewhat more centrally.

Evolutionarily younger species of the Section *Sitopsis* (Jaub. & Spach) Zhuk., i.e. *Ae. longissima, Ae. searsii* and *Ae. bicornis*, are found in the southern latitudes and form the southern cluster (S-cluster). The map in Fig. 3 shows the younger *Ae. bicornis* as the most distant species of the Section *Sitopsis*. The well-defined S-cluster includes all diploid and polyploid *Aegilops* spp. with the S genome, except for *Ae.speltoides*. The presence of *T. dicoccoides* in this cluster might indicate a similarity of its B genome with the S genome of some of the diploids.

Four diploid species are found in the central cluster (C-cluster); the evolutionarily old *Ae.speltoides* and the more derived *Ae. umbellulata* and the two wild *Triticum* diploids. However, *T. urartu* is somewhat separated from the other species and located towards the S-cluster. This geographical position indicates that the species may be more distant from the common ancestor than the closely-related *T. baeoticum*. The latter also has anthers that are much longer (6.0 mm) than those of *T. urartu* (2.5 mm) (Gandilyan, 1972), which again implies a less-advanced evolutionary stage.

Ae. tauschii, a single diploid species of the Section *Vertebrata* Zhuk. emend. Kihara, has spread far to the east of the Near East centre and is located in the eastern cluster (E-cluster). This cluster includes two D-genome polyploid species, *Ae. crassa and Ae. juvenalis.*

The distribution pattern of the *Aegilops* and wild *Triticum* diploids has resulted from the development of adaptive mechanisms at the species level, such as the mode of seed dispersal and spike morphology, to different ecological niches of the highly diverse environment of the region.

The species-specific adaptation to distinct geographical sub-regions is well- illustrated in the map of five *Aegilops* diploids in Fig. 3. *Ae. speltoides* occupies the northern part of the Near East arc with fertile soils and favorable rainfall, while the other S-genome species, *Ae.searsii* and *Ae. bicornis* are adapted to dry highlands and lowlands of the southeastern Mediterranean, respectively. The D-genome species, *Ae. tauschii*, can withstand the cold winter season and periods of drought and heat stress of Central Asia and the Caucasus highlands, whereas the M-genome *Ae. comosa* prefers the mild climate of the Aegean region.

The distinct character of the species' adaptation is shown in Fig. 4 in relation to collection site latitude, where most species show significant differences in their geographical position. The plot of means and 95% confidence intervals was computed from latitude data on 8878 collection sites (populations). A similar picture displaying
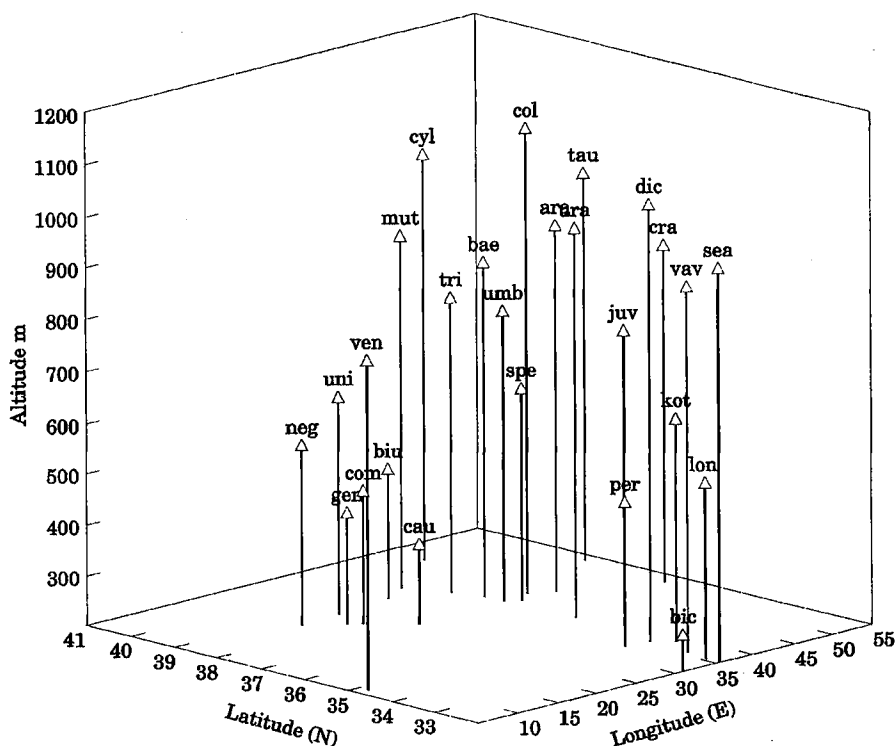

Figure 5. Tri-dimensional plot of latitude, longitude and altitude means for 26 wild wheat species.

substantial variation between species can also be obtained from site longitude and altitude data (not shown).

Polyploid species of the *Aegilops–Triticum* complex have evolved later in the region from occasional crosses between different diploids, followed by spontaneous polyploidization (amphidiploidy). Consequently, their ecological adaptation depends more on the genomes provided by the diploid donors than on the taxonomic classification. For example, *Ae. kotschyi* and *Ae. peregrina* of the Section *Aegilops* are located in the southern cluster (Fig. 2), while other polyploid species of this Section are concentrated in northern latitudes. The adaptation to higher summer temperature and terminal drought stress of these two species and *Ae. vavilovii* (Section *Vertebrata*) is conditioned by the presence of the S genome. *Ae. juvenalis* and *Ae. crassa*, polyploids of the Section *Vertebrata*, obviously inherited their drought and cold tolerance from the D-genome donor, *Ae. tauschii,* and spread far to the eastward to regions with a distinct continental climate.

When altitude is added to latitude and longitude as the third dimension, species within a cluster are further differentiated, as for example diploid *Ae. searsii, Ae. bicornis* and *Ae. longissima* or tetraploid *Ae. peregrina, Ae. kotschyi* and *T. dicoccoides* in the S-cluster or *Ae. speltoides, T. baeoticum* and *T. araraticum* in the C-cluster (Fig. 5).

Geographical aspects of the intra-specific diversity

We have demonstrated that wild *Triticum* and *Aegilops* species differ in their adaptation to specific ecological conditions, in spite of all being annual plants adapted to the Mediterranean climate, i.e. hot and dry summer and cool and rainy winter. An additional typical feature of this climate is its increasing continental character eastwards and the high year-to-year fluctuations, producing irregular periods of drought, cold and heat stresses and occasional outbreaks of diseases.

These particular climatic conditions, together with diverse soil, topographical and hydrological conditions of the West and Central Asia and Mediterranean region create many micro-ecological niches that stimulated the development of high intra-specific diversity, sometimes in a short distance or even within the same population. Some traits which are related to within-species ecological adaptation, such as glume colour, glume hairness and awn characteristics, have been used for lower taxa classification, particularly by wheat taxonomists of the former USSR (Dorofeev *et al.*, 1979; Gandilyan, 1980). Intra-specific diversity in other less conspicuous traits of major effects on plant local adaptation often went unnoticed by taxonomists, but their value for wheat breeding may be much higher.

Plant phenology certainly belongs to this category, because the optimum timing of developmental phases, e.g. flowering and maturity, dictates the survival of the plant population and its success in competition with other well- adapted members of the ecosystem. The phenology of cereals, including wheat, and pulses of Near East origin, results from a plant response to temperature (earliness *per se* and vernalization) and photoperiod. Our unpublished data for *T. baeoticum, T. urartu* and *T. dicoccoides* indicate that most of the phenotypic variation for photoperiod sensitivity is among populations or sites. Therefore, when one is interested in the manipulation of photoperiod sensitivity using wild wheats, the geographical origin of the wild parent

may be more important than the choice of the species. Similarly, disease response in wild wheat populations often displays a within-species geographical pattern depending on the frequency and severity of the disease in a given location and within-population variation may also be high (ICARDA, 1995; 26–27). Therefore, more attention should be paid to mapping the geographical distribution of the intra-specific genetic diversity in useful traits.

Future challenges relating to wild wheat geography

The above study and discussion of the geographical distribution of wild wheats was based on only three compound ecological variables: latitude, longitude and altitude. The new information technologies, such as the Global Positioning System (GPS), Geographical Information System (GIS) and Remote Sensing (RS), provide means for more accurate and detailed ecological characterization of wild wheats. It will be based on the elementary ecological variables, e.g. on monthly temperature, monthly rainfall, parent rock and soil characteristics, vegetation cover, etc. However, the prerequisite to exploring the full potential of the GIS and RS technologies is the quality and completeness of latitude and longitude data in databases compiled from the genebank and/or herbarium accession information. Transcription of the usually narrative collection site description into site co-ordinates and computerization of the data is a tedious and time-consuming task that will need a concerted effort of genetic resources collection and herbarium curators and documentation specialists.

It has been widely recognized that wild progenitors and relatives of wheat have accumulated a rich reservoir of genes for adaptation and survival in the harsh natural environment during their long existence in the region. Useful genes have already been transferred from the crop wild gene pool to the cultivated wheats, particularly those related to biotic stress tolerance. In future, the rich natural genetic diversity of wild wheats may be indispensable for wheat breeding to meet the challenges posed by the rapidly-growing human population and possible climatic changes. Even if the recent advances in bio- technology make the gene transfer between unrelated organisms possible, wild wheats of the primary gene and secondary wheat gene pool, as defined by Harlan & De Wet (1971), are still the most feasible wild source of genes for conventional breeding programs, and will remain so for some time.

Archeological data show that geographical distribution of wild wheats was a dynamic phenomenon even before the onset of agriculture and plant domestication, that was dependent on the climatic changes in the region (Wilcox, 1998). The spread of agriculture from the Near East centre of domestication had a two-fold effect on the geographical distribution of wild wheat. On the one hand wild species, particularly those which developed weedy races, were moved with the seed of cultivated species far away from the original area of the natural distribution, while on the other hand agriculture caused the major loss and fragmentation of the natural habitats of the wild wheats. Unfortunately, this process has accelerated dramatically in the last few decades and the rapid genetic erosion of the wild wheat gene pool is primarily related to the high rates of population growth in most countries of West Asia and North Africa. Since the wild wheat progenitors and close wild relatives occupy an ecological niche similar to that of cultivated cereals and pulses, most natural habitats have been converted into fields and the demand for arable land is still growing.

To save at least a part of the remaining genetic diversity, joint teams of scientists from international and national organizations have conducted numerous collection missions to sample the genetic diversity of natural populations and conserve them *ex situ* in genebanks. However, the *ex situ* conservation of genetic resources has its limitations, especially regarding wild species (Frankel, 1978; Plucknett *et al.*, 1987). Moreover, our results suggest that the very high genetic diversity, encountered in some natural populations of wild wheats, cannot be sampled adequately and maintained as a bulk in a genebank (Valkoun & Damania, 1992). Consequently, a complementary method, *in situ* conservation in the original habitat, has been recommended for wild species, including crop wild relatives (Ingram & Williams, 1984).

New tools are now available for germplasm characterization at the DNA level. Molecular characterization of data based on the application of polymerase chain reaction (PCR) techniques will provide new insight into the extent and structure of genetic diversity and its geographical pattern in wild wheat genebank holdings, as well as in natural populations in the original habitat. Molecular marker techniques will also reveal the cryptic genetic richness of wild wheats. The detailed eco-geographical data, supported by the new knowledge coming from the molecular characterization, will facilitate the development of the optimal strategy for conserving wild wheats, both *ex situ* and *in situ*. The use of the new tools will also promote the efficient utilization of these invaluable genetic resources in wheat breeding and research for the present and future needs of the mankind.

THE FINAL NOTE

Even if we are proud of the recent advances in wheat research using modern technology, we have to appreciate the enormous contribution of generations of scientists who, working with much simpler and modest tools, have built the solid foundations of today's achievements. In this context, we also owe much to John Percival for his scientific legacy, which has been a major cornerstone of modern wheat science and breeding.

ACKNOWLEDGEMENTS

REFERENCES

Aaronsohn A. 1910. *Agricultural and botanical explorations in Palestine*. USDA, Bureau of Plant Industry, Bulletin No. 180, Washington, USA: Government Printing Office.

Dorofeev VF, Filatenko AA, Migushova EF, Udachin RA, Jakubziner MM. 1979. *Flora of cultivated plants. Vol. 1. Wheat*. Leningrad: Kolos [in Russian].

Frankel O. 1978. Conservation of plant genetic resources and their wild relatives: an overview. In: Hawkes JG (ed.) *Conservation and agriculture*. London: Duckworth, 123–149.

Gandilyan PA. 1972. On the wild-growing *Triticum* species of the Armenian SSR. (in Russian). *Botanicheskyi Zhurnal* 57: 173–181.

Gandilyan PA. 1980. *Opredelitel pshenitzi, aegilopsa, rzhi i jachmenja. [Key to wheat, Aegilops, rye and barley].* Acad. Sci. Armenian SSR, Erevan [in Russian].

Hammer K. 1980. Vorarbeiten zur monographischen Darstellung von wildpflanzensortimenten: *Aegilops* L. *Kulturpflanze* **28**: 33–180.

Harlan JR. 1992. *Crops and man.* 2nd edition. Madison, WI: American Society of Agronomy and Crop Science Society of America.

Harlan JR, de Wet JMR. 1971. Toward a rational classification of cultivated plants. *Taxon* **20**: 509–517.

Harlan JR, Zohary D. 1966. Distribution of wild wheats and barley. *Science* **153**: 1074–1080.

Harris DR. 1998. The spread of Neolithic agriculture from the Levant to western Central Asia. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origins of agriculture and crop domestication.* Aleppo: ICARDA, 65–82.

Hawkes JG. 1983. *The diversity of crop plants.* Cambridge, MA and London: Harvard University Press.

Kimber G, Feldman M. 1987. *Wild wheat: An introduction.* Special Report 353, Colombia, Missouri: College of Agriculture, University of Missouri.

Ingram GB, Williams JT. 1984. In situ conservation of wild relatives of crops. In: Holden JWH, Williams JT (eds). *Crop genetic resources: conservation and evaluation.* London: George Allen & Unwin, 163 – 179.

ICARDA. 1995. *ICARDA Annual report 1994.* Aleppo: ICARDA.

Johnson BL. 1975. Identification of the apparent B-genome donor of wheat. *Canadian Journal of Genetics and Cytology* **17**: 21–39.

Plucknett DL, Smith NJH, Williams JT, Murthi Anishetty N. 1987. *Gene banks and the world's food.* Princeton, NJ: Princeton University Press.

van Slageren MW. 1994. *Wild wheats: A monograph of Aegilops L. and Amblyopyrum (Jaub. & Spach) Eig (Poaceae).* Wageningen Agricultural University Papers 94–7, Wageningen, The Netherlands: Wageningen Agricultural University and Aleppo: ICARDA.

Valkoun J, Damania AB. 1992. Gliadin diversity in populations of *Triticum urartu* and *T. dicoccoides* in Syria. In: *Reproductive Biology and Plant Breeding, Book of Poster Abstracts. XIIIth EUCARPIA Congress*, Angers, France, 499–500.

Valkoun J, Waines JG, Konopka J. 1998. Current geographical distribution and habitat of wild wheats and barley. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origin of agriculture and crop domestication.* Aleppo: ICARDA, 293–299.

Vavilov NI. 1997. *Five continents.* Rome: International Plant Genetic Resources Institute.

Waines JG, Barnhart D. 1992. Biosystematic research in *Aegilops* and *Triticum*. *Hereditas* **116**: 207–212.

West JG, McIntyre CL, Appels R. 1988. Evolution and systematic relationships in the Triticeae (Poaceae). *Plant Systematics and Evolution* **160**: 1–20.

Willcox G. 1998. Archeological evidence for the beginnings of agriculture in Southwest Asia. In: Damania AB, Valkoun J, Willcox G, Qualset CO (eds). *The origin of agriculture and crop domestication.* Aleppo: ICARDA, 25–38.

Zohary D, Hopf M. 1988. *Domestication of plants in the Old World.* Oxford: Clarendon Press.

Zohary D, Hopf M. 1993. *Domestication of plants in the Old World: the origin and spread of cultivated plants in West Asia, Europe, and the Nile Valley*, 2nd edition. Oxford: Clarendon Press.

Germplasm and Collections

Introduction:
Germplasm and collections

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Keywords: germplasm – collections – accessions

According to the genepool concept of Harlan & de Wet (1971) several genera belong to the genepool of *Triticum*: *Aegilops, Secale, Dasypyrum, Elymus, Elytrigia, Leymus* and *Agropyron* (von Bothmer, Seberg & Jacobsen, 1992). They have to be considered as useful germplasm sources, but the most important germplasm comes from the genus *Triticum* itself, which comprises 27 species, with many subspecies and convarieties and several hundred botanical varieties, according to Dorofeev *et al.* (1979). Although the number of species seems to be too high for a modern evolutionary approach and the number of infraspecific taxa is difficult to keep in mind and is not easy to handle, this and similar systems (e.g. Percival, 1921) provide a unique basis for judging the diversity of *Triticum* using mainly morphological characters.

In recent decades, large collections of wheats have been brought together. According to the *Report on the State of the World's Plant Genetic Resources for Food and Agriculture* (FAO, 1996) the genebanks of the world contain 784,500 accessions of *Triticum*. They comprise diploid, tetraploid and hexaploid forms of *Triticum* and some related genera, e.g. *Aegilops*, which are sometimes included in the genus *Triticum*.

In the last ten years in particular, the wild relatives in the species complex have been considered for the collections because they show a great variation with respect to molecular markers. These species are often difficult to distinguish morphologically (e.g. *T. baeoticum – T. urartu, T. araraticum – T. dicoccoides*) and the collections are therefore not well-determined. There are several recent cases of misinterpretation based on wrongly-determined material.

Whereas the wild taxa of *Triticum* and related genera are well-collected (see e.g. van Slageren, 1994; Valkoun, Waines & Konopka, 1998), the cultivated races are currently neglected, even though they are far from being sufficiently known. Many rare types are disappearing or have already disappeared in recent years because they are affected by

genetic erosion in agriculture and cannot find niches outside the agro-ecosystems. As a striking example Ethiopia can be mentioned. On the other hand, even new botanical varieties have been detected and described (Filatenko & Hammer, 1997).

For wild species a special approach has to be taken by genebanks, especially in the process of reproduction (see e.g. Hammer, 1997). *In situ* conservation is an excellent method for wild species. On-farm conservation for cultivated races is proposed as a new approach, but so far there are only a few results. Zeven (1996) has provided information in this direction.

Though the number of wheat accessions in genebanks is already very high, there is really no time to lose to secure the genetic basis of this most important crop (see e.g. Peña-Chocarro, 1996).

The high numbers in the FAO report stress the importance of the search for unwanted duplicates (Hammer *et al.*, 1998) but they are not good signals for stressing conservation priorities.

REFERENCES

Dorofeev VF , Filatenko AA, Migušova EF, Udačin RA, Jakubziner MM. 1979. *Wheat. Flora of cultivated plants.* Leningrad: Kolos.

FAO 1996. *Report on the State of the World's Plant Genetic Resources for Food and Agriculture.* Rome: FAO, 75 pp.

Filatenko AA, Hammer K. 1997. New descriptions of hulled wheats on the infraspecific level. *Genetic Research and Crop Evolution* 44: 285–288.

Hammer K. 1997. The management of germplasm of wild relatives of crop plants at Gatersleben. *Bocconea* 7: 263–272.

Hammer K, Knüpffer H, Filatenko A, Zuev E. 1998. Diploid wheats in the Gatersleben genebank. In: Jaradat AA (ed.). *Triticeae III,* 37–44.

Harlan JR, de Wet JMJ. 1971. Toward a rational classification of cultivated plants. *Taxon* 20: 509–517.

Peña-Chocarro L. 1996. In situ conservation of hulled wheat species: The case of Spain. In: Padulosi S *et al.* (eds). *Hulled Wheats,* 129–146.

Percival J. 1921. *The Wheat Plant. A Monograph.* London: Duckworth & Co.

Valkoun J, Waines JG, Konopka J. 1998. Current geographical distribution and habitat of wild wheats and barley. In: Damania AB *et al.* (eds). *The Origins of Agriculture and Crop Domestication,* 293–299.

Van Slageren MW. 1994. Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig. *Wageningen Agricultural University Papers* 49–7.

Von Bothmer R, Seberg O, Jacobsen N. 1992. Genetic resources in the Triticeae. *Hereditas* 116: 141–150.

Zeven AC. 1996. Results of activities to maintain landraces and other material in European countries *in situ* before 1945 and what we may learn from them. *Genetic Research and Crop Evolution* 43: 337–341.

The collection and use of wild and landrace wheats

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Keywords: Wheat – diaspore – seed dispersal - isozymes - roots

Abstract

A collection of wild and landrace wheats allows for many avenues of research. An historical approach illustrates the ability of collectors to observe morphological differences between *Triticum monococcum* and *T. urartu*. It allows study of genetic diversity among species, identifies possible intermediate forms in species differentiation and pinpoints isolating mechanisms between populations of *Aegilops speltoides* and *T. urartu*. Tetraploid and hexaploid forms of *Ae. neglecta* are morphologically similar, but can be differentiated by the size and frequency of stomata. Many goatgrasses have synaptospermic diaspores where the spike is disseminated intact. Possible selection forces needed to maintain these are rodents or other grazing animals. There is a series of genes for toughness of rachis in these diaspores, from one-gene control, to two, to possibly four or six in hexaploid *Ae. neglecta*. Pollination biology of *Ae. triuncialis* needs study, for the evolutionary advantages of disseminating hill populations of full-sibs and half-sibs may be another selection pressure to maintain the tough-rachised diaspore. Wheat roots have been neglected since Percival's monograph. Improved root characters are needed in wheats for rainfed and sustainable areas. Ditelosomic lines of landrace wheat, lacking a pair of chromosome arms, may exhibit root or shoot biomass overproduction.

INTRODUCTION

The University of California, Riverside collection of wheats and goatgrasses numbers around 4500 accessions of wild and domesticated types mostly from the genera *Aegilops* and *Triticum*. As with the Percival and Watkins collections, the UCR collection was started by one man, the late Professor B. Lennart Johnson. He learned the new technique of electrophoresis of seed proteins in Dr. Ove Hall's laboratory in Sweden in 1959 and thought an analysis of seed proteins in diploid and polyploid wheats might shed light on the controversial donor of the B genome of durum and bread wheat. In that study, which lasted from 1961 to 1976, Lennart amassed a large collection of germplasm and became convinced that earlier collections of wild wheats in the Near East had been superficial. He organized two collecting trips, one in 1965 to Turkey, and a second in 1972–73 to Israel, Lebanon, Turkey, Iraq and Iran.

TRITICUM URARTU IN USDA COLLECTIONS PRIOR TO 1970

Triticum urartu was first observed by Tumanian in Armenia (Tumanian, 1929–1930; Gandilian, 1972). Knowledge of the paper, written in Russian, was limited in Western Europe and North America. Moreover, many botanists thought that Soviet taxonomists recognized as species a number of taxa that should more correctly be considered to be varieties. I was a graduate student at the University of California, Los Angeles in 1964–67, and at Riverside in 1967–68. My job was to obtain kernel samples of *Aegilops* and *Triticum* species available in seed lists from germplasm collections. Kernel accessions were germinated, the chromosome number counted, plants grown out, herbarium specimens made and kernels harvested and threshed for protein extraction. As a post-doctoral fellow at the University of Missouri, Columbia, I was able, through Dr. Ernest R. Sears' contacts with USDA and Soviet wheat workers, to obtain seed of recently-described taxa from the Vavilov Institute in Leningrad, which included *Triticum urartu,* in 1969 and 1970.

The collection that first gave a clue to the presence of *T. urartu* growing outside Armenia was PI 245726 (G827) obtained as *Aegilops speltoides,* from the Plant Introduction Station at Ames, Iowa, in June 1965. It was collected by a member (possibly J.R. Harlan) of the US Operations Mission at Ankara in 1957, or earlier, from Ceylanpinar, Urfa province, Turkey. Lennart realized that this accession was mis-named and called it *Triticum boeoticum*. This wild diploid wheat had a seed protein pattern with two fast bands, different from those of other diploid wheats with one fast band or none. In December 1968, at Columbia, Missouri, I received two accessions from the USDA collection, PI 227669 (G1545) and PI 230133 (G1546), originally named *Hordeum* species, and both collected by Howard Scott Gentry in Iran. PI 227669 was collected August 1955 from a mountain pass above Dashte Arjan, west of Shiraz, at 2400m. PI 230133 was collected July 9, 1955, at Dastan, south of Shahre Kord, at 2260m. These diploid wheats were entered into the Riverside accession book as *T. boeoticum* in January, 1969, but were later found to have two fast-moving bands in their seed protein profile (Table 1).

It was the existence of these three diploid wheats from Turkey and Iran with an unusual endosperm protein profile that stimulated Lennart to return to the Near East in

TABLE 1. Accessions of *Triticum urartu** in the USDA small grains collection prior to 1970.

Accession	Location	Identity	Collector
PI245726	Ceylanpinar, Urfa, Turkey	*Aegilops speltoides*	Member US Mission, 1957
PI227669	Dashte Arjan, Shiraz, Iran, 2400m	*Hordeum* sp.	Howard S. Gentry, August 1955
PI230133	Dastan, Shahre Kord, Iran, 2260m	*Hordeum* sp.	Howard S. Gentry, July 9, 1955

*Robert Metzger says that several of the accessions of *Triticum boeoticum* collected by J.R. Harlan in Turkey in the 1950's and 1960's were later re-identified by him as *T. urartu*.

the summers of 1972 and 1973 (Johnson, 1972). Working with robust material that he collected from Urfa and Mardin provinces, Turkey, that looked like wild tetraploid wheat, but which was diploid, Lennart recognised that the types with two fast-migrating protein bands were morphologically similar to *T. urartu*. He had already received *T. urartu* collected from Armenia in1970 from Leningrad. These three accessions demonstrated that *T. urartu* was present in Turkey and Iran. The 1972 and 1973 collecting trips found it to be common in Lebanon and Turkey, less so in Iraq and Iran. None of the wild wheats Lennart collected in Turkey in 1965 in Urfa and Mardin was *T. urartu*. Professor Zohary had also collected this area in 1962 and had not found *T. urartu*. However, a collection of wild wheats received from the Agricultural Research and Introduction Centre, Menemen, near Izmir, in January 1973, but made between 1967 and 1972, contained mostly wild and domesticated forms of *T. monococcum*, but three accessions were later identified as *T. urartu*. The more thorough collection of wild wheats in southeastern Turkey in the early 1970s was beginning to sample *T. urartu*.

Today, we recognize that *T. urartu* is common in the Fertile Crescent from Jordan, but not Israel, proceeding northwards through southern Syria and the Bekaa Valley of Lebanon into northern Syria and southeastern Turkey, Armenia, Iraq and Iran. The two countries where we know least of the distribution of *T. urartu* are Iraq and Iran. The International Center for Agricultural Research in the Dry Areas (ICARDA) has collected recently in northern Iraq, but there are few recent collections of wild wheats in western Iran, especially from the areas where Gentry collected in 1955. There is need to investigate the distribution of wild wheats in the Zagros Mountains, especially above 2000m. Botanists have still to determine how far south of Shiraz wild wheats grow in the mountains.

The occurrence of *T. urartu* in the USDA collections before 1970, when Johnson first received grains from Leningrad, demonstrates three points. First, it is unwise to disregard the views of local botanists without translating, reading and testing their observations. Second, even famous botanists, such as H.S. Gentry, and possibly J.R.

Harlan, can make mistakes in identifying grasses, especially in geographic regions where they are less familiar with the flora. All three accessions were mis-named, which might mean that the collectors recognised something unfamiliar about the plants. Third, it is advisable for students of germplasm to make their own determinations, and not rely on those of a resident curator. Often large collections such as the USDA Small Grains, containing mostly domesticated material, do not have specialists who are familiar with foreign literature nor with the minor morphological differences used to separate wild species. Cryptic or sibling species in wild cereals are common, for example *Ae. bicornis* and *Ae. sharonensis*, *T. turgidum* and *T. timopheevii*, *T. monococcum* and *T. urartu* and *Ae. longissima* and *Ae. searsii*.

Triticum urartu is now recognized as the source of the paternal AA genome of the BBAA tetraploid wheats, with an ancestor of *Ae. speltoides* contributing the maternal BB genome (Chapman *et al.*, 1976; Dvořák, 1976; Dvořák & Zhang, 1990). Lennart did not question the hypothesis that *T. monococcum* ssp. *aegilopoides* had contributed the AA genome (Johnson, 1975). Perhaps because he made this mistake, many cytogeneticists were reluctant to accept *T. urartu* as a distinct species. Kimber & Sears (1987), Kimber & Feldman (1987) and Zohary & Hopf (1993) have all questioned the validity of *T. urartu*, even though the sterility of the F1 hybrid with *T. monococcum* was published immediately afterwards (Johnson & Dhaliwal, 1976). Moreover, Tumanian's morphological characters that distinguished *T. urartu* from *T. monococcum* have stood the test of time (Gandilian, 1972; van Slageren, 1994).

INTERMEDIATE ACCESSIONS

The above implies that wild *T. monococcum* always has only one fast-migrating band in the disc electrophoresis system, or none, whereas *T. urartu* has two or more. This is largely correct, but there are a few exceptions. The accessions G1150 and G1173, collected by Johnson in 1965 near Erzarum and Malatya, Turkey, have two fast-migrating bands, but have the morpho- logical characters of *T. monococcum* ssp. *aegilopoides*. Accession G1016, collected north-east of Cardak, Turkey, in 1965, has only one band, but shows some morphological characters similar to *T. urartu*. One accession, *T. boeoticum* No.18, will cross with *T. urartu* (G1944), collected near Viransehir, Turkey, and produce some fertile hybrids (Metzger, pers. comm.). There do appear to be a few intermediate types that warrant investigation to ascertain the genetic differences that separate these two diploid species.

POPULATION DIVERSITY IN WILD WHEATS

Although there has been considerable research on genetic diversity in wild wheat populations in Israel and Jordan, there has been less in Syria, Lebanon, Turkey, Iraq and Iran. Populations of *Ae. speltoides*, *T. monococcum* ssp. *aegilopoides*, *T. urartu*, and *T. turgidum* ssp. *dicoccoides* from Syria and Lebanon were collected in 1994, when I was at the Genetic Resources Unit at ICARDA, and we have assayed isozyme diversity in them (Hegde, Valkoun & Waines, 1998). These results suggest populations of *Ae. speltoides* cluster distinctly from those of the two diploid wheats, which overlap. The tetraploid species had relatively less genetic diversity than the diploids, and it was highly homozygous (Table 2) (Hegde, Valkoun & Waines, 1999).

TABLE 2.   Summary of genetic diversity based on a mean of 10 loci for 35 populations of wild wheats and goatgrass.

Species		Diversity index (He)	Fixation index (F)
Aegilops speltoides			
Populations (12)	(P)	0.10	0.43
Species	(S)	0.22	0.77
Triticum monococcum ssp. *aegilopoides*			
Populations (8)	(P)	0.07	0.58
Species	(S)	0.21	0.90
T. urartu			
Populations (7)	(P)	0.06	0.31
Species	(S)	0.31	0.94
T. Turgidum ssp. *dicoccoides*			
Populations (8)	(P)	0.05	0.64
Species	(S)	0.14	0.96

RE-SYNTHESIS OF TETRAPLOID WHEAT

We need to make the allotetraploid between *Ae. speltoides* and *T. urartu*, and to compare this with wild tetraploid wheat, *T. turgidum* or *T. timopheevii*. Gill & Waines (1978) were able to make an F1 hybrid between *Ae. speltoides* G1316 from near Haifa, Israel and *T. urartu* G1785 from Kiziltepe, Mardin, Turkey. It was sterile and we did not make the allotetraploid. Many attempts to re-make this cross using other accessions of these parents have been unsuccessful (Waines & Barnhart, 1992; Waines *et al.*, 1999). Attempts to make interspecific F1 hybrids among accessions from Turkey and Lebanon, or from adjacent geographic areas in Syria, have met with failure. The endosperm appears to break down and/or the embryos show hybrid lethality. This implies that isolating mechanisms exist among many populations of *Ae. speltoides* and *T. urartu*.

STOMATAL SIZE AND FREQUENCY BETWEEN TETRAPLOID AND HEXAPLOID FORMS OF *AEGILOPS NEGLECTA*

In his monograph of wild wheats, van Slageren, (1994) was unable to distinguish morphologically between the tetraploid and hexaploid forms of *Ae. neglecta and Ae. crassa*. We have looked at stomatal size and frequency between the ploidy levels of *Ae. neglecta* and we were able to distinguish the two forms (Tables 3, 4) (Aryavand *et al.*, 1999).

EXPLANATIONS OF SYNAPTOSPERMIC DIASPORES IN *AEGILOPS*

In the final chapters of *The Wheat Plant*, Percival (1921) outlined his ideas for the origin of the polyploid wheats and invoked hybridisation of tetraploid wheat with *Ae. geniculata (Ae. ovata)* or *Ae. cylindrica* as a possible ancestry for hexaploid wheat.

TABLE 3.   Mean stomatal size (μm) of L2 and L3 (basal leaves) and penultimate (PL) and flag (FL) upper leaves of tetraploid and hexaploid forms of *Aegilops neglecta.*

Ploidy	L2	L3	Mean	PL	FL	Mean
Mean 4x	43.46	44.20	43.83	51.88	49.16	50.52
Mean 6x	55.29	53.87	54.58	67.43	63.79	65.61

Percival was doubtless aware of the unusual mechanisms in the genus *Aegilops* for dissemination of the fruits. A review of the multi-fruited dissemination units found in *Aegilops* occurs in the doctoral thesis of Laura Morrison (1994). Morrison recognised three primary types of wild wheat diaspores, where the term diaspore applies to the whole dispersal unit, spikelet or spike. (Fig. 1) First she recognised the wedge diaspore, produced by multiple wedge disarticulations; second the synaptospermic diaspore produced by a single disarticulation; and third the barrel diaspore produced by multiple barrel disarticulations. The four wild *Triticum* species all have wedge diaspores, where the spike breaks at maturity into individual spikelets that have a sharp-pointed rachis segment with hairs, bristles and awns that direct the spikelet down through the vegetation and insert it into a crack in the soil. There it is safe from predator animals and fires until germination takes place after the winter rains. *Aegilops bicornis*, *Ae. sharonensis* and one morph of the dimorphic species *Ae. speltoides*, namely ssp. *ligustica* also have the wedge diaspore. Seven diploid species of *Aegilops* have a spike that stays intact at maturity and breaks at one point near the base of the spike, called a synapto- spermic diaspore (Morrison, 1994). *Aegilops caudata*, *Ae. comosa*, *Ae. longissima*, *Ae. searsii*, *Ae. speltoides* ssp. *speltoides*, *Ae. umbellulata* and *Ae. uniaristata* are diploid examples of this diaspore type. The difference between these wild *Aegilops* species and domesticated wheats lies in the toughness of the rachis, and the presence of the one break-point near the base of the spike. *Aegilops caudata*, *Ae. comosa*, *Ae. umbellulata* and *Ae. uniaristata* all have rachises as tough as domesticated tetraploid and hexaploid wheat.

TABLE 4.   Mean stomatal frequency (No/mm^2) of L2 and L3 (basal leaves) and penultimate (PL) and flag (FL) upper leaves of tetraploid and hexaploid forms of *Aegilops neglecta.*

Ploidy	L2	L3	Mean	PL	FL	Mean
Mean 4x	49.29	52.71	51.00	51.33	54.99	52.97
Mean 6x	38.97	40.87	39.92	44.24	48.35	46.30

Aegilops tauschii is an example of the barrel diaspore, which is also found in many polyploids containing the *tauschii* genome. A detailed discussion of the morphological variation to be found in dissemination units in *Aegilops* and *Triticum* is presented in Morrison (1994). My point is that the character of tough rachis, which we normally
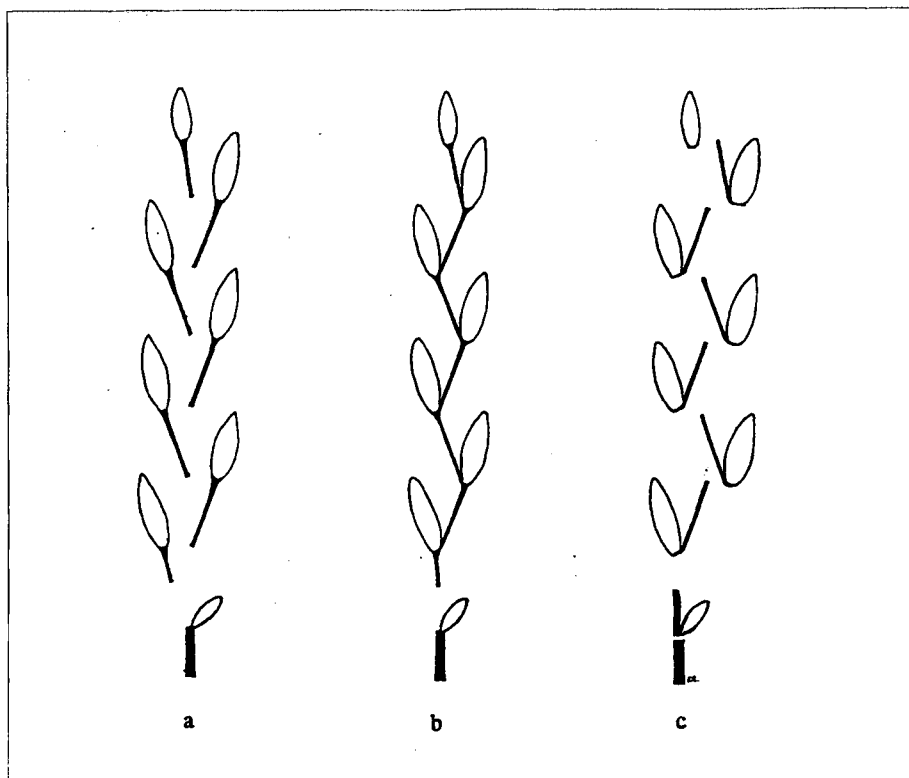
Figure 1. Schematic of the three types of wild-wheat diaspores: (a) Wedge diaspore produced by multiple wedge disarticulations; (b) Synaptospermic diaspore produced by a single disarticulation; (c) Barrel diaspore produced by multiple disarticulations (after Morrison, 1994).

associate with domestication by man, is common in wild *Aegilops* species, where we have no evidence of selection by man! If man is not selecting, how does the tough rachis arise in these species? What are the selection forces for the various forms of tough rachis found among *Aegilops* species? If we assume the wedge diaspore is primitive in *Aegilops*, as exemplified by *Ae. speltoides* ssp. *ligustica,* what is the selection force that maintains the other morph of that species, namely the synaptospermic diaspore, found in ssp. *speltoides*. Previously, I hypothesized that wedge diaspores are selected by large ants (*Messor* species) or small rodents or birds that gather the individual spikelets and carry them to their nest or threshing area, in the process of which some spikelets are carried to new locations and discarded (Waines, 1998). This would allow the fruits to germinate. Large ants do gather *Aegilops*, *Hordeum* and *Triticum* spikelets in the Near East. They may also be able to gather the barrel-type spikelets of *Ae. tauschii*.

Animals (rodents of unknown genera) have been observed to gather the wedge diaspore of *T. turgidum* ssp. *dicoccoides* in the Jebel Druz of southern Syria, and the barrel-type spikelets of *Ae. crassa* in the Jebel Abdul Aziz in northern Syria. Rodent threshing areas with threshed spikelets are common in the latter location (Waines, 1998). What is the selection force for the synaptospermic diaspore found in *Ae. speltoides* ssp. *speltoides* which is too large to be gathered by ants or small rodents? It might be gathered by larger rodents and birds, or disseminated by sheep and goats.

Agricultural botanists and conservation biologists might pay attention to the generally neglected question of what agents disseminate the fruits and seeds of the wild relatives of our crop plants.

THE GENETICS OF TOUGH RACHIS IN *AEGILOPS* SPECIES

The number of genes that determine tough rachis in *Aegilops* species is of interest. Two alleles at a single (complex) locus control the two sympatric morphs in *Ae. speltoides* and the two geographically separated morphs in *Ae. tauschii* where some Afghani and Chinese accessions have a tough rachis, but Near Eastern accessions have barrel-type diaspores (Zohary & Imber, 1963; Metzger & Silbaugh, 1968). Tough rachis in *T. monococcum* is controlled by contrasting alleles at one or two loci (Sharma & Waines, 1980), with the majority of domesticated types having tough alleles at both loci. The rachis of *Ae. caudata, Ae. comosa, Ae. umbellulata* and *Ae. uniaristata* is so tough as to imply it is conditioned by alleles for toughness at two loci, just as in diploid wheat or barley. Therefore, tetraploids formed from these tough-rachised diploids could have alleles for toughness at four loci, two in each parental genome, and hexaploid *Ae. neglecta* could have six. Most of the synaptospermic tetraploid goatgrass species involve combinations from among these four diploids.

POLLINATION BIOLOGY OF SYNAPTOSPERMIC DIASPORES OF *AEGILOPS TRIUNCIALIS*

The wedge diaspore of wild wheats and goatgrasses, or the barrel diaspore of goat grasses contains one to three, but mostly two fertile florets that develop later into kernels. These two fruits have the same mother, but could have the same or different fathers contributing the sperms that fertilize the eggs. The kernels in a spikelet can show multiple paternity, depending on the extent of out-crossing common to each species. If each wedge or barrel spikelet can exhibit multiple paternity, we would expect all the spikelets in a synaptospermic diaspore to exhibit multiple paternity. This is so in *Ae. triuncialis*, barbed goatgrass, the species with the widest distribution of any goatgrass. This allotetraploid, of *Ae. umbellulata* and *Ae. caudata*, genome formula UUCC, is a notorious weed of rangelands. It has taken over the Hopland Research and Extension Center, near Ukiah, Mendocino County, in northern California. *Aegilops triuncialis* is classed as a noxious weed in California. Isozyme electrophoresis indicates that barbed goatgrass is a fixed heterozygote, as are many successful tetraploids. The spike contains three to five fertile spikelets, each with one or two kernels. During the first winter, five or more seedlings germinate from the diaspore, and these are either full-sibs or half-sibs, depending on the extent of multiple paternity in the spike. Seedlings from one synaptospermic diaspore of *Ae. triuncialis* from Hopland show genetic polymorphism for three enzyme systems, Phosphoglucose isomerase-1, Triosephosphate isomerase-2 and 6-Phosphogluconate dehydrogenase (Hegde & Waines, unpublished). These half-sib seedlings do not appear to suffer from seedling competition, but grow together as though they are tillers of the same plant (Wiersma & Waines, unpublished). At flowering, a "plant" of barbed goatgrass, is a small population of full-sibs and half-sibs, which are able to out-cross within this population and reproduce synaptospermic diaspores that again show multiple

paternity, so repeating the cycle. Synaptospermic diaspores, which are very common in *Aegilops,* being found in 15 species out of 23, are a very efficient mechanism for disseminating populations of full-sibs and half-sibs or what in plant breeding terms we call hill plots. Could the genetic advantages of disseminating a hill population of full-sibs and half-sibs be another selective force that maintains the diaspore dimorphism in *Ae. speltoides* and the tough rachis in those diploid *Aegilops* species with synaptospermic diaspores? Is the ability of one spike to disseminate hill populations of full-sibs and half-sibs a reason why these species, especially the polyploids, which are fixed heterozygotes, are such aggressive weeds, that are able to produce more synaptospermic diaspores and hill populations in the next generation? Clearly, a tough rachis conditioned by two, four or six alleles, will keep the hill population of full-sibs and half-sibs in close proximity.

In barbed goatgrass, not all the kernels in a spikelet germinate in the first year. The spike is sufficiently tough to resist breakdown in the first year and to protect the dormant kernels through a second summer. These kernels generally germinate in the second winter and also produce a hill population. Dormancy that lasts beyond two winters has not been investigated in *Aegilops* species.

Barbed goatgrass is a worse weed in California than in the Near East. At Hopland, no native animals appear to gather and thresh the spikes to extract the nutritious kernels. Nor have I seen spike diseases such as smuts and bunts infesting the plants as they do in Syria and Turkey. Barbed goatgrass is very efficient at disseminating its diaspores, for few fields at Hopland are free of the weed. Hopland is a site for experiments with sheep. Whether sheep aid in dissemination still has to be determined. Once the immature spike has emerged from its leaf sheath and the many awns are extended, few sheep or cattle will eat the spikes, which irritate their nostrils. Nine species of *Aegilops*, including one diploid, seven tetraploids and one hexaploid have a synaptospermic diaspore with spreading awns, that discourage grazing by animals. It will be interesting to determine how many species have multiple paternity among the fruits in a spike. The genus *Medicago,* where out-crossed seeds are often retained in coiled, or indehiscent pods, may have a similar reproductive strategy in the legume family. Aggregate fruits and seeds are also common in the Chenopodiaceae (*Beta*) and Moraceae (Waines, 1998).

Jointed goatgrass, *Ae. cylindrica,* (DDCC), parents *Ae. tauschii* and *Ae. caudata,* is another tetraploid species that is a noxious weed in the USA. Similarly to *Ae. triuncialis*, it prefers areas with higher rainfall, and is common in northern California, but it has small populations in the south on the coast near Santa Barbara, and in the San Bernardino Mountains at Crestline. It appears to be associated in California with cattle, which will eat the mature spikes and thereby spread the barrel diaspores. In contrast to the two-kerneled diaspores of diploid wheats, the Santa Barbara population of jointed goatgrass exhibits little seed dormancy. Both kernels germinate in the first winter and grow together to form a single plant-clump with many tillers. Although electrophoresis of seedlings shows that they are fixed heterozygotes, since they are allotetraploid, we have found little genetic variation so far between seedlings in a barrel diaspore, or among plants within a population. In contrast to bearded goatgrass, jointed goatgrass appears to be monomorphic for the common enzyme systems.

AN EXPERIMENTAL WHEAT POPULATION

With knowledge of the half-sibs that appear to make the synaptospermic diaspore of *Ae. triuncialis* so successful as an aggressive weed, can we consider how we might use this in experimental breeding of bread and durum wheat? Can we design a wheat spike that promotes multiple paternity among the different fruits in the spike? Are there any genetic advantages for reproductive fitness and grain yield from growing a wheat population composed of full-sibs and half-sibs that is able to reproduce itself and not have to be always re-made by the plant breeder, as is so with F1 hybrids? This idea is not new. Norman Borlaug suggested a strategy similar to this in a paper entitled "The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants" (Borlaug, 1958). He was mostly concerned with disease tolerance by the population. Perhaps we could take another look at this idea from the point of view of reproductive fitness and grain yield. One characteristic common to many domesticated crops is that domestication imposed a genetic bottleneck that often had more to do with ease of harvest or threshing than to do with reproductive fitness. Selection of the domestication syndrome (Hammer, 1984) in common beans may have enforced a higher degree of self-pollination, with a subsequent increase in genetic homozygosity among plants in the population. This could have resulted in a decrease in seed yield, compared with that of a bean crop grown as a mixed-mating population that encouraged tripping and cross-pollination by insects (Ibarra-Perez *et al.*, 1996, 1997, 1999). If left undisturbed, domesticated common bean in southern California would form mixed-mating populations. I suspect that this will also be so for wild common bean populations. The same might be so for durum and bread wheat where wind would promote cross-pollination in place of insects. Perhaps this may happen to some extent in landraces. I am not aware that anyone has compared out-crossing in landrace wheats with that in modern domesticated populations and wild populations using molecular markers as well as isozymes.

WHEAT ROOTS – EIGHTY YEARS OF NEGLECT

Chapter four in *The Wheat Plant* is devoted to wheat roots. Since 1921 there have been only about ten significant papers published on genetic variation and inheritance of root characters in wheat. Even today, no genes are known that specifically affect wheat roots (O'Tool & Bland, 1987). After over 100 years of breeding the above ground part of the plant this is short-sighted. One must ask who is determining agricultural research policy in the world? If John Percival could study wheat roots, why cannot we devise methods to study genetic variation and inheritance of root characteristics? If man can travel to the moon, why can't he do research on roots?

When I first returned to Riverside in 1975, and found I was located in a semi-desert that received on average 250 mm annual rainfall, in a distinctly Mediterranean climate, I realized that drought and heat stress might be good topics on which to do research. Johnson's wheat collection was available. I was encouraged to use the germplasm, that had been brought together to study wheat evolution, for desirable physiological, biochemical, pest, disease and product quality characteristics.

Sitting in my office one afternoon, I had just finished reading Percival's slim chapter on roots when a prospective Masters student came to ask for ideas for a thesis research topic. That is how Barbara Robertson began her study of seminal roots in wild and domesticated wheats at three ploidy levels (Robertson, Waines & Gill, 1979). In it she demonstrated that the number of seminal-root initials present in the resting embryo is the same in species of *Triticum*, whether diploid, tetraploid, hexaploid, wild or domesticated, but that the number of root initials that develop on germination is genetically controlled and is correlated with seed weight. Heavy kernels, with large endosperm reserves, tend to develop more seminal-root initials, at least in the first seven days after germination. A question that Barbara did not ask is do the undeveloped root initials grow out later in response to the energy available from photosynthesis in the seedling leaves in the first month? Or, do kernels with small endosperm always have smaller root systems? It would be useful to study this in goatgrasses, where the range of seed weight is larger, as well as in wheat species.

A BREAD WHEAT IDIOTYPE FOR SUSTAINABLE AGRICULTURE

The bread wheat Yecora Rojo was bred by the CIMMYT programme and has been the most popular cultivar in southern California for more than 30 years. It is a two-gene dwarf that requires no vernalization, but is grown in California as a winter wheat. Sowing takes place from November to mid-February, in irrigated or rainfed conditions. This cultivar has the advantage that a dry-land farmer can wait to see if rain falls before New Year. If it does, he can sow Yecora Rojo and be reasonably sure that rain will continue to fall throughout the remainder of the winter to give enough moisture to mature the crop. In the winter of 1996–97 an unusual rainfall pattern occurred. Hardly any rain fell before New Year, but 250 mm fell by January 31, after which the dry-land farmers of western Riverside County sowed Yecora Rojo. Surprisingly, no more rain fell that season in southern California. The wheat seed germinated and developed well, but by flowering in late March and early April the crop was beginning to show drought stress. By late April and early May the crop was a disaster. Dry-land wheat farmers harvested little grain in southern California in 1997.

Why was this so? Was the poor distribution of rainfall, 250 mm in one month, the only reason for the poor harvest? The plant breeders selected a wheat cultivar with high protein content, with the right high molecular weight glutenin bands to produce good bread quality, but by paying attention only to the above-ground part of the plant, the

TABLE 5.   Means of single plants for spring bread wheat grown in irrigated pots under glasshouse conditions in 1992 and 1993.

Genotype	Dry Matter (g/plant)	
	Root	Shoot
Yecora Rojo	1.6	9.0
Chinese Spring	4.8	15.0
Iran No. 49	4.2	11.6

breeders had unknowingly produced a cultivar that performed poorly under drought stress. In Table 5 the root biomass of Yecora Rojo is compared with those of two landraces 'Chinese Spring' and 'Iran No. 49'. Yecora Rojo produces a very small and shallow root system compared with the landraces (Ehdaie & Waines, 1997). Moreover, when the landraces are drought stressed, they increase their root biomass relative to well-watered plants. It appears that the plants put energy into root growth to search for water (Table 6). Stressed Yecora Rojo does not do this, or it produces less root biomass than well-watered plants.

A project we would like to do at Riverside is to cross Yecora Rojo with Chinese Spring and Iran No. 49 to combine the good shoot characteristics of the CIMMYT wheat with the good root characters of the landraces. Iran No. 49 has another advantage. It is resistant to toxicity caused by the Russian wheat aphid (*Diuraphis noxia* Mordvilko), whereas Chinese Spring and Yecora Rojo are susceptible to this insect pest. Resistance is controlled by two genes (Ehdaie & Baker, 1999). It should be possible to select for the high root biomass and aphid resistance of the landrace as well as the stem height and grain quality characteristics of the Yecora Rojo to produce a high quality cultivar suitable for sustainable rainfed and irrigated regimes in Mediterranean climates.

We do not know the mechanism by which some landraces, when drought stressed, are able to increase their root biomass and depth, whereas some modern wheats do not do so or produce less roots in response to stress. However, we suspect that the genetic control is quantitative (Ehdaie & Waines, 1999). Clearly, a more thorough study of roots and rooting in wheat would be useful for production of cultivars for sustainable or rainfed agricultural systems.

TABLE 6. Means of root and shoot biomass of bread wheat genotypes grown in wet and dry experiments.

Genotype	Wet		Dry	
	Root (g/plant)	Shoot (g/plant)	Root (g/plant)	Shoot (g/plant)
Yecora Rojo	4.6	53.3	3.7	14.5
Chinese Spring	6.8	74.6	9.1	33.5

BIOMASS OVER-PRODUCTION IN WHEAT

Recently we evaluated water-use efficiency of aneuploids of the bread wheat landrace Chinese Spring, a model wheat in which to study physiology and genetics (Ehdaie & Waines, 1997). We used the ditelosomic lines lacking a pair of chomosome arms, to determine which arms carry genes that affect root – and shoot – biomass production and water use in a well-watered regime. Compared with normal euploid Chinese Spring, three ditelosomic lines had phenotypes exhibiting "biomass over-production". The characteristics of these lines appear in Table 7.

TABLE 7.   Components of yield of Chinese Spring ditelsomics that show biomass over-production.

Genotype	Plant ht (cm)	No. of tillers	Shoot biomass (g/plant)	Root biomass (g/plant)	Vegetative DM (g/plant)	Grain yield (g/plant)
Chinese Spring	128	12	23	5.5	28.3	18.7
Dt 4AS	68	36	27	4.3	31.3	1.9
Dt 4AL	128	23	44	8.1	52.1	9.9
DT 5DS	111	19	39	8.8	48.7	19.3

Bread wheat, *T. aestivum* (BBAADD), is an allohexaploid with 42 chromo- somes, which arose under domestication from the spontaneous hybridisation of a domesticated tetraploid (BBAA) wheat and a weedy goatgrass (DD). Kernel size in wild and domesticated tetraploid wheat (*T. turgidum*) is normally larger than that in hexaploid wheat. Perhaps the optimum ploidy level in wheats is naturally tetraploid, with hexaploids occurring only as a result of human selection under domestication for specific purposes such as stress tolerance or bread-making quality. There are natural hexaploid species in *Aegilops,* but none is as successful as the tetraploid species, and often less so than diploid species. Perhaps we should not be surprised that bread wheat lacking a pair of chromosome arms can produce more biomass than the complete hexaploid. This biomass over-production is often expressed as increased root biomass, or increased number of tillers and shoot biomass. Sometimes grain yield is less, sometimes it is the same as euploid.

What might be the cause of biomass over-production? Does biomass overproduction occur only in a well-watered situation, or also under drought stress? One cause alluded to already is that in the hexaploid, three doses of a gene system codes for inefficiency, and that loss of specific loci on chromosomes 4AS, 4AL and 5DL, thereby simulating the tetraploid condition, might raise the efficiency of particular biochemical and physiological systems. Another approach is to ask what known genes are carried on these three chromosome arms. Chromosome 4A, along with 4B, is reported to carry major genes that control the levels of ribulose-1,5-bisphosphate carboxylase in Chinese Spring wheat (Jellings *et al.*, 1983). Chromosome 4AL carries a locus *D3* that controls grass-clump dwarfing, with increased tillers (Hermsen, 1963; Worland & Law, 1980; McIntosh, 1998). Chinese Spring carries the recessive allele of this locus, but removal of the locus could have the same effect as the dominant grass-dwarf allele. Another dwarfing gene locus might be on chromosome 5D (Knott, 1989). Genes that either increase or decrease the level of plant growth hormones such as auxins, cytokinins, and gibberellins might be associated with these three chromosome arms. One association is of interest, namely the increase in root biomass of the ditelocentric line for 4AS, with arm 4AL missing. This might be the same result as having the grass-clump dwarf *D3* locus present. Perhaps this kind of grass-clump dwarf also has increased root biomass. I do not think that root biomass of the different grass-clump dwarf genes has been investigated relative to shoot biomass. If this is so, it might

explain why grass-clump dwarf genes are found in some semi-dwarf wheat cultivars bred for sub-tropical climates, which also exhibit drought tolerance (Moore & Haider, 1998). This is another reason why agricultural botanists should pursue root studies.

THE COST OF MAINTAINING GERMPLASM COLLECTIONS

John Percival undoubtedly discovered that maintaining a germplasm collection of wild, landrace and modern wheats consumes a great deal of time, energy and research funds. The University of California, Riverside collection is no different, even though it is stored in walk-in freezers at $-18°$ C. A major expense is the cost of curation and to grow out those accessions that need to be rejuvenated. Unfortunately, in an effort to reduce costs, the University of California has discontinued permanent Staff Research Associate positions and replaced them with temporary post-doctoral fellows. While this might be good for laboratory research, it is of little use for field-based programs, which is what germplasm conservation is. Fortunately, the California Genetics Resources Conservation Program does help with small grants for seed increase and collection maintenance. In the process of doing this it is possible to study genetic diversity in populations, ideally before they are increased in California. However, the University's need to reduce costs and to reduce diversity of employment for its staff is at odds with its stated goals of conserving plant biodiversity. I suspect that Percival's collection faced much the same problems. There is a continuing need to monitor the upkeep and fate of these large germplasm collections.

REFERENCES

Aryavand A, Ehdaie B, Tran B, Waines JG. 1999. Stomatal frequency and size and ploidy level in *Aegilops neglecta* (Poaceae). (Submitted).

Borlaug NE. 1958. The use of multilineal or composite varieties to control airborne epidemic diseases of self-pollinated crop plants. In: Jenkins BC (ed.). *Proceedings of the 1st International Wheat Genetics Symposium.* Winnipeg: University of Manitoba Press, 12–27.

Chapman V, Miller TE, Riley R. 1976. Equivalence of the A genome of bread wheat and that of *Triticum urartu. Genetical Research, Cambridge* 27: 69–76.

Dvorak J. 1976. The relationship between the genome of *Triticum urartu* and the A and B genomes of *T. aestivum. Canadian Journal of Genetics and Cytology* 18: 371–377.

Dvorak J, Zhang HB. 1990. Variation in repeated nucleotide sequences sheds light on the phylogeny of the wheat B and G genomes. *Proceedings of the National Academy of Sciences, USA* 87: 9640–9644.

Ehdaie B, Baker CA. 1999. Inheritance and allelism for resistance to Russian wheat aphid in an Iranian spring wheat. *Euphytica* 107: 71–78.

Ehdaie B, Waines JG. 1997a. Growth and evapotranspiration efficiency in landrace and dwarf spring wheats. *Journal of Genetics and Breeding* 51: 201–209.

Ehdaie B, Waines JG. 1997b. Chromosomal location of genes influencing plant characters and evapotranspiration efficiency in bread wheat. *Euphytica* 96: 363–375.

Ehdaie B, Barnhart D, Waines JG. 1999. Inheritance of root and shoot biomass in a bread wheat cross. (Submitted).

Gandilian PA. 1972. On the wild growing *Triticum* species of the Armenian SSR. *Botany Journal* 57: 173–181.

Gill BS, Waines JG. 1978. Paternal regulation of seed development in wheat hybrids. *Theoretical & Applied Genetics* 51: 265–270.

Hammer K. 1984. Das domestikaationssyndrom. *Kulturpflanze* 32: 11–34.

Hegde SG, Valkoun J, Waines JG. 1998. Allozyme variation in diploid and tetraploid wild wheats from northern Syria. In: Slinkard AE (ed.). *Proceedings of the 9th International Wheat Genetics Symposium,* Saskatoon, Canada: University of Saskatchewan Extension Press. Vol. 2, 218–220.

Hegde SG, Valkoun J, Waines JG. 1999. Genetic diversity of wild wheat and goat-grass. (in prep.).

Hermsen JGT. 1963. The localization of two genes for dwarfing in the variety Timstein by means of substitution lines. *Euphytica* **12:** 126–129.

Ibarra-Perez FJ, Ellstrand NC, Waines JG. 1996. Multiple paternity in common bean (*Phasolus vulgaris* L. Fabaceae). *American Journal of Botany* **83:** 749–758.

Ibarra-Perez FJ, Ehdaie B, Waines JG. 1997. Estimation of outcrossing rate in common bean. *Crop Science* **37:** 60–65.

Ibarra-Perez FJ, Barnhart D, Ehdaie B, Knio KM, Waines JG. 1999. The effect of insect tripping on seed yield of common bean. *Crop Science* **39:** 428–433.

Jellings AJ, Leese BM, Leech RM. 1983. Chromosomal location of the control of Ribulose bisphosphate carboxylase levels in wheat. *Molecular and General Genetics* **192:** 272–274.

Johnson BL. 1972. Protein electrophoretic profiles and the origin of the B genome wheat. *Proceedings National Academy of Sciences,USA* **69:** 1398–1402.

Johnson BL. 1975. Identification of the apparent B-genome donor of wheat. *Canadian Journal of Genetics & Cytology* **17:** 21–39.

Johnson BL, Dhaliwal HS. 1976. Reproductive isolation of *Triticum boeoticum* and *T. urartu* and the origin of the tetraploid wheats. *American Journal of Botany* **63:** 1088–1094.

Kimber G, Feldman M. 1987. *Wild Wheat: An Introduction.* Special Report No. 353. Columbia, Missouri: College of Agriculture, University of Missouri.

Kimber G, Sears ER. 1987. Evolution in the genus *Triticum* and the origin of cultivated wheat. In: Heyne, EG (ed.). *Wheat and Wheat Improvement* (2nd. edition). Madison, WI: American Society of Agronomy, 154–164.

Knott DR. 1989. The mode of inheritance of a type of dwarfism in common wheat. *Genome* **32:** 932–933.

McIntosh RA. 1998. Unpublished results. In: Slinkard AE (ed.). *Proceedings of the 9th International Wheat Genetics Symposium.* Saskatoon, Canada: University of Saskatchewan Extension Press. Vol. **5:** 75–76, 208.

Metzger RJ, Silbaugh BA. 1968–69. Aneuploid studies at Oregon State University. *European Wheat Aneuploid Cooperative Newsletter* **2:** 60.

Moore K, Haider SA. 1998. Reduced height and grass-clump dwarf genes in drought stress tolerant genotypes of spring wheat (*Triticum aestivum*). In: Slinkard AE (ed.). *Proceedings of the 9th International Wheat Genetics Symposium.* Saskatoon, Canada: University of Saskatchewan Extension Press. Vol. **4:** 60–62.

Morrison LA. 1994. Re-evaluation of systematic relationships in *Triticum* L. and *Aegilops* L. based on comparative morphological and anatomical investigations of dispersal mechanisms. Unpublished Ph.D. Thesis. Oregon State University, Corvallis, Oregon.

O'Toole JC, Bland WL. 1987. Genotypic variation in crop plant root systems. *Advances in Agronomy* **41:** 91–145.

Percival J. 1921. *The Wheat Plant. A Monograph.* London: Duckworth.

Robertson BM, Waines JG, Gill BS. 1979. Genetic variability for seedling root numbers in wild and domesticated wheats. *Crop Science* **19:** 843–847.

Sharma HC, Waines JG. 1980. Inheritance of tough rachis in crosses of *Triticum monococcum* and *T. boeoticum. Journal of Heredity* **71:** 214–216.

Slageren van MW. 1994. *Wild wheats: a monograph of Aegilops L. and Amblyopyrum* (Jaub, & Spach) Eig. *Wageningen Agricultural University Papers* 94–7.

Tumanian MG. 1929–1930. Wild einkorns and emmers in Armenia. *Bulletin of Applied Botany, of Genetics and Plant-Breeding (Trudy po Prikladnoi, Botanike, Genetike i Selektsii)* **24:** 1–14.

Waines JG. 1998. *In situ* conservation of wild relatives of crop plants in relation to their history. In: Damania AB, Valkoun J, Wilcox G, Qualset CO (eds). *The Origins of Agriculture and Crop Domestication. The Harlan Symposium.* Aleppo: ICARDA, IPGRI, FAO, UC/GRCP, 300–306.

Waines JG, Barnhart D. 1992. Biosystematic research in *Aegilops* and *Triticum. Hereditas* **116:** 207–212.

Waines JG, Abu Mazour I, Damania AB, Valkoun J. 1999. Unpublished results from 1994–1995.

Worland AJ, Law CN. 1980. The genetics of hybrid dwarfing in wheat. *Zeitschrift Fur Pflanzenzuchtung* **85:** 28–39.

Zohary D, Hopf M. 1993. *Domestication of Plants in the Old World* (2nd ed.) Oxford: Oxford Science Publications.

Zohary D, Imber D. 1963. Genetic dimorphism in fruit types in *Aegilops speltoides. Heredity* **18:** 223–231.

The Watkins Collection
of landrace-derived wheats

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Abstract

During the 1920s and 1930s A.E. Watkins established at Cambridge a collection of wheats from around the world. These were selected largely from landraces of macaroni wheat, *Triticum durum*, and bread wheat, *T. aestivum*. The accessions were classified in terms of ear characteristics with the elucidation of the genetic control of awning being a major outcome. A part of the collection is still maintained at the John Innes Centre, Norwich. This is currently being regenerated and a new current and archival database is being constructed.

INTRODUCTION

During the early decades of this century there was a rapidly expanding interest in wheat and wheat improvement. In the UK, this was especially the case at the University of Reading where John Percival was Professor of Agricultural Botany, and at the Plant Breeding Institute of the University of Cambridge with Roland (later Sir Roland) Biffen as its Director. Throughout the 1920s and 1930s Arthur Ernest Watkins was a lecturer in genetics in the School of Agriculture at the University of Cambridge. From 1932–37 he was Secretary of The Genetical Society; he was also author of a book entitled *Heredity and Evolution* (Watkins, 1935).

THE COLLECTION

During the late 1920s and early 1930s Watkins established a considerable collection of wheats from virtually all the wheat-growing countries of the world. It was largely achieved through the official channels of the Board of Trade in London and its contacts

with overseas officials, especially in the then British Commonwealth and Dependencies. Samples were even obtained from Burma, a country that does not grow wheat today. Many of the original letters that accompanied the samples are archived at the John Innes Centre. They contain information on the origin and cultivation of the samples, although not in all cases, as the local source of the samples was very varied. In some cases they were obtained direct from farmers, but in others were simply purchased in local markets. Watkins also exchanged material with other wheat workers and letters in the archive show that he was in contact with John Percival at Reading, N.I. Vavilov (Fig. 1) and C.A. Flacksberger in St. Petersberg, T. Shen in Shanghi and O.H. Frankel in New Zealand. The original collection contained several thousand accessions of diploid, tetraploid and hexaploid species. Unfortunately, many were lost when the collection was put into storage for the duration of the Second World War, where they suffered the ravages of grain moth. Today the collection, which is now held at the John Innes Centre, is reduced to around 1,300 accessions from 34 countries (Table 1). The
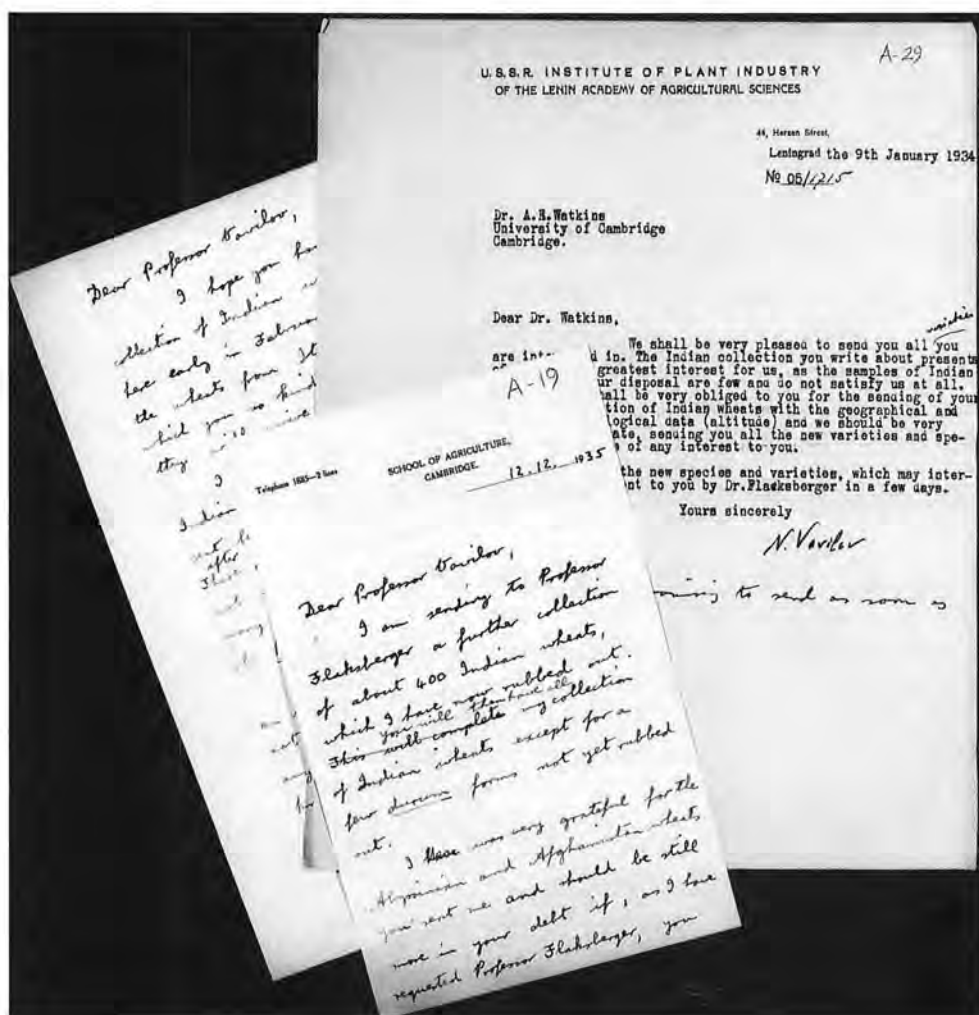
Figure 1. Correspondence between A.E. Watkins and N.I. Vavilov.

TABLE 1.   Geographical distribution of the accessions in the current Watkins wheat collection.

Country	No. of accessions	Country	No. of accessions
Afghanistan	36	India	145
Algeria	36	Iran	64
Australia	34	Iraq	13
Brazil	1	Israel	11
Bulgaria	18	Italy	25
Burma	4	Lebanon	2
China	94	Malta	3
Crete	34	Morocco	54
Cyprus	16	Poland	19
Czechoslovakia	1	Portugal	67
Egypt	14	Romania	7
Ethiopia	20	Spain (incl. Canary Is.)	147
Finland	1	Syria	26
France	21	Tunisia	34
Germany	4	Turkey	33
Greece	62	USSR	142
Hungary	6	Yugoslavia	62

largest groups consist of 830 accessions of *Triticum aestivum* L. and 350 of *T. durum* Desf. with the remaining 100 accessions comprising smaller numbers of *T. dicoccum* (Schrank.) Schlubl., *T. carthlicum* evski, *T. timopheevi* Zhuk., *T. turgidum* L., *T. polonicum* L., *T. compactum* Host., *T. sphaerococcum* Perc. and *T. macha* Dek. & Men. The John Innes Centre also holds a further collection of wheat species including *T. urartu* Tum., *T. boeoticum* Boiss., *T. monococcum* L. and *T. spelta* L. Some of the early accessions of *T. boeoticum* and *T. spelta* in all probability were originally part of the collection amassed by Watkins, some are also known to have originated from Percival's collection at Reading.

Originally the collection was regenerated on a three-year rotational cycle. It is currently being regenerated but otherwise is now held as seed in secure medium term storage (2.5°C and 10% RH). For further security the collection has been duplicated at the Australian Winter Cereals Collection, Tamworth, NSW, Australia. The John Innes Centre also holds herbarium specimens of ears of the original collection (Fig. 2).

USING THE COLLECTION

Watkins' main interest in the wheats was in the genetics of a range of ear characteristics including awning and colouration of the glumes and grains. Consequently, the accessions are classified in terms of these characters. Table 2 shows his treatment of bread wheat, *T. aestivum*. As can be seen in the table a fully awned (Bearded) hexaploid wheat with smooth white glumes, black awns and red grains is placed in category 13. The table also shows how his categorization related to the subdivision of the species into botanical varieties. The same categorization was used for the other hexaploid species, but a second similar classification was created for the tetraploid wheats.

The major outcome of Watkins' studies was the elucidation of the genetic control of awning in wheat (Watkins & Ellerton, 1940). Together with his PhD student Sydney Ellerton he identified the three major awn suppressing genes, Tipped 1(*B1*), Tipped 2(*B2*) and Hooded (*Hd*). He also published on the inheritance of glume shape relative to species differentiation (Watkins, 1940). Sydney Ellerton's thesis (Ellerton, 1939) was based on the collection and contains valuable data on the geographical distribution of awning (Fig. 3) and glume characteristics.

Figure 2. An example of the herbarium specimen cards of the Watkins wheat collection.

THE PRESENT

Since the work of Watkins and Ellerton there have been few studies involving the collection. Some years ago the *T. aestivum* accessions were spring sown in Canada to determine which had winter and which had spring habit. Recently, a preliminary screen of the hexaploid accessions for disease resistance has been undertaken. They have been grown in disease nurseries in the field and assessed for resistance to powdery mildew, *Erysiphe graminis*, and yellow (stripe) rust, *Puccinia striiformis*. Little resistance to mildew was observed but there appears to be potentially valuable rust resistance. It is hoped that future screening for resistance to other pathogens will also show the potential of the collection as a valuable genetic resource. A certain amount of electrophoretic screening of grain storage protein composition has also been carried out and this has indicated a considerable range of sub-unit profiles. Morphological characterization of small parts of the collection has also occurred (Silwimba, 1997; Kloda, 1998).
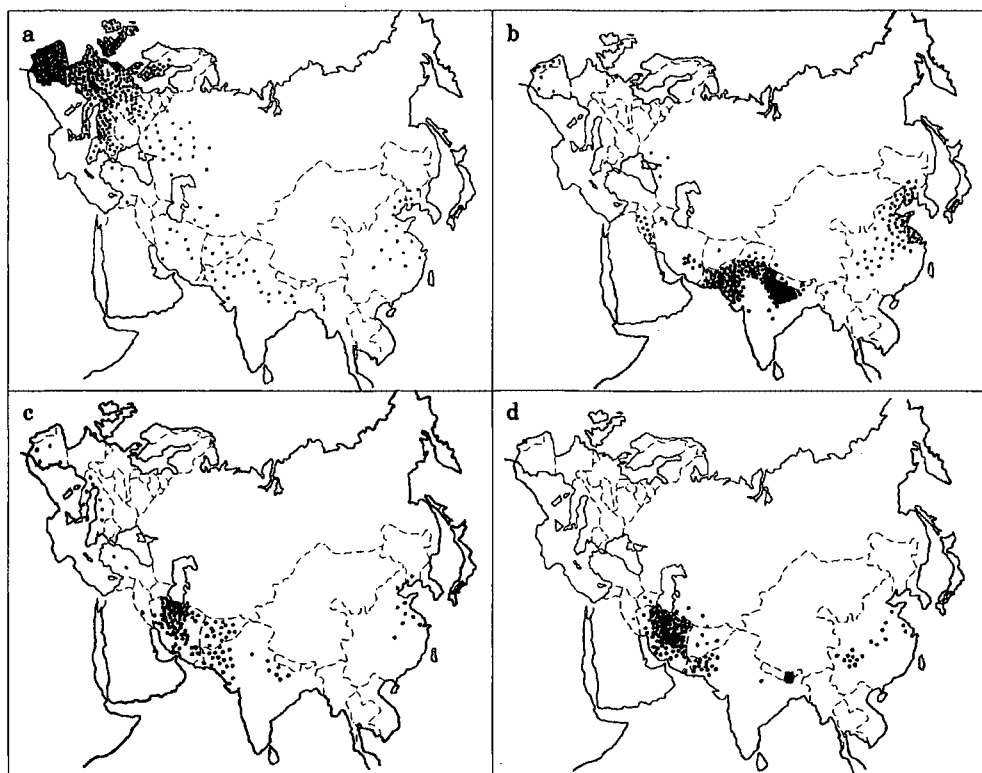
Figure 3. Distribution maps of the different suppressed awning types of *Triticum aestivum* in the Watkins collection: a. Awnless; b. Awnless 2; c. Half-awned; d. Hodded awned.

TABLE 2. Watkins' categorization of hexaploid wheat, *Triticum aestivum* L.

Awn type	Glume type	Glume colour	Awn colour	Grain colour	Category	Variety
Awnless 1 *muticum*	Smooth	White		White	1	*albidum* Al.
				Red	2	*lutescens* Al.
		Red		White	3	*alborubrum* Körn.
				Red	4	*milturum* Al.
	Rough	White		White	5	*leucospermum* Körn.
				Red	6	*velutinum* Schübl.
		Red		White	7	*delfi* Körn
				Red	8	*pyrothrix* Al.
		Grey		Red	9	*cyanothrix* Körn.
		Black-dark brown		Red	10	*nigrum* Körn.
Bearded *aristatum*	Smooth	White	White	White	11	*graecum* Körn.
				Red	12	*nigro-aristatum* Flaksb.
			Black	Red	13	*erythrospermum* Körn.
		Red	?Red	White	14	*erythroleucon* Körn.
			Red	Red	15	*ferrugineum* Al.
			Black	Red	16	*sardoum* Körn.
		Grey on white	White	Red	17	*nigro-erythrospermum* Jakush.
		Grey on red	Red	Red	18	*caesium* Al.
		Black on white	Black	Red	19	*nigricans* Howard
		Black on red	Black	White	20	*indicum* Howard
				Red	21	*bengalense* Howard
	Rough	White	White	White	22	*meridionale* Körn.
			Black	Red	23	*pseudo-meridionale* Flaskb.
			White	Red	24	*hostianum* Clem.
			Black	Red	25	*pseudo-hostianum* Flaksb.
		Red	Red	White	26	*Turcicum* Körn
			Black	White	27	*Pseuoturcicum* Vav.
			Red	Red	28	*barbarossa* Al.

TABLE 2. *continued*

			Black	Red	29	*pseudobarbarossa* Vav.
		Grey	???	White	30	*griseum* Vav.
				Red	31	*coeruleovelutinum* Körn.
		Black on white	?Black	?	32	*mesopotanicum* Vav.
				Red	33	*fuliginosum* Al.
		Black on red	?Black	White	34	*iranicum* Vav.
				Red	35	*kurdistanicum* Vav.
		White, black margin	Black	White	36	*hamadanicum* Vav.
				Red	37	*kazvinicum* Vav.
		Red, black margin	Black	White	38	*kermanshachi* Vav.
				Red	39	*luristanicum* Vav.
Half-awned *breviaristatum*	Smooth	White	White	White	40	*subgraecum* Vav.
				Red	41	*suberythrospermum* Vav.
		Red	?Red	White	42	*suberythroleucon* Vav.
		Red	Red	Red	43	*subferrugineum* Vav.
	Rough	White	White	White	44	*submeridionale* Vav.
			Black	White	45	*sub-pseudo-meridionale* Vav.
			White	Red	46	*sub-hostianum* Vav.
		Red	Red	White	47	*subturcicum* Vav.
				Red	48	*subbarbarossa* Vav.
		Brown-black	?	Red	49	*subfuliginosum* Vav.
Awnless 2 Hooded *inflatum*	Smooth	White		White	50	*albinflatum* Flaksb
				Red	51	*lutinflatum* Flaksb.
		White, black edges		?	52	*triste* Flaksb.
		Red		White	53	*alborubro-inflatum* Vav.
				Red	54	*rubinflatum* Flaksb.
	Rough	White		White	55	*khorassanicum* Vav.
				Red	56	
		Red		White	57	*transcaspicum* Vav.
				Red	58	*nigroinflatum* Vav.

FUTURE USE

The Watkins Collection is a valuable wheat genetic resource, which is largely derived from landraces prior to the widespread introduction of the recently-bred monoculture cultivars. However, it must be remembered that it represents only a 'snapshot' of the wheats of that period and single accessions are not a true representation of the land race from which they were derived. On receiving a sample of wheat Watkins selected plants with phenotypes displaying the characters in which he was interested. The samples were frequently mixed and often contained both tetraploid and hexaploids, thus more than one accession may be derived from a single sample. Unfortunately, at sometime in the past during regeneration, a harvesting error appears to have occurred with part of the *T. durum* section such that it is no longer at present possible to relate some of the current accessions to the original specimens. In time, it may be possible to resolve this by a detailed comparison of the current and original specimens. However, these lines still represent a valuable collection of early 20th century tetraploid wheat.

A new archival database is being established, which aims to bring together all available information into a single resource. This will include passport data, morphological characterization and evaluation, scanned original correspondence, taxonomic keys and images of specimen ears from the original cards and from the accessions as they are today. The use of the collection by a range of different research areas is envisaged via the development of multiple entry points into the system, thus maximizing the potential of the resource. Examples of potential users are archivists, plant breeders interested in the characterization data and the accessions, and research students carrying out eco-geographical studies. This, along with the current regeneration programme, should ensure the survival and availability of the collection for the future.

ACKNOWLEDGEMENTS

REFERENCES

Ellerton S. 1939. *Genetics and gene distribution in* Triticum vulgare *Vill. and other* Triticum *species.* PhD thesis, University of Cambridge.

Kloda JM. 1998. Characterisation of accessions of *Triticum turgidum* from the Watkins collection of wheats and the John Innes Centre wheat collection. MSc. thesis, University of Birmingham.

Silwimba J. 1997. Characterisation of landrace wheats from the Watkins collection. Msc. thesis, University of Birmingham.

Watkins AE. 1935. *Heredity and Evolution.* London: John Murray.

Watkins AE. 1940. The inheritance of glume shape in *Triticum. Journal of Genetics* **39:** 249–264.

Watkins AE, Ellerton S. 1940. Variation genetics of the awn in *Triticum. Journal of Genetics* **40:** 243–270.

Evolution and Genetics

Wheat evolution and genetics: discovery and use of genes in crop improvement

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John Percival was intrigued by relationships of wild species related to wheat. While he did not extend his life's work on wheat to genetics of traits, he did produce many hybrids among *Aegilops* species. He also had success in breeding wheats for England, building on his extensive knowledge of variation within his large collection of wheat varieties. Percival also did not contribute directly to the understanding of the evolutionary history of wheat, although he was certainly aware of the origin of durum and bread wheats through natural interspecific hybridizations. The major features of the origin of wheat are well known, but several questions remain, especially about the time scale and sequence of development and adoption by farmers of various types of wheat. Evidence is gathered from archeobotanical studies and, more recently, from molecular studies of the wheat genomes and particular genes. From these studies appears information regarding the origin of wheat and the domestication process and, further, information that can be used for developing wheat varieties to meet future food needs.

It is fitting that the following two papers build on the Percival legacy in wheat evolution and breeding. Dvořák examines one of the important domestication genes controlling the hardness of seed covering structures, the glumes, lemmas, and paleas. Rajaram shows how intensive plant breeding and extensive distribution of the derived varieties have resulted in very large increases in global wheat production over a relatively short period of time, in a crop evolution sense. These papers bear on the theme of the Percival Symposium, 'Wheat – Yesterday, Today and Tomorrow'. Yesterday's wheats were farmer- selected landraces that were domesticated from wild forms, previously harvested from natural stands of wild-appearing wheat plants. Today's wheats are largely the products of directed plant breeding efforts, but there are large pockets of traditional or landrace varieties still being grown in many countries where wheat is a primary food crop. What will tomorrow's wheats look like, how will

they be developed, and who will develop them? These are critical questions bearing on food production and distribution.

Domestication of wheat is a continuous process, with farmers and breeders shaping its directions (Fig. 1). For example, landraces and progenitor species are continually being used as sources of genes for wheat variety development and farmers continue to select and improve their crops, especially in centres of crop diversity. The scientific basis for domestication is being discovered through genetic analyses, thus permitting directed

Wild Species (A and B)

Hybridization, Diploidization

↓

Wild Crop Progenitors (2x, 4x)

Monococcum and Dicoccum wheats
Gatherers
Nomadic Cultures

↓

Farmers

Sedentary or Transhumance Cultures
Planting, Harvesting, Seed-saving, Seed transport
(non-brittle rachis, free threshing)

↓

Hybridization - 4x X 2x (D genome)

Aestivum, common, bread wheat

↓

Farmers

Sedentary or Migratory, Seed-saving, Seed Transport
Landraces, locally adapted
Hybridization among landraces, broad adaptation

↓

Farmers and Plant Breeders

Selection within landraces
Hybridization among landraces and selection

↓

Plant Breeders

Local distribution of varieties
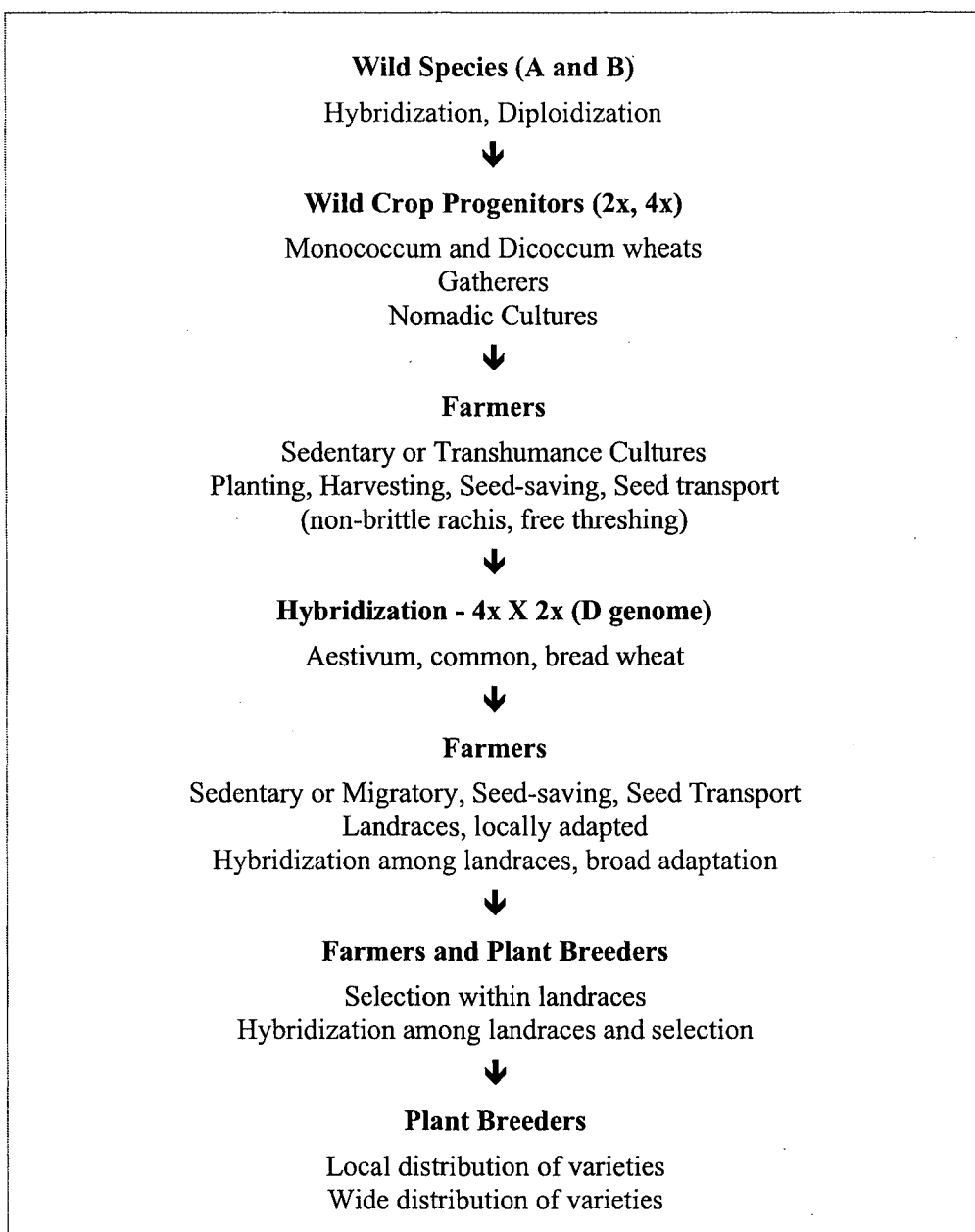Wide distribution of varieties

Figure 1. Domestication process for wheat.

TABLE 1.   Some traits of adaptive significance in wheat.

Trait	Approx. gene no.	Basis	Reference
Male and female fertility	3	Segregational	Jan & Qualset (1977a,b)
Coleoptile length	3	Segregational Pleiotropy with *Rht*	Fick & Qualset (1976)
Height reduction			
Dw	4	Segregational	Fick & Qualset (1973)
Rht	2+	Segregational	Fick & Qualset (1973), many others
Amylase activity	1	Pleiotropic with *Rht4*	Fick & Qualset (1975)
Flowering initiation			
Photoperiod,	3	Segregational	Klaimi & Qualset (1973a)
Vernalization	3	Segregational Multiple alleles	Klaimi & Qualset (1973b)
Canopy architecture			
Leaf angle	2	Segregational	De Carvalho & Qualset (1978)
Leaf size	3	Segregational	De Carvalho & Qualset (1978)
Liguleless/auricleless	1	Segregational	Unpublished
Spike density (sphaerococcum)	2	Segregational	De Carvalho & Qualset (1978)
Spike ramification			
Supernum. spikelets	2	Segregational	Gavira & Qualset (unpublished)
Branched rachis	3	Segregational	Gavira & Qualset (unpublished)
Tiller reduction (Israeli)	2	Segregational	Gavira & Qualset (unpublished)
Seed size	3	Selection response rate	Minella & Qualset (unpublished)
Nitrogen transformations Nitrate reductase,			
nra	1	Segregational	Gallagher, Qualset & Rains (1980)
Nitrate assimilation	2	Segregational	Cox, Qualset & Rains (1985a,b; 1986)
Stomatal conductance	3	RFLP	Qualset, McGuire, Lu & Zeiger (unpub.)

breeding to meet specific needs and environmental conditions. Two approaches can be taken, that are not mutually exclusive. One is the traditional plant-breeding approach whereby genetic diversity is identified and hybrids made among types having complementary traits, in the hope of recovering the desired new combinations of traits. This is the empirical approach and it has served very well in wheat improvement. The second may be called analytical breeding *sensu* Mac Key (1966) and Donald (1968), where specific traits are identified to match the targeted goals for breeding. Phenotypic analyses are used to identify potential parents and hybrids are made to search for the desired new combinations of traits. The analytic approach has not been applied widely and the various models (ideotypes) of plants predicted to produce high yield have not been rigorously tested.

It is the analytical approach that seems to hold promise for tomorrow's wheats, when used along with the traditional breeding efforts. Analytical breeding will move beyond phenotypic analysis to gene analysis, whereby specific genes will be identified and targeted for transfer to achieve productive gene complexes. This is the *modus operandi* of biotechnology or molecular breeding through parasexual gene transfer, but it can be applied in traditional sexual gene transfer breeding. Identification of genes and thereby determination of the potential for use in breeding can be done in a gross way through traditional Mendelian genetic analysis. For example, this is illustrated in my research program in California, in which genetic analysis of important traits was done to support methodologies and genetic resources for the California wheat breeding program. Remarkably, most of the traits studied were shown to be controlled largely by a few major genes that could be detected through traditional Mendelian segregation analysis (Table 1 and Qualset, 1979). This is only a start towards designing varieties. Creating the desired combinations of traits is a major breeding effort. However, detailed mapping, gene isolation or identification of these genes through molecular approaches are powerful tools for designing and developing tomorrow's wheats to meet the breeders' targets and the farmers' and the end-users' requirements.

REFERENCES

Cox MC, Qualset CO, Rains DW. 1985a. Genetic variation for nitrogen assimilation and translocation in wheat. I. Dry matter and nitrogen accumulation. *Crop Science* **25**: 430–435.

Cox MC, Qualset CO, Rains DW. 1985b. Genetic variation for nitrogen assimilation and translocation in wheat. II. Nitrogen assimilation in relation to grain yield and protein. *Crop Science* **25**: 435–440.

Cox MC, Qualset CO, Rains DW. 1986. Genetic variation for nitrogen assimilation and translocation in wheat. III. Nitrogen translocation in relation to grain yield and protein. *Crop Science* **26**: 737–740.

De Carvalho FIF, Qualset CO. 1978. Genetic variation for canopy architecture and its use in wheat breeding. *Crop Science* **18**: 561–567.

Donald, CM. 1968. The breeding of crop ideotypes. *Euphytica* **17**: 385–403.

Fick GN, Qualset CO. 1973a. Inheritance and distribution of grass-dwarfing genes in short-statured wheats. *Crop Science* **13**: 31–33.

Fick GN, Qualset CO. 1973b. Genes for dwarfness in wheat, *Triticum aestivum* L. *Genetics* **65**: 531–539.

Fick GN, Qualset CO. 1975. Genetic control of endosperm amylase activity and gibberellic acid responses in tall and short-statured wheats. *Proceedings of the National Academy of Science, USA* **72**: 892–895.

Fick GN, Qualset CO. 1976. Seedling emergence, coleoptile length, and plant height relationships in crosses of dwarf and standard-height wheats. *Euphytica* **25:** 679–685.

Gallagher LW, Soliman KM, Qualset CO, Huffaker RC, Rains DW. 1980. Major gene control of nitrate reductase activity in common wheat. *Crop Science* **20:** 717–721.

Gallagher L.W, Soliman KM, Rains DW, Qualset CO, Huffaker RC. 1983. Nitrogen assimilation in common wheats differing in potential nitrate reductase activity and tissue nitrate concentrations. *Crop Science* **23:** 913–919.

Jan, Chao-Chien, Qualset CO. 1977a. Genetic male sterility in wheat (*Triticum aestivum* L.): Reproductive characteristics and possible use in hybrid wheat breeding. *Hilgardia* **45:** 152–171.

Jan, Chao-Chien, Qualset CO. 1977b. Genetic male-sterility in wheat: Inheritance. *Crop Science* **17:** 791–794.

Klaimi YY, Qualset CO. 1973a. Genetics of heading time in wheat (*Triticum aestivum* L.). I. The inheritance of photoperiodic response. *Genetics* **74:** 139–156.

Klaimi YY, Qualset CO. 1973b. Genetics of heading time in wheat (*Triticum aestivum* L.). II. The inheritance of vernalization response. *Genetics* **76:** 119–133.

Mac Key, J. 1966. The wheat plant as a model in adaptation to high productivity under different environments. *Proceedings of the Fifth International Yugoslav Symposium on Wheat Research. Savrem. Poljopr. (Contemporary Agriculture)* **14 (11–12):** 37–48.

Qualset CO. 1979. Mendelian genetics of quantitative characters with reference to adaptation and breeding in wheat. *Proceedings of the Fifth International Wheat Genetics Symposium. Indian Society of Genetics and Plant Breeding, New Delhi,* **2:** 577–590.

Evolution of free-threshing and hulled forms of *Triticum aestivum*: old problems and new tools

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Keywords: spelt – *Triticum macha* – *Triticum spelta* – *Triticum turgidum* – RFLP

Abstract

Hulled forms of *Triticum aestivum* have been considered to be either ancestral to the free-threshing forms of *T. aestivum* or derived by hybridization of free-threshing *T. aestivum* with hulled emmer (*T. turgidum* ssp. *dicoccon*). Restriction fragment length polymorphism (RFLP) is being employed to discriminate between these hypotheses and shed light on the origin of each form of wheat. The cultivated forms of tetraploid wheat are essentially monomorphic for allele *Xpsr920a* on chromosome 4A whereas wild emmer is nearly monomorphic for allele *Xpsr920b*, indicating that all forms of cultivated tetraploid wheat evolved from cultivated emmer. Surprisingly, both alleles occur in *Triticum aestivum*. This evidence and genetic distances suggest that *T. aestivum* ssp. *macha* and its sibling tetraploid, *T. turgidum* ssp. *paleocolchicum*, are segregants from a cross between hexaploid wheat and wild emmer. It is concluded that European spelt originated in Europe by introgression of the speltoid syndrome into European free-threshing wheat. A general scenario of the origin of *T. aestivum* is discussed.

INTRODUCTION

Classical cytogenetic studies established that hexaploid wheat, *Triticum aestivum* L. ($2n = 6x = 42$, genomes AABBDD) originated from interspecific hybridization of tetraploid emmer wheat ($2n = 4x = 28$, genomes AABB) with *Aegilops tauschii* Coss. ($2n = 2x = 14$, genomes DD) (Kihara, 1944; McFadden & Sears, 1946). It is now generally accepted that the tetraploid wheat parent of *T. aestivum* was cultivated emmer (*Triticum turgidum* L. ssp. *dicoccon* Schrank, further *T. dicoccon*) rather than wild emmer (*Triticum turgidum* L. ssp. *dicoccoides* Korn. ex Schweinf., further *T. dicoccoides*) (Tsunewaki, 1966; Kimber & Sears, 1987). Since amphiploids from emmer x *Ae. tauschii* crosses resemble spelt (*T. aestivum* ssp. *spelta* Mac Key), McFadden & Sears (1946) suggested that spelt is the ancestral form of *T. aestivum*. At that time, spelt was known only from Europe, which was a dilemma for McFadden's & Sears' hypothesis. *Triticum aestivum* could not have originated in Europe because of

the absence of *Ae. tauschii* there. Rediscovery of spelt cultivation in Iran (Kuckuck & Schiemann, 1957) resolved this dilemma. Spelt could have pre- existed in Asia and been brought to Europe with other forms of wheat.

Although the ancestral position of spelt in the scheme of evolution of *T. aestivum* has been widely accepted, it has not been accepted universally, and counter-proposals have repeatedly been made (for a review of the early hypotheses see Andrews, 1964). Geographic considerations led Flaksberger (1925) and Schiemann (1932) to consider evolutionary schemes by which spelt could have originated in Western Europe. Archaeological records show that a free-threshing club wheat (*T. aestivum antiquorum*) was cultivated in the European Alps in the 3rd millenium BC, preceding thus the first appearance of spelt in Europe. Schiemann (1932) therefore speculated that spelt originated from a cross between club wheat and the European cultivated emmer. Since cultivated emmer has adhering glumes and some forms have a partially brittle rachis, spelt-like plants could segregate in the progeny of these hybrids. The feasibility of this scenario was substantiated by Mac Key (1966). He crossed *T. aestivum* ssp. *compactum* with cultivated emmer and obtained spelt-like segregants with lax spikes, partially brittle rachis and adhering glumes. These crosses were recently repeated by Ohtsuka (1998) with identical results. Obviously, the presence of the *C* gene, which is responsible for the club phenotype, in the D genome does not preclude emergence of lax-spike segregants, even though the D genome chromosomes cannot recombine in those crosses.

Spelt has been collected in Transcaucasia, Iran, Tadjikistan, and Afghanistan. In addition to spelt, several other hulled wheats have been described. Hulled, brittle-rachis *T. aestivum* ssp. *macha* (Dekapr. & Menabde) Mac Key (further *T. macha*) is grown in Georgia. A hulled wheat with elongated rachillae, *T. aestivum* spp. *vavilovii* (Jakubz.) A. Love is endemic to eastern Turkey. In Tibet, a semi-wild wheat (*T. aestivum* ssp. *tibetanum* Shao) with brittle rachis and partially adhering glumes grows in barley fields (Shao, 1980). A non-free threshing wheat (*T. aestivum* ssp. *yunanense* King) is cultivated in upper reaches of the Lanchang and Nu Rivers, China.

Jaaska (1978) found that European spelt differs from the Asian spelt by being polymorphic for the NADP-dependent aromatic ADH-B allozymes B1 and B2 in the A genome, whereas all accessions of the Asian spelt are monomorphic for allozyme B1. On the basis of this evidence, he concluded that European spelt is likely of a separate origin from the Asian spelt and from *T. macha* which is monomorphic for the B1 allele.

The free-threshing tetraploid *T. turgidum* ssp. *carthlicum* Nevski (further *T. carthlicum*) holds an intriquing position for the evolution of free-threshing forms of *T. aestivum*. In *T. aestivum,* the free-threshing habit is determined by the presence of the dominant *Q* allele on chromosome 5A (Sears, 1948; Mac Key, 1954) and the recessive allele at the *Tg* locus on chromosomes of homoeologous group 2 (Kerber & Rowland, 1974). *Triticum carthlicum* is the only tetraploid wheat in which the free-threshing habit is based on the dominant *Q* allele (Mac Key, 1966). All other tetraploid wheats, irrespective of whether hulled or free-threshing, have the *q* allele (for review see Mac Key, 1966).

DNA can potentially provide an unlimited number of loci for studies of relationships among wheat taxa, and studies of molecular variation have a potential to shed light on

the evolution of free-threshing forms of wheat. Liu & Tsunewaki (1991) compared restriction fragment length polymorphisms (RFLPs) between European spelt and bread wheat at single- or low-copy number loci in the A, B and D genomes. They pointed out that if spelt originated by mutation of Q to q in free-threshing wheat (Mac Key, 1954), the level of polymorphism between bread wheat and spelt would be similar among the three genomes. If, however, spelt originated by hybridization of bread wheat or club wheat with emmer, the A and B genomes would be more polymorphic than the D genome. Since the latter is true, they argued that this evidence supports the origin of spelt from a 4x × 6x hybrid, a conclusion reached earlier by Tsunewaki (1968) on the basis of other genetic evidence. However, since the A and B genomes are generally more polymorphic than the D-genome even between bread wheat cultivars, the argument of Liu & Tsunewaki provides rather weak support for the hypothesis.

To gain insight into the evolution of *T. turgidum* and *T. aestivum*, and to assess the position of hulled hexaploid wheats in the evolution of free-threshing forms of hexaploid wheat, we initiated investigation of RFLP at single copy loci in the three wheat genomes and those of their close relatives, *Ae. tauschii* and einkorn wheats. On the basis of these studies, most of the *Ae. tauschii* accessions could be assigned to one of two distinct genepools, designated "strangulata" and "tauschii" (Dvořák *et al.*, 1998). These genepools do not coincide with the classification of *Ae. tauschii* on the basis of morphology (Dvořák *et al.*, 1998). The D genome of European spelt, Asian spelt, *T. macha*, *T. aestivum* ssp. *vavilovii* and bread wheat were closely related to the "strangulata" genepool (Dvořák *et al.*, 1998). Assessment of genetic distances suggested that *T. aestivum* originated in a geographic region ranging from Armenia to southwestern Caspian Iran (Dvořák *et al.*, 1998; 1999).

At a number of loci, wheat and *Ae. tauschii* were found to share more than a single allele, indicating that more than one *Ae. tauschii* source was responsible for the formation of the D genome of *T. aestivum* (Dvořák *et al.*, 1999). Alleles at polymorphic loci shared by *T. aestivum* with *Ae. tauschii* were usually encountered in more than one form of *T. aestivum* (Dvořák *et al.*, 1999). Additionally, polymorphisms which were not encountered in *Ae. tauschii*, and presumably evolved in the D genome of wheat since the origin of hexaploid wheat, were shared by the various hulled and free-threshing forms of *T. aestivum* (Dvořák *et al.*, 1998). These findings and genetic distances based on variation in the D genome showed that all forms of hexaploid wheat share a common D-genome genepool and all have probably radiated from a single ancestral hexaploid population (Dvořák *et al.*, 1998, 1999).

MATERIAL AND METHODS

DNAs were isolated from accessions of diploid, tetraploid, and hexaploid wheats. The number of accessions of each taxon is indicated in Table 1. Southern blots of DraI-digested genomic DNAs were hybridized with cDNA or PstI clones as described previously (Dvořák *et al.*, 1998). Forty loci, 21 in the A genome and 19 in the B genome were investigated. The A genome loci were previously mapped in einkorn wheat (Dubcovsky *et al.*, 1996). In polyploid wheats, each investigated DNA fragment was assigned to a genome by hybridization of the clones with a panel of DNAs of Chinese Spring nullisomic-tetrasomics (Sears, 1966). For homoeologous group 4, *Lophopyrum*

TABLE 1.   Frequencies of the psr920a and psr920b alleles on chromosome 4A in wheat.

| Species	Subspecies	Origin	No. of accessions	*psr920a*	*psr920b*
T. urartu	*urartu*		88	0.00	1.00
T. turgidum	*dicoccoides*		202	< 0.01	0.99
	dicoccon		189	0.99	< 0.01
	durum		55	1.00	0.00
	turgidum		3	1.00	0.00
	turanicum		54	1.00	0.00
	polonicum		4	1.00	0.00
	carthlicum		10	1.00	0.00
	ispahanicum		7	1.00	0.00
T. aestivum	*spelta*	Europe	51	0.04	0.96
	macha		13	0.00	1.00
	compactum	Alps	36	0.08	0.92
	compactum	Turkey	11	0.28	0.72
	compactum	Afghan.	13	0.54	0.46
	aestivum	West	16	0.69	0.31
	aestivum	Turkey	57	0.28	0.72
	aestivum	Iran	92	0.49	0.51
	aestivum	China	144	0.93	0.07

elongatum / Chinese spring disomic substitution lines were used (Dvořák, 1980). Allelic designations were assigned to RFLP and allelic variation was scored. The DNA fragments of Chinese Spring were used as a reference in different blots. Nei's genetic distances (Nei, 1978) among morphological forms or geographic groups were computed using variation at 39 loci (*Xpsr920* was not used) with the GDA computer program (Lewis & Zaykin, 1997).

RESULTS

Xpsr920

Allelic variation at locus *Xpsr920* on the long arm of chromosome 4A provided intriguing insights into the origin of hexaploid wheat. The locus is polymorphic among the A genomes (Fig. 1). Wild emmer is essentially monomorphic for allele *Xsr920b*, whereas cultivated emmer is essentially monomorphic for allele *Xpsr920b* (Fig. 1, Table 1). *Triticum urartu,* the source of the A genome of polyploid wheats (Dvořák *et al.*, 1993), is monomorphic for the *Xpsr920b* allele and *T. monococcum* is monomorphic for allele *Xpsr920c* (Fig. 1). Sharing of the *Xpsr920b* allele by *T. urartu*
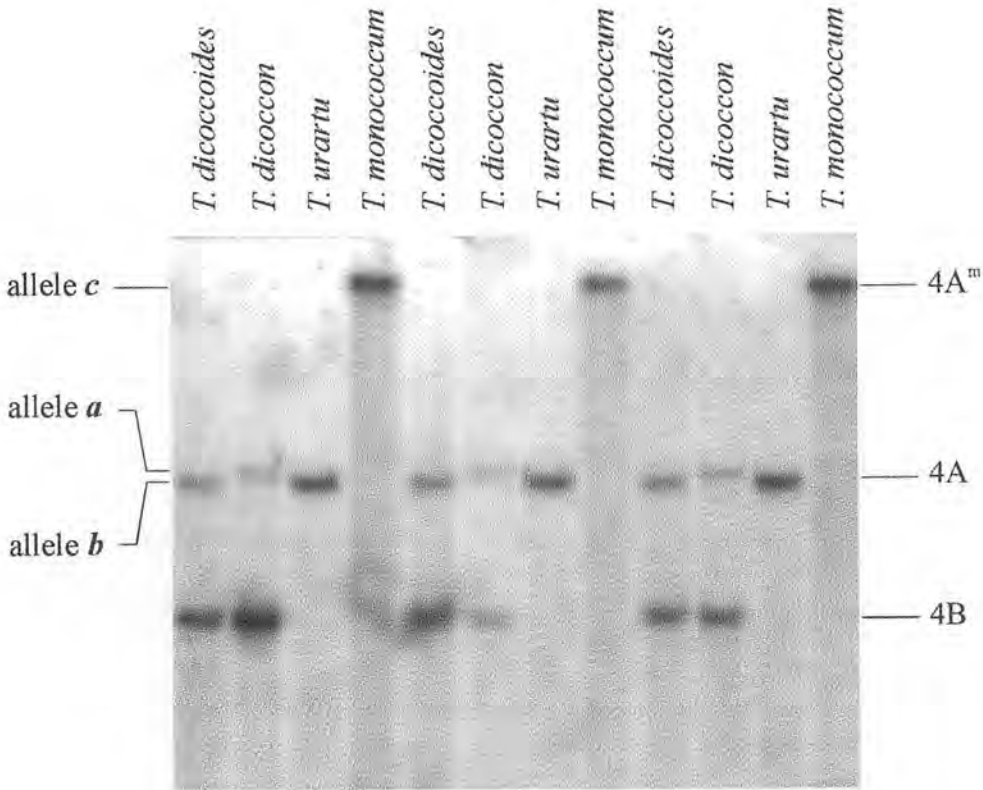
Figure 1. Restriction fragment length polymorphism at the psr920 locus in *T. turgidum* ssp. *Dicoccoides* (*T. dicoccoides*), *T. turgidum* ssp. *dicoccon* (*T. dicoccon*), *T. urartu*, and *T. monococcum* ssp. *Aegilopoides* (*T. monococcum*). *Triticum dicoccoides* and *T. urartu* genepools are characterized by the b allele, that of *T. dicoccon* by the a allele, and that of *T. monococcum* by the c allele.

and wild emmer indicates that the *b* allele is ancestral. The *Xpsr920a* allele must have been derived from the *Xpsr920b* allele early during the domestication of cultivated emmer since it is nearly fixed in cultivated emmer across its entire range.

All forms of cultivated tetraploid wheat so far investigated (ssp. *durum,* ssp. *turgidum,* ssp. *turanicum,* ssp. *ispahanicum,* ssp. *carthlicum,* and ssp. *polonicum*) have allele *Xpsr920a* (Table 1). If *T. aestivum* originated from hybridization of cultivated emmer with *Ae. tauschii* and if the free-threshing forms of *T. aestivum* evolved from hulled wheats by mutation, then all forms of *T. aestivum* are expected to have the *Xpsr920a* allele. Surprisingly, both alleles are present (Table 1). *Triticum macha* and European spelt are in fact monomorphic and nearly monomorphic for the *Xpsr920b* allele, respectively. There appears to be a west-east cline in the frequency of the *Xpsr920b* allele in the free-threshing forms of wheat. The highest frequency was encountered in the Alpine ssp. *compactum* (0.92) followed by Turkish ssp. *compactum* and ssp. *aestivum* (0.72). The frequency of the allele decreases to 0.51 in Iran and 0.07 in China.

Genetic distances

Genetic distances were calculated from allelic variation at 39 loci. *Xpsr920* was not used in order to have a line of evidence independent of the variation at the *Xpsr920* locus. To clarify the fixation of the *Xpsr920b* allele in *T. macha* and European spelt, genetic distances were examined between these wheats and other tetraploid and hexaploid wheats (Table 2). *Triticum macha* appeared to be more closely related to wild emmer and tetraploid *T. turgidum* ssp. *paleocolchicum* than to any other wheat. European spelt was closely related to all groups of bread wheat and club wheat; the closest relationship was to Alpine club wheat. The distance of European spelt to emmer was twice to three times as great as to the European club wheat or western bread wheat (Table 2). Of the three groups of cultivated emmer included in Table 2, emmer accessions from Europe were as a group more closely related to European spelt than those from Turkey and regions east of Turkey.

DISCUSSION

Cultivated emmer precedes temporally other cultivated forms of tetraploid wheat in the archeological record (for recent review see Nesbitt & Samuel, 1996). Virtual monomorphism for the *Xpsr920*a allele in all forms of cultivated tetraploid wheat indicates that none was independently domesticated from wild emmer. The fact that virtually all accessions of cultivated emmer have the *psr920a* allele indicates that a mutation of the *psr920b* to *psr920a* occurred early in the process of domestication of emmer and that all domesticated emmer today arose from a single ancestral population.

Triticum aestivum

The near monomorphism of the *psr920a* allele in the domesticated tetraploid wheat but polymorphism for both alleles in hexaploid wheat is striking and suggests that the evolution of hexaploid wheat is more complex than the evolution of tetraploid wheat. One possibility is that polymorphism at the *Xpsr920* locus on chromosome 4A in *T. aestivum* is due to reverse mutation from *Xpsr920a* to *Xpsr920b*. The *Xpsr920a* allele is characterized by increased DraI DNA fragment length relative of the ancestral allele. This could have been caused by a DNA insertion in tetraploid wheat. An excision of the inserted DNA element in hexaploid wheat could have caused a reversion of *Xpsr920a* to *Xpsr920b* allele. If this scenario is true, this reverse mutation would have to have occurred early in the evolution of the hexaploid genepool since the *Xpsr920b* allele is present in all forms of *T. aestivum*. It is very unlikely that the *Xpsr920a* allele is unstable and reverses to *Xpsr920b* in a high frequency. If that were the case, cultivated tetraploid wheats would be polymorphic, which is not the case.

Another possibility is that the *Xpsr920b* allele was contributed to *T. aestivum* by wild emmer. Since *Ae. tauschii* populations which contributed the D genome of *T. aestivum* (Armenia-southwestern Caspian Iran region) are not sympatric with wild emmer, it is unlikely that wild emmer was the primary tetraploid that contributed of the A and B genomes to *T. aestivum*. Geographic considerations dictate that the primary parent was cultivated emmer. Hybridization of the primary hexaploid with *T. dicoccoides* could have happened in Turkey. The interspecific hybridization would have broadened the genepool of the A and B genomes of hexaploid wheat, potentially producing extensive morphological variation that characterizes modern *T. aestivum*.

TABLE 2. Nei's genetic distances based on RFLP at 39 loci in the A and B genomes between groups of *T. aestivum* ssp. *macha* (*T. macha*) and *T. Aestivum* ssp. *spelta* (spelt) and groups of *T. aestivum* ssp. *aestivum*, ssp. *compactum*, and ssp. *spelta* and groups *T. turgidum* ssp. *dicoccon*, ssp. *dococcoides* and ssp. *Paleocolchicum*.

Taxon	Geographical origin	*T. macha*	European spelt
T. aestivum ssp. *aestivum*	West	0.24	0.09
	Turkey	0.23	0.11
	Iran	0.23	0.16
	China	0.24	0.16
T. aestivum ssp. *compactum*	Alps	0.28	0.09
	Turkey	0.29	0.17
	Iran	0.34	0.22
T. aestivum ssp. *spelta*	Europe	0.21	-
	Iran	0.33	0.20
	Afghanistan	0.40	0.18
	Tadjikistan	0.36	0.22
T. aestivum ssp. *macha*	Georgia	-	0.21
T. turgidum ssp. *dicoccoides*	Fertile crescent	0.18	0.26
T. turgidum ssp. *dicoccon*	Europe	0.24	0.22
	Turkey	0.25	0.26
	East of Turkey	0.33	0.31
T. turgidum ssp. *paleocolchicum*	Georgia	0.17	0.35
T. turgidum ssp. *durum*	Global	0.30	0.26
T. turgidum ssp. *carthlicum*	Turkey	0.41	0.31

Following this scenario, the existence of a cline of the *Xpsr920b* allele suggests that the western wheats, such as European club wheat, originated in Turkey, whereas the eastern wheats, Iranian and in particular Chinese wheats, which have high frequencies of the *Xpsr920a* allele, have a more eastern origin and are more closely related to the ancestral hexaploid population. A similar differentiation between eastern and western forms of *T. aestivum* was reported by Tsunewaki (1968).

European spelt

While McFadden & Sears (1946) considered European spelt to be ancestral to free-threshing wheat, other workers speculated that European spelt originated from hybridization of European bread or club wheat with cultivated European emmer (Mac Key, 1966; Tsunewaki, 1968; Ohtsuka, 1998). Jaaska (1978) concluded from the distribution of the NADP-dependent aromatic alcohol dehydrogenase allozymes that the European spelt is of a separate origin from the Asian spelt. European spelt shares the

Ne_2 allele with European wheat (Tsunewaki, 1968) which led Tsunewaki to concluded that it is a result of introgression of q gene from European emmer into European free-threshing wheat. European spelt is characterized by a virtual monomorphism for the *Xprs920b* allele and close genetic proximity to Alpine club wheat and western bread wheat. Both observations are consistent with the hypothesis that European spelt originated in Europe from hybridization of European *T. aestivum* and cultivated emmer.

The A and B genomes of European spelt are far more closely related to European and western free-threshing wheats than to European emmer. Additionally, if European spelt is a hybrid or a direct segregant from 4x × 6x crosses, it would be polymorphic for both *Xprs920* alleles. Instead, it has the same high frequency of the *Xprs920b* allele as Alpine club wheat. Both lines of evidence strongly suggest that European spelt is not a simple hybrid or direct segregant from a 4x × 6x cross but a result of introgression of the spelt syndrome into free-threshing European wheat. The same conclusion was reached by Tsunewaki (1968) in his study of the distribution of hybrid necrosis alleles.

In view of the fact that the A and B genomes of European spelt are closely related to Alpine club wheat, it is not surprising that European spelt appeared different from the Asian spelt in previous studies examining variation at several loci in the A and B genomes (Tsunewaki, 1968; Jaaska, 1978). Nei's genetic distances based on variation in the A and B genomes showed that European spelt is only distantly related to Asian spelt.

It can be also argued that European spelt originated in Turkey and was introduced to Europe. In that case, it would have to be assumed that hybridization and introgression occurred between European emmer and European *T. aestivum,* to explain the greater proximity of European spelt to European emmer than to Turkish emmer. Genetic evidence argues against this introgression, and hence against this hypothesis. First, European emmer is monomorphic for the *Xpsr920a* allele while European *T. aestivum* has a high frequency of the *Xpsr920b* allele. Second, western bread wheat and Alpine club wheat are not any closer to European emmer (Nei's genetic distances of 0.165 and 0.233, respectively) than to Turkish emmer (0.151 and 0.209, respectively); actually, a reverse may be true.

The survival of the spelt syndrome among European wheats for close to four millennia suggests that it either provided *T. aestivum* with some advantage or was for some reason preferred by farmers, or both (for a recent review see Nesbitt & Samuel, 1996). Quantitative trait analysis of a segregating population from European spelt X bread wheat revealed a strong association between resistance to pre-harvest sprouting and the q region on chromosome 5A of spelt (Zannetti *et al.*, 1998). It is tempting to speculate that one reason for the selection of the spelt phenotype and the q region was resistance to pre-harvest sprouting associated with q in environments with heavy summer rains that are typical of regions in which spelt was cultivated in the past.

Triticum macha

This hulled wheat is endemic to Georgia. It has a brittle rachis and compact spikes. On morphological grounds, it has been speculated to be the ancestor of *T. aestivum* (Swaminathan, 1966; Kandelaki, 1967; and others) although other workers considered it derived (e.g. Tsunewaki, 1968). *Triticum macha* is almost equidistant between wild emmer and *T. turgidum* ssp. *paleocolchicum*. Additionally, it is monomorphic for the

Xprs920b allele. This is consistent with the hypothesis that wild emmer rather than cultivated emmer is the tetraploid ancestor of *T. macha*. *T. macha* has a fragile rachis with the same disarticulation of spikes as wild emmer (wedge type) in which it differs from European spelt (barrel type disarticulation). Since *T. macha* is strongly isolated from other hexaploid wheats by the hybrid chlorosis *Ch1* allele which it shares with emmer (Tsunewaki, 1968), it maintained its intermediate genetic position between the parental *T. aestivum* and wild emmer, rather than being subjected to introgression with other hexaploid wheats. Genetic distances in Table 2 show that *T. macha* is distant from all forms of spelt and free-threshing wheat. This is consistent with the suggested hybrid origin and inconsistent with an ancestral position of *T. macha* in the evolution of hexaploid wheat. The monomorphism for the *Xpsr920b* allele also contradicts an ancestral position of *T. macha* for other forms of *T. aestivum*, because additional hybridization with domesticated emmer would have to be postulated in the east. Since *T. turgidum* ssp. *paleocolchicum* is closer to *T. macha* than to other populations of emmer and other forms of tetraploid wheat, *T. turgidum* ssp. *paleocolchicum* appears to be derived from, rather parental to *T. macha*. Most likely, *T. turgidum* ssp. *paleocolchicum* is a tetraploid segregant from the same hybrid population which gave rise to *T. macha*.

REFERENCES

Andrews AC. 1964. The genetic origin of spelt and related wheats. *Zuchter* **34**: 17–22.

Dubcovsky J, Luo MC, Zhong GY, Bransteitter R, Desai A, Kilian A, Kleinhofs A, Dvořák J. 1996. Genetic map of diploid wheat, *Triticum monococcum* L., and its comparison with maps of *Hordeum vulgare* L. *Genetics* **143**: 983–999.

Dvořák J. 1980. Homoeology between *Agropyron elongatum* chromosomes and *Triticum aestivum* chromosomes. *Canadian Journal of Genetics and Cytology* **22**: 237–259.

Dvořák J, di Terlizzi P, Zhang HB, Resta P. 1993. The evolution of polyploid wheats: Identification of the A genome donor species. *Genome* **36**: 21–31.

Dvořák J, Luo M-C, Yang Z-L, Zhang H-B. 1998. The structure of *Aegilops tauschii* genepool and the evolution of hexaploid wheat. *Theoretical and Applied Genetics* **97**: 657–670.

Dvořák J, Luo M-C, Yang Z-L 1999. Genetic evidence on the origin of *T. aestivum* L. In: Damania A (ed.). *The origins of agriculture and the domestication of crop plants in the Near East.* ICARDA, Aleppo: ICARDA, in press.

Flaksberger CA. 1925. Pshenitsa odnozernyaki. *Trudy po Prikladnoi Botaniky i Selektsii* **15**: 207–227.

Jaaska V. 1978. NADP-dependent aromatic alcohol dehydrogenase in polyploid wheats and their relatives. On the origin and phylogeny of polyploid wheats. *Theoretical and Applied Genetics* **53**: 209–217.

Kandelaki GV. 1967. On the origin of *Triticum macha* Dek. et Men. (in Russian) *Genetika (Moscow)* **1**: 34–36.

Kerber ER, Rowland GG. 1974. Origin of free threshing character in hexaploid wheat. *Canadian Journal of Genetics and Cytology* **16**: 145–154.

Kihara H. 1944. Discovery of the DD-analyser, one of the ancestors of *Triticum vulgare* (in Japanese). *Agriculture and Horticulture (Tokyo)* **19**: 13–14.

Kimber G, Sears ER. 1987. Origin of the genus *Triticum* and the origin of cultivated wheat. In: *Wheat and wheat improvement.* Monographs of the American Society of Agronomy 154–164.

Kuckuck H, Schiemann E. 1957. Uber das Vorkommen von Speltz und Emmer (*Triticum spelta* L. und *Tr. dicoccum* Schubl.) im Iran. *Zeischrift fur Pflanzenzuchtung* **38**: 383–396.

Lewis PO, Zaykin D. 1997. Genetic data analysis: Computer program for the analysis of allelic data. Version 1.0. A free internet program distributed by the authors from the GDA Home Page at http://chee.unm.edu/gda.

Liu Y-G, Tsunewaki K. 1991. Restriction fragment length polymorphism (RFLP) analysis in wheat. II. Linkage analysis of the RFLP sites in common wheat. *Japanese Journal of Genetics* **66:** 617–633.

Mac Key J. 1954. Neutron and X-ray experiments in wheat and a revision of the speltoid problem. *Hereditas* **40:** 65–180.

Mac Key J. 1966. Species relationship in *Triticum.* In: Mac Key JM (ed.). *2nd International Wheat Genetic Symposium.* Lund, Sweden: *Hereditas* 237–275.

McFadden ES, Sears ER. 1946. The origin of *Triticum spelta* and its free-theshing hexaploid relatives. *Journal of Heredity* **37:** 81–89, 107–116.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* **89:** 583–590.

Nesbitt M, Samuel D. 1996. From staple crop to extinction? The archaeology and history of hulled wheats. In: Padulosi S, Hammer K, Heller J (eds). *Hulled Wheats. Promoting the conservation and use of underutilized and neglected crops. 4. Proceedings of the first international workshop on hulled wheats.* Castelvecchio Pacoli, Italy: International Plant Genetic Resources Institute, Rome, Italy 41–100.

Ohtsuka I. 1998. Origin of central European spelt wheat. In: *9th international wheat genetics symposium.* Slinkard AE. (ed.). Saskatoon: University of Saskatchewan Extension Press, 303–305.

Schiemann E. 1932. Pfahlbauweizen – historiches und Phylogenetisches. *Zeitschrift fur Pflanzenzuchtung* **17:** 36–54.

Sears ER. 1948. The cytology and genetics of the wheats and their relatives. *Advances in Genetics* **2:** 239–270.

Sears ER. 1966. Nullisomic-tetrasomic combinations in hexaploid wheat. In: Riley R, Lewis KR (eds). *Chromosome manipulations and plant genetics.* Edinburgh: Oliver & Boyd, 29–44.

Shao Q. 1980. Some-wild wheat from Xizang (Tibet). *Acta Genetica Sinica* **7:** 149–156.

Swaminathan MS. 1966. Mutational analysis of the hexaploid *Triticum* complex. In: Mac Key JM (ed.). *Proceedings of the 2nd International Wheat Genetics Symposium, Lund, Sweden: Hereditas,* **Suppl. 2:** 418–437.

Tsunewaki K. 1966. Comparative gene analysis of common wheat and its ancestral species. II. Waxiness, growth habit and awnedness. *Japanese Journal of Botany* **19:** 175–229.

Tsunewaki K. 1968. Origin and phylogenetic differentiation of common wheat revealed by comparative gene analysis. In: Finley KW, Shepherd KW (eds). *3rd International Wheat Genetics Symposium.* Canberra, Australia: 71–85.

Zannetti S, Keller M, Winzeler M, Saurer W, Keller B, Messmer M. 1998. QTL for quality parameters for bread-making in a segregating wheat by spelt population. In: Slinkard AE. (ed.) *9th International Wheat Genetics Symposium.* Saskatoon, Canada: University of Saskatchewan Extension Press 1: 273–276

Half a century of international wheat breeding

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INTRODUCTION

Wheat is the most widely grown and consumed food crop. It is the staple food of nearly 35% of the world population and demand for wheat will grow more rapidly than for any other major crop. The forecast global demand for wheat in the year 2020 varies between 840 (Rosegrant *et al.*, 1995) to 1050 million tons (Kronstad, 1998). To reach this target, global production will need to increase by 1.6 to 2.6% annually from the present production level of 560 million tons. Increases in realized grain yield have provided about 90% of the growth in world cereal production since 1950 (Mitchell *et al.*, 1997) and by the first decade of the next century most of the increase needed in world food production must come from higher absolute yields (Ruttan, 1993). For wheat, the global average grain yield must increase from the current 2.5 t ha^{-1}, to 3.8 t ha^{-1}. In 1995, only 18 countries world wide had average wheat grain yields of more than 3.8 t ha^{-1}, the majority located in Northern Europe (CIMMYT, 1996).

The formidable challenge to meet this demand is not new to agricultural scientists who have been involved in the development of improved wheat production technologies for the past half-century. For all developing countries, wheat yields have grown at an average annual rate of over 2% between 1961 and 1994 (CIMMYT, 1996). In Western Europe and North America the annual rate of growth for wheat yield was 2.7% from 1977 to 1985, falling to 1.5% from 1986 to 1995. Recent data have indicated a decrease in the productivity gains being achieved by major wheat producing countries (Brown, 1997). In Western Europe, where the highest average wheat grain yield is obtained in the

Netherlands (8.6 t ha^{-1}), yield increased from 5 to 6 t ha^{-1} in five years, but it took more than a decade to raise yields from 6 to 7 t ha^{-1}. Worldwide, annual wheat grain yield growth decreased from 3.0% between 1977–1985, to 1.6% from 1986–1995, excluding the USSR (CIMMYT, 1996). Degradation of the land resource base, together with a slackening of research investment and infrastructure, has contributed to this decrease (Pingali & Heisey, 1997). Production constraints affected by physiological or genetic limits are hotly debated, however future increases in food productivity will require substantial research and development investment to improve the profitability of wheat production systems through enhancing input efficiencies. Due to a continuing necessity for multi-disciplinary team efforts in plant breeding, and the rapidly changing development of technologies, three overlapping avenues can be considered for raising the yield frontier in wheat: continued investments in "conventional breeding" methods; use of current and expanded genetic diversity; and, investigation and implementation of biotechnology assisted plant breeding.

In this presentation, we attempt to give a brief summary of CIMMYT's international wheat breeding program. We would also attempt to describe emerging strategies that might be applied in the future.

CONVENTIONAL WHEAT BREEDING

It is likely that gains to be achieved from conventional breeding will continue to be significant for the next two decades or more (Duvick, 1996), but these are likely to come at a higher research cost than in the past. In recent surveys of wheat breeders (Braun *et al.*, 1998; Rejesus *et al.*, 1996), more than 80 % of respondents expressed concern that plant variety protection (PVP) and plant or gene patents will restrict access to germplasm. This may have deleterious consequences for future breeding success since Rasmusson (1996) stated that nearly half of the progress made by breeders in the past can be attributed to germplasm exchange. Regional and international nurseries have been an efficient means of gathering data from varied environments and exposing germplasm to diverse pathogen selection pressures, while providing access and exchange of germplasm. Breeders utilize these cooperative nurseries extensively in their crossing programs (Braun *et al.*, 1998). However, the numbers of co-operatively-distributed wheat yield and screening nurseries have been greatly reduced during the past decade. Today, only the International Maize and Wheat Improvement Center (CIMMYT) and the International Center for Agricultural Research in Dryland Areas (ICARDA) distribute international nurseries for spring wheat, with the National Wheat Improvement Program of Turkey, CIMMYT, ICARDA and Oregon State University distributing international winter wheat nurseries.

Investments needed for breeding efforts increase with increasing yield levels. Further, progress to develop higher yielding cultivars is reduced with every objective added to a breeding program. Though the list of important traits may become longer and longer, little if any assistance has been provided by economists to prioritize breeding objectives. Considering that a wheat breeding program like CIMMYT allocates around 60% of its resources to "Durable Resistance Breeding", i.e. the need for research in this field is obvious. Due to high cost, we see durable resistance breeding as one of the first fields where transformation should be applied by breeders through introgression of one or more genes controlling disease resistance.

BREEDING FOR WIDE ADAPTATION

CIMMYT's breeding methodology is tailored to develop widely adapted, disease resistant germplasm with high and stable yield across a wide range of environments. The impact of this approach has been significant. The total spring bread wheat (*Triticum aestivum* L.) area in developing countries, excluding China, is around 63 million ha of which 36 million ha or 58 % are planted to varieties derived from CIMMYT germplasm (Byerlee & Moya, 1993; Rajaram, 1995). During the period of 1966 to 1990, 1317 bread wheat cultivars were released by developing countries, of which 70% were either direct releases from CIMMYT advanced lines or had at least one CIMMYT parent (Byerlee & Moya, 1993). For the period from 1986 to 1990, 84% of all bread wheat cultivars released in developing countries had CIMMYT germplasm in the pedigree. Simultaneously the use of dwarfing genes has continued to increase over time and today, regardless of the type of wheat, more than 90% of all wheat varieties released in developing countries are semi-dwarfs, which covered 70% of the total wheat area in developing countries by the end of 1990 (Byerlee & Moya, 1993). The continuous adoption of semi-dwarf spring wheat cultivars in the post-Green Revolution period from 1977–1990 resulted in about 15.5 million tons of additional wheat production in 1990, valued at about US$3 billion, of which 50% or US$1.5 billion are attributed to the adoption of new Mexican semi-dwarf wheat cultivars (Byerlee & Moya, 1993). In 1990, an estimated 93% of the total spring bread wheat production in developing countries, excluding China, comes from semi-dwarf spring wheats, which cover about 83% of the total spring bread wheat area in developing countries (Byerlee & Moya, 1993).

The cornerstones of CIMMYT's breeding methodology are targeted breeding for ME, the use of a diverse gene pool for crossing, shuttle breeding, selection for yield under optimum conditions, and multi-locational testing to identify superior germplasm with good disease resistance. In this paper we would like to present some of the recent developments at CIMMYT's wheat program.

Targeted breeding – the mega-environment concept

To address the needs of diverse wheat growing areas, in 1988 CIMMYT introduced the concept of mega-environment (ME) (Rajaram *et al.*, 1994). A ME is defined as a broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental, defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences, and, for convenience, by a volume of production. Germplasm generated for a given ME is useful throughout it, accommodating major stresses, but perhaps not all the significant secondary stresses. Within a ME, millions of ha are addressed with a certain degree of homogeneity as it relates to wheat. By 1993, 12 ME have been defined, 6 for spring wheats (ME1–ME6), 3 for facultative wheats (ME7–ME9) and 3 for winter wheats (ME9–ME12). Details for each ME are given in Table 1.

Use of a diverse genepool for crossing to maintain genetic diversity

Broad-based plant germplasm resources are imperative for a sound and successful breeding program. Utmost attention is given to the genetic diversity within the CIMMYT germplasm to minimize the risk of genetic vulnerability, since it is grown on large areas

TABLE 1. Classification of mega-environments (MEs) used by the CIMMYT Wheat Program. Adapted from Rajaram *et al.* (1995).
SPRING WHEAT

ME	Latitude (degrees)	Area (mill./ha)	Moisture regime	Temperature regime	Growth habit	Sown	Major breeding objectives	Representative locations/ regions	Year breeding began at CIMMYT
1	Low	32.0	Low rainfall irrigated	Temperate	Spring	A	Resistance to lodging, SR, LR, YR	Yaqui Valley, Mexico Indus Valley, Pakistan Gangetic Valley, India Nile Valley, Egypt	1945
2	Low	10.0	High rainfall	Temperate	Spring	A	As for ME1 + resistance to YR, *Septoria* spp., sprouting	North African Coast, Highlands of East Africa, Andes, and Mexico	1972
3	Low	1.7	High rainfall	Temperate	Spring	A	As for ME2 + acid soil tolerance	Passo Fundo, Brazil	1974
4A	Low	10.0	Low rainfall, winter dominant	Temperate	Spring	A	Resistance to drought, *Septoria* spp., YR	Aleppo, Syria; Settat, Morocco	1974
4B	Low	5.8	Low rainfall, summer dominant	Temperate	Spring	A	Resistance to drought, *Septoria* spp., *Fusarium* spp., LR, SR	Marcos Juarez, Argentina	1974
4C	Low	5.8	Mostly residual moisture	Hot	Spring	A	Resistance to drought, and heat in seedling stage	Indore, India	1974
5A	Low	3.9	High rainfall/ irrigated, humid	Hot	Spring	A	Resistance to heat, *Helminthosporium* spp., *Fusarium* spp., sprouting	Joydepur, Bangladesh Londrina, Brazil	1981
5B	Low	3.2	Irrigated, low humidity	Hot	Spring	A	Resistance to heat and SR	Gezira, Sudan; Kano, Nigeria	1975
6	High	5.4	Moderate rainfall/ summer dominant	Temperate	Spring	S	Resistance to SR, LR, *Helminthosporium* spp., *Fusarium* spp., sprouting, photoperiod sensitivity	Harbin, China	1989

TABLE 1. *Continued*
WINTER/FACULTATIVE WHEAT

ME	Latitude (degrees)	Area (mill./ha)	Moisture regime	Temperature regime	Growth habit	Sown	Major breeding objsectives	Representative locations/ regions	Year breeding began at CIMMYT
7	High		Irrigated	Moderate cold	Facultative	A	Rapid grain fill, resistance to cold, YR, PM, BYD	Zhenzhou, China	1986
8A	High		High rainfall/ irrigated, long season	Moderate cold	Facultative	A	Resistance to cold, YR, *Septoria* spp.	Chillan, Chile	1986
8B	High		High rainfall/ irrigated, short season	Moderate cold	Facultative	A	Resistance to *Septoria* spp., YR, PM, *Fusarium* spp., sprouting	Edirne, Turkey	1986
9	High		Low rainfall	Moderate cold	Facultative	A	Resistance to cold, drought	Diyarbakir, Turkey	1986
10	High		Irrigated	Severe cold	Winter	A	Resistance to winterkill, YR, LR, PM, BYD	Beijing, China	1986
11A	High		High rainfall, irrigated, long season	Moderate cold	Winter	A	Resistance to *Septoria* spp., *Fusarium* spp., YR, LR, PM	Temuco, Chile	1986
11B	High		High rainfall/ irrigated, short season	Severe cold	Winter	A	Resistance to LR, SR, PM, winterkill, sprouting	Lovrin, Romania	1986
12	High		Low rainfall	Severe cold	Winter	A	Resistance to winterkill, drought, YR, bunts	Ankara, Turkey	1986

a Low = less than about 35-40 degrees. b Refers to rainfall just before and during the crop cycle. High = >500mm; low = <500mm
c Hot = mean temperature of the coolest month > 17.5 degrees; cold = <5.0 degrees. d A = autumn, S = spring
e Factors additional to yield and industrial quality. SR=stem rust, LR=leaf rust, YR=yellow (stripe) rust, PM=powdery mildew, and BYD=barley yellow dwarf . f Further subdivided into (1) optimum growing conditions, (2) presence of Karnal bunt, (3) late planted, and (4) problems of salinity.

and is widely used by NARS. We also believe that the use of genetically diverse material is mandatory for future increase of yield potential and yield stability. Parental groups of lines considered for crossing in any year consist of 500 – 800 lines. Twice a year around 30% of the parental stocks are replaced with outstanding introductions. About 2000 out of 8000 crosses/year are made to these introductions. In addition, commercial varieties from NARS, and non-conventional sources such as durum wheat, and alien species are used to incorporate desired traits by recombination or translocation. The introductions are mostly used as female to preserve cytoplasmic diversity.

The most recent example of the potential impact of generating new diversity is the reconstitution of bread wheat by the CIMMYT wide crossing program by crossing durum wheat (*Triticum durum*) with the D-genome donor *Triticum tauschii*. Lines derived from backcrosses to bread wheat showed substantial morpho-agronomic variation, resistance to Karnal Bunt *(Tilletia indica)* and scab *(Fusarium graminearum)* and a TKW of up to 53 g (Villareal, 1995). Yield potential is close to that of bread wheat and grain yield of the best synthetic wheat reached 7.7 t/ha (Table 2.).

TABLE 2.   Grain yield and tkw of two crosses of bread wheat with synthetic wheats in yield trials at cd. Obregon, Mexico in 1993.

Entry	Grain yield (kg/ha)	1000 KW (g)
Chen/*T. tauschii*//BCN	7740a[1]	53a
Cndo/R143//Ente/Mexi/3/ T.tauschii/4/Weaver	6830b	52a
Bacanora 88 (BW check)	6770b	40b

[1]Means within columns followed by different letters are significantly different at the 0.05 level of probability. Source:Villareal (1995).

Other sources exploited for new variability are:

- *Triticum dicoccoides* (emmer wheat) as a source of resistance to stripe rust, leaf rust, powdery mildew, *Septoria* spp. and Wheat Streak Mosaic Virus, tolerance to drought, high protein content and higher yield potential.

- Bread wheat is crossed with durum wheat to increase grain size. The six highest yielding lines derived from this program out-yielded their breadwheat parent by 5 to 20 % in yield trials in Cd. Obregon, Mexico.

Shuttle breeding between Cd Obregon and Toluca

Young & Frey (1994) provide two factors which influence the success of a shuttle program: "(a) the use of a germplasm pool encompassing genotypes with broad adaptation and (b) the use of selection environments eliciting different responses from plant types" and state further "The wheat breeding program of Borlaug met these

conditions". When N.E. Borlaug started the shuttle breeding approach in 1945 the only objective was to accelerate breeding for stem rust resistance. Since then, segregating populations have been shuttled 100 times between the two environmentally contrasting sites in Mexico, Cd. Obregon and Toluca (for a detailed description of the two locations see Braun et al., 1992). We would like to stress this point since the discussion of breeding for wide versus specific adaptation has not come to an end (Ceccarelli, 1989). We believe that comparisons between breeding methodologies for different species should not only consider selection parameters like heritabilities but also the breeding investments into the respective crop. At CIMMYT alone, more than 200 000 crosses have been made since 1945 and today, more than 4000 advanced spring wheat lines are annually screened worldwide. We are of the opinion that such a large scale testing and crossing program using a diverse genepool will most probably have higher chances of identifying widely adapted germplasm, break genetic linkages and pyramid desired genes than programs which test the germplasm in a narrow environmental range and restrict the genetic diversity in the crossing program. The wide acceptance of CIMMYT germplasm by NARS and by farmers supports this approach. This is said without disparaging other approaches.

One of the important results of this shuttle was the selection of photo- insensitive wheat genotypes. Initially, selection for photoperiodic insensitivity was unconscious, but only this trait permitted the wide spread of the Mexican semi-dwarfs (Borlaug, 1995). Today, this trait has been incorporated into basically all spring wheat cultivars grown below 48° latitude and is now also spreading to wheat areas above 48° N (Worland et al., 1994).

Selection under optimum conditions and breeding for yield potential

Selection of segregating populations and consequent yield testing of advanced lines is paramount for identification of high yielding and input responsive wheat genotypes. The increase in yield potential of CIMMYT cultivars developed since the 60's is shown in Fig. 1. (Rees et al., 1993). The average increase per year was 0.9% and there is no evidence that a yield plateau is reached. This genetic progress in increasing the yield potential is closely associated with an increase in the photosynthetic activity (Rees et al., 1993). Both photosynthetic activity and yield potential increased over the 30 year period by some 25%. These findings may have major implications on CIMMYT's future selection strategy since there is evidence that wheat genotypes with a higher photosynthesis rate have a lower canopy temperature, which can be easily, rapidly and cheaply measured using a hand-held thermometer. If verified in future trials, breeders may be able to use this trait to increase selection efficiency for yield potential. This technique may be, in particular, useful to select wheat genotypes adapted to environments where heat is a production constraint.

Yield per se is closely associated with input responsiveness. Increasing the input efficiency at low production levels can shift cross over points, provided they exist, and enhance residual effects of high genetic yield potential. Furthermore, combining input efficiency with high yield potential will allow a farmer to benefit from such cultivars over a wide range of input levels. The increase in N-use-efficiency is shown in Fig. 2. (Ortiz-Monestario et al., 1995).
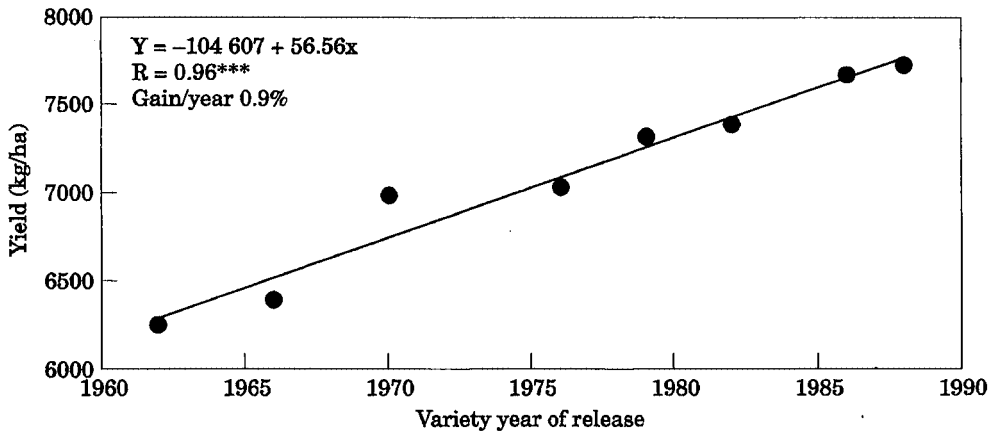
Figure 1. Mean grain yields for the historical series of bread wheat varieties for the years 1990–93 at Cd. Obregon, Mexico. (Data from Rees *et al.*, 1993.)

Multi-locational testing

Around 1500 sets of yield trials and screening nurseries consisting of around 4000 advanced bread wheat lines are sent annually to more than 200 locations. Multi-locational testing plays a key-role in identifying best performing entries for crossing. Since the shuttle program (see above) permits two full breeding cycles/year, it takes around five to six years from crossing to international distribution of advanced lines to cooperators. This "recurrent selection program" ensures a continuous and fast pyramiding of desirable genes.

Ceccarelli (1989) pointed out that the widespread cultivation of some wheat cultivars should not be taken as a demonstration of wide adaptation, since a large proportion of these areas are similar or made similar by use of irrigation and/or fertilizer and therefore, the term wide adaptation has been used mainly to describe geographical rather than environmental differences. If this is true, the genotypic variation should be considerably higher than the GxE - interaction in ANOVAs of CIMMYT trials. Braun *et al.* (1992) showed that this is not the case. When subsets of locations were grouped on geographical and/or environmental similarities, the GxE interaction was mostly greater than the genotypic variance. The environmental diversity of sites where CIMMYT's 21st International Bread Wheat Screening Nursery was grown and the diversity amongst genotypes in this nursery was demonstrated by Bull *et al.* (1994). They classified similarities among environments by forming subsets of genotypes from the total dataset and compared it with the classification based on the remaining genotypes. Using this procedure they concluded that it was not possible to come to a stable grouping of environments, because little or no relationship existed among them.

Conclusions drawn from trials carried out on research stations are always open to critics who argue, that these results do not necessarily reflect farmers' field conditions. However, the wide acceptance of CIMMYT germplasm by farmers in ME 1 to ME 5 (see above) does not support the view that the wide adaptation of CIMMYT germplasm is based on geographical rather than environmental differences.

Strategy for durability of resistance

From its beginning, incorporation of durable, non specific disease resistance into CIMMYT's germplasm was a high priority since breeding of widely adapted germplasm with stable yields without adequate resistance against the major diseases would be impossible. The concept goes back to Niederhauser *et al.* (1954), Borlaug (1966) and Caldwell (1968) who proposed the application of general resistance in the CIMMYT program versus the specific or hypersensitive type. Intentionally very diverse sources of resistance for rusts and other diseases are used in the crossing program. The major sources are germplasm from national programs, advanced CIMMYT lines, germplasm received from the CIMMYT or other genebanks and CIMMYT's wide crossing program.

CIMMYT's strategy in the case of cereal rusts is to breed for general resistance (slow rusting) based on historically proven stable genes. This non specific resistance can be further diversified by accumulating several minor genes and combine them with different specific genes to provide a certain degree of additional genetic diversity. This concept is also applied to other diseases like *Septoria* leaf blotch, *Helminthosporium* spot blotch, *Fusarium* head scab etc. Following is the present situation of the CIMMYT germplasm regarding resistance to major diseases.

- Stem rust (*Puccinia graminis* f.sp. *tritici*). Resistance has been stable after 40 years of utilization of the genes derived from the variety Hope and losses due to stem rust have been negligible since the late 1960s. The resistance is based on the gene complex Sr2, which actually consists of Sr2 plus 8–10 minor genes pyramided into three to four gene combinations (Rajaram *et al.*, 1988). Sr 2 alone behaves as a slow rusting gene. Since there has been no major stem rust epidemic in areas where CIMMYT germplasm is grown, the resistance seems to be durable.
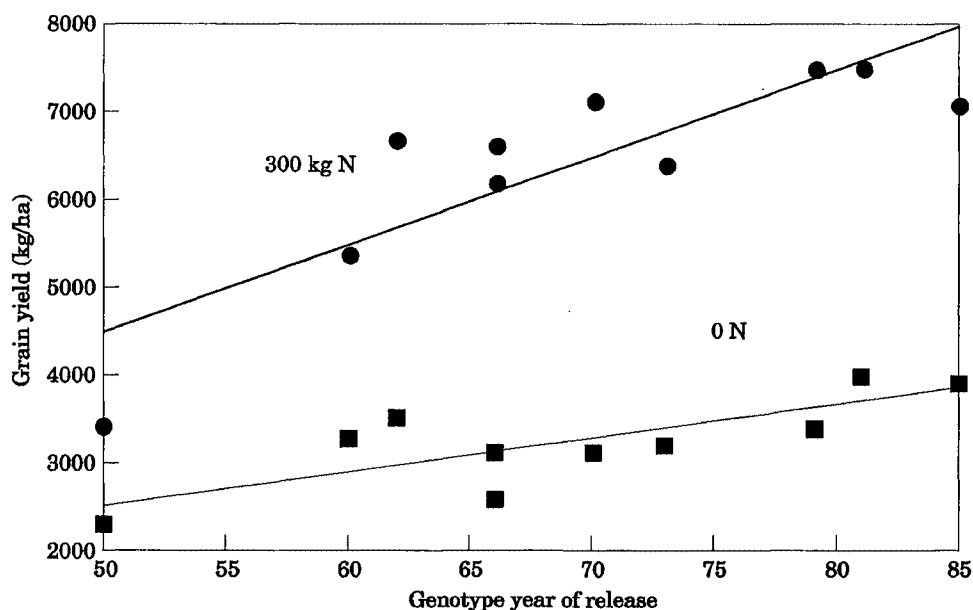

Figure 2. Grain yield of the historical series of bread wheats at Cd. Obregon, Mexico at 0 and 300 kg/ha N application. (Data from J.I. Ortiz-Monasterio *et al.*, 1995.)

- Leaf rust (*Puccinia recondita* f.sp. *tritici*). Resistance has been stabilized by using genes derived from many sources, in particular the Brazilian cultivar Frontana (Singh & Rajaram, 1992). No major epidemic has been observed for almost twenty years. Four partial resistance genes including Lr 34 give a slow rusting response and have been the reason for the containment of leaf rust epidemics in the developing world during the last 15 years wherever the varieties carry these minor genes. About 60% of the CIMMYT germplasm carries one to four of these partial resistance genes. Lr 34 is linked to Yr 18 as well as to a morphological marker leaf tip necrosis which makes the gene particularly attractive for breeders (Singh, 1992a, b). CIMMYT continues to look for new sources of partial resistance.

- Stripe rust (*Puccinia striiformis*). Slow rusting genes like Yr 18 have been identified (Singh, 1992b); however their interaction is less additive than for leaf and stem rust. More basic research is needed to understand the status of durable resistance in high yielding germplasm. The breakdown of Yr 9 in West Asia and North Africa and the present yellow rust epidemics underline the need for the release of cultivars with accumulated durable resistance.

- *Septoria tritici*: Initially all semi-dwarf cultivars developed for irrigated conditions were susceptible. Today more than eight genes have been identified in CIMMYT germplasm and two to three genes in combination provide acceptable resistance. Future activities will concentrate on pyramiding these genes and spread them more widely in the CIMMYT germplasm (Jlibene M., 1992; Matus-Tejos, 1993).

- Karnal Bunt (*Tilletia indica*). More than five genes have been identified and most of them are partially dominant. Genes providing resistance to Karnal Bunt have been incorporated into high yielding lines (Singh *et al.*, 1995).

- Powdery Mildew (*Erysiphe graminis* f.sp. *tritici*). CIMMYT's germplasm is considered to be vulnerable to this disease. The disease is absent in Mexico and the responsibility to transfer resistance genes has been delegated to CIMMYT's regional breeder in South America.

Adaptation of recent CIMMYT cultivars

CIMMYT's breeding strategy has resulted in the development of widely grown varieties, such as Siete Cerros, Anza, Sonalika, Seri 82 which at their peak were grown on several million ha. Seri 82 as released for irrigated as well as rainfed environments. Reynolds *et al.* (1994) reported that Seri 82 was the highest yielding entry in the 1st and 2nd International Heat Stress Genotype Experiment. Seri 82 can be considered as the first wheat genotype truly adapted to several ME, particularly to ME1, ME2, ME4 and ME5. A comparison between Seri 82 and a Pastor, a recently developed CIMMYT cultivar, demonstrates the progress made in widening adaptation during the last ten years. Fig. 3. shows the performance of Pastor (Pfau/Seri// Bow), in the CIMMYT's 13th Elite Spring Wheat Yield Nursery. In 50 trials grown in al 6 ME, Pastor yielded only in 8 trials significantly (P=0.01) lower than the highest yielding entry. This figure also demonstrates that Pastor has no tendency for a cross over at any yield level. While we do not reject that such a cross over may exist for some cultivars, Pastor and Seri 82 are clear examples that it is possible to combine abiotic stress tolerance with high yield

potential. Fig. 4 shows the yield difference between Seri 82 and Pastor. In only 16 out of 50 trials Seri had a higher yield than Pastor. The latter cultivar proves that breeding for wide adaptation has not yet reached its limit.

BREEDING FOR DROUGHT TOLERANCE

There has been a large transformation in the productivity of wheat due to the application of Green Revolution technology. This has resulted in a doubling and tripling of wheat production in many environments, but especially in irrigated areas. The high yielding varieties of semi-dwarf-statured wheats have continuously replaced the older tall types at a rate of 2 million ha per year since 1977 (Byerlee & Moya, 1993).

There is a growing recognition that the dissemination, application and adoption of this technology has, however, been slower in marginal environments, especially in the semiarid environments affected by poor distribution of water and drought. The annual gain in genetic yield potential in drought environments is only about half that obtained in irrigated, optimum conditions. Many investigators have attempted to produce wheat varieties adapted to these semi-arid environments, but with limited success. Others have criticized the Green Revolution technology (Ceccarelli et al., 1987) for inadequately addressing productivity constraints in semi-arid environments, although their own recommended technology has had limited impact, in particular in farmers' fields. This criticism is in clear contrast to the actual acceptance of semi-dwarf wheat cultivars in rainfed areas, since most of the 16 million ha increase in the area sown to Mexican semi-dwarf wheats in the mid 80's occurred in rainfed areas and in 1990, more than 60% of the dryland area in developing countries was planted with semi-dwarfs (Byerlee & Moya, 1993).
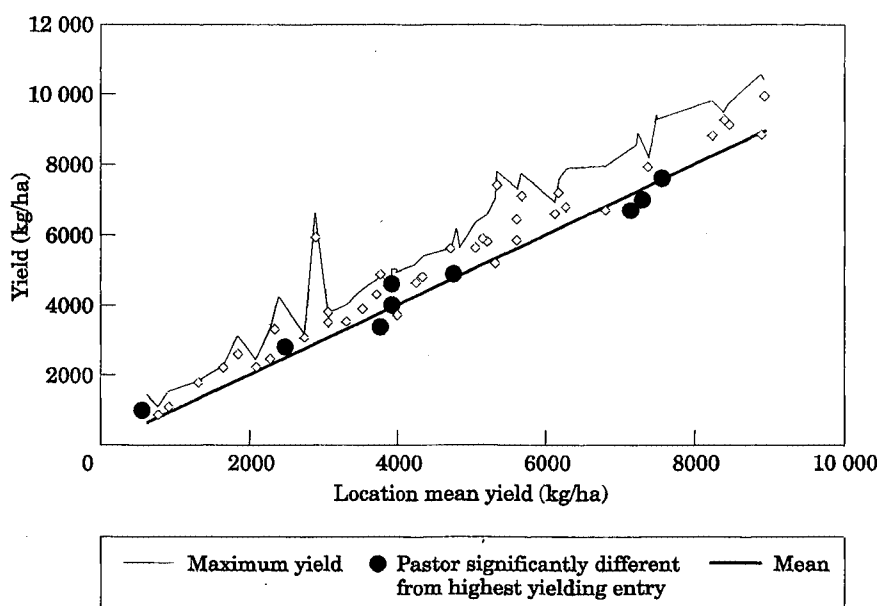

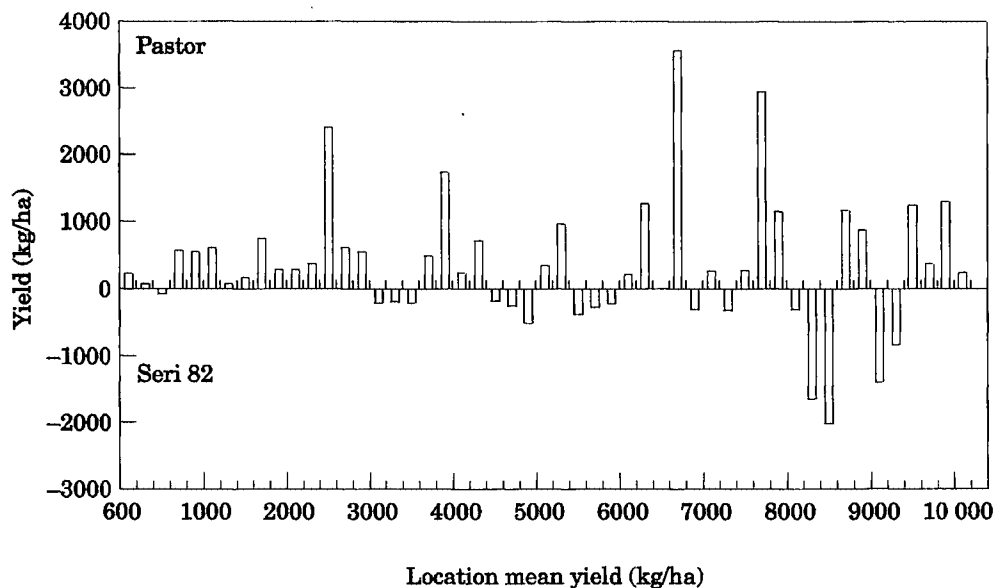Figure 3. Yield of Pastor at 50 locations of the 13th ESWYT.

Figure 4. Yield difference between Pastor and Seri 82 at 50 locations of the 13th ESWYT.

In this paper, we wish to give a presentation of why CIMMYT wheat germplasm has had considerable adaptive success in semi-arid environments. We also wish to draw conclusions regarding an effective methodology for a breeding program addressing drought-prone areas. While doing so, we do not intend to belittle any other methodology or approach followed elsewhere, but we do wish to put forward the adoption by farmers as the decisive criteria of success for any methodology.

Definition of semiarid environments and description of distinct drought patterns

In Table 1, the major global drought patterns observed in wheat production are presented (Edmeades *et al.*, 1989; Rajaram *et al.*, 1994). Through respectively dealing with spring (ME4A), facultative (ME9), and winter wheat (ME12), these three mega-environments are characterized by sufficient rainfall prior to anthesis, followed by drought during the grain-filling period. In South America, the Southern Cone type of drought (ME4B) is characterized by moisture stress early in the crop season, with rainfall occurring during the post anthesis phase. In the Indian Subcontinent type of drought stress (ME4C), the wheat crop utilizes water reserves left from the monsoon rains during the previous summer season. In the Subcontinent also irrigated wheat crop (ME1) may suffer drought due to a reduced or less than optimum number of irrigations.

Traditional methodology of breeding for drought stress

The traditional methodology, which has been practised for many years in varying forms, is typified by handling of all segregating populations under target conditions of drought, and recommends the use of local landraces in the breeding process (Ceccarelli *et al.*, 1987). What is not particularly evidenced by this methodology is any impact on

yield, farmers' adoption or final national production. This traditional methodology is based on the assumption that the agro-ecological situation facing the farmer does not vary in its expression over time. It assumes that responsiveness of varieties to improved growing conditions will not be needed. Also it presumes that there always occurs a crossover below a certain yield level under dry conditions, where modern high yielding varieties of a responsive nature would always yield less than traditional land race based genotypes. Such crossovers may occur for selected genotypes and one should always be open to the possibility that there are real "drought tolerance" traits operating at the 1 $t.ha^{-1}$ and below yield level, that adversely affect high yield potential at the $4tha^{-1}$ and higher yield levels. So far at CIMMYT such traits were not identified. In any case, cross-over would be restricted to such harsh conditions, where in fact farmers choose – rightfully so – not to grow wheat at all, but rather other known more drought tolerant crops such as barley or sorghum, or resort to grazing practices.

Alternative methodology of combining yield responsiveness and adaptation to drought.

At CIMMYT we advocate a "open-ended system" of breeding in which yield responsiveness is combined with adaptation to drought conditions. Most semi-arid environments differ significantly across years in their water availability and distribution pattern. Hence it is prudent to construct a genetic system in which plant responsiveness provides a bonus wherever environmental situations improve due to higher rainfall. With such a system, improved moisture conditions immediately translate into greater gain to the farmer. Why do we believe this can be done?

The tale of the VEERY

In the early 1980's when the advanced lines derived from the spring × winter cross Kavkaz/Buho//KAL/BB (CM33027) were tested in 73 global environments of the 15th International Wheat Yield Nursery (15th ISWYN) (Fig. 5), their performance was quite untypical compared to any previously known high yielding varieties. In later tests, we found that these lines, called VEERY's, carry the 1B/1R translocation from rye, and that general performance of such germplasm was superior not only in high-yielding environments but particularly under drought conditions (Villareal et al., 1995, Table 3). From the VEERY cross 43 varieties were released, excluding those released in Europe.

However, in addition to the creation of a new class of superior germplasm, there is an important lesson in breeding to be learned here. The VEERY's represent a genetic system in which high-yield performance in favourable environments and adaptation to drought could be combined in one genotype. The two genetic systems are apparently not always incompatible, although others have claimed that their combination would not be possible. Based on this revelation, it is possible to hypothesize a plant system in which efficient input use and responsiveness to improved levels of external inputs (in this case available water) can be combined to produce germplasms for marginal (in this case semi-arid) environments, that at least maintain minimum traditional yields and express dramatic increases whenever the environment improves.
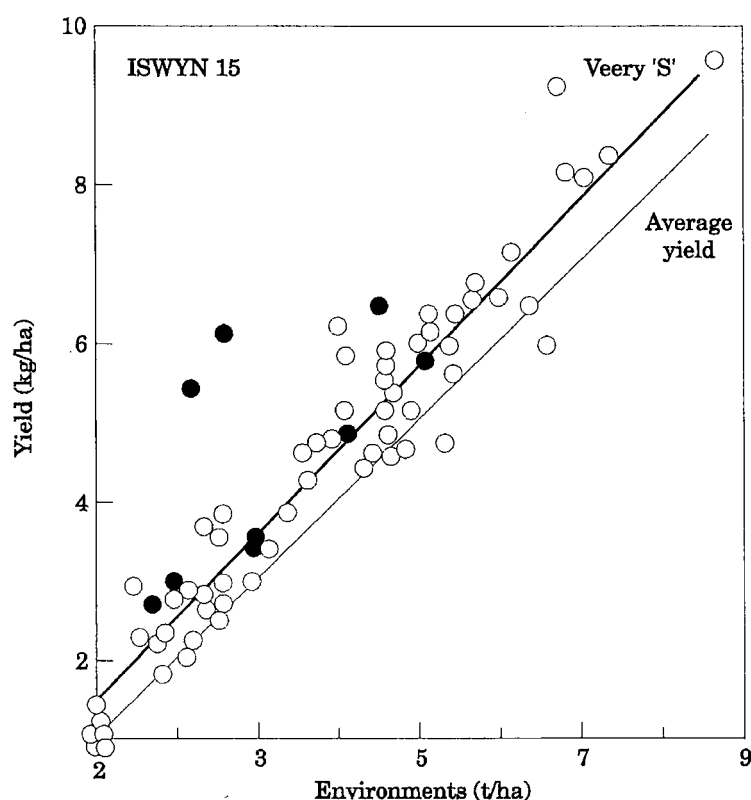
Figure 5. Performance of VEERY in 73 Global environments (ISWYN 15).

Evidence supporting promotion of this methodology

1. By the mid 1980's CIMMYT bred germplasm occupied 45% of the semiarid wheat areas with rainfall between 300–500 mm, and 21% of the area less than 300 mm (Morris et al., 1991), including large tracks in West Asia/North Africa (WANA). By 1990, 63% of the dryland areas, in especially ME4A and ME4B, was planted with semi-dwarf wheats (Byerlee & Moya, 1993), many carrying the 1B/1R translocation. This represents clear acceptance by farmers, who widely adopted the new responsive germplasm over their traditional varieties. The positive trend among the final users of our products can not be ignored. Indirectly, it supports our view that the modern genotypes have adaptation to ME4A and ME4B drought areas while expressing high yields in improved conditions.

2. To support the above assumptions, an experiment was conducted to determine how the most modern and widely (spatially) adapted germplasm compared to commercial germplasm from countries representing the Mediterranean region (ME4A), the Southern Cone of South America (ME4B) and the Indian Subcontinent (ME4C), under conditions artificially simulating those three MEs (Calhoun et al., 1994; Tables 4, 5). The most widely (spatially) adapted CIMMYT

TABLE 3. Effect of the 1BL/1RS translocation on yield characteristics of 28 random F2-derived F6 lines from the cross Nacozari 76/Seri 82 under reduced irrigation conditions.

Plant characteristics	1BL/1RS	1B	Mean diff.
Grain yield	4945	4743	202[*]
Above-ground biomass at maturity (t/ha)	12600	12100	500[*]
Grains/m^2	14074	13922	152NS
Grains/spike	43.5	40.6	2.9[*]
1000-grain weight (g)	37.1	36.5	0.5[*]

Source: Villareal *et al.* (1995). NS: Not significant   *Significant at the 0.05 level

lines outyielded the commercial varieties in all artificially simulated environments. The recent adoption trend of CIMMYT germplasm in these difficult marginal environments supports the model of input efficiency/input responsiveness.

3. The story of Nesser

Nesser is an advanced line with superior performance in drought conditions bred at CIMMYT/Mexico and. identified at ICARDA/Syria. The cross combines a high yielding CIMMYT variety Jupateco and a drought tolerant Australian variety W3918A. The performance of Nesser in WANA's ME4A environments has been widely publicized (ICARDA, 1993), and the line is considered by ICARDA to represent a uniquely drought tolerant genotype. However, it was selected at CIMMYT/Mexico under favourable environments, and carries a combination of input efficiency and high yield responsiveness. It performs similarly to the VEERY lines in the absence of rust.

Based on the above evidence, our proposed operational methodology is to combine input efficiency and input responsiveness.

Application

A breeding scheme that we use to achieve the combination of the two genetic systems is described below. Two contrasting selection environments are alternated, allowing alternate selection for input efficiency and input responsiveness.

TABLE 4. Wheat genotypes representing adaptation to different moisture environments.

ME$_1$	Irrigation	Super Kauz, Pavon 76, Genaro 81, Opata 85
ME$_4$A	(Mediterranean)	Almansor, Nesser, Sitta, Siete Cerros
ME$_4$B	(Southern Cone)	Cruz Alta, Prointa Don Alberto, LAP1376, PSN/BOW CM69560
ME$_4$	(Subcontinent)	C306, Sonalika, Punjab 81, Barani

Source: Calhoun *et al.* (1994).

TABLE 5.   Grain yields of selected wheat genotypes grouped by adaptation and tested under moisture regimes in the Yaqui Valley, Mexico, 1989–90 and 1990–91.

Adaptation group		Full irrigation[1]	Late drought[2]	Early drought[3]	Residual moisture[4]
ME[1]	Irrigation	6636 a*	4198 a	4576 a	3032 a
ME[4]C	Mediterranean	6342 b	3990 ab	4390 b	2883 b
ME[4]B	Southern Cone	5028 c	3148 bc	4224 b	2359 c
ME[4]C	Subcontinent	4778 c	3245 bc	3657 c	2704 b

Source: Calhoun et al. (1994)
[1] received 5 irrigations; [2] received 2 irrigations early before heading; [3] received one irrigation for germination and two post heading; [4] received one irrigation for germination only. * Means in the same column followed by the same letter are not significantly different at P = 0.05.

F1. Crosses involving spatially widely adapted germplasm representing yield stability and yield potential, with lines with proven drought tolerance in the specific setting of either ME4A, ME4B or ME4C. Winter wheats and synthetic germplasm are emphasized.

F2. The individual plants are raised under irrigated and optimally fertilized conditions, and inoculated with a wide spectrum of rust virulence. Only robust and (horizontally) resistant plants are selected. These may represent adaptation to favourable environments.

F3, F4. The selected F2 plants are evaluated in a modified pedigree/bulk breeding system (Rajaram & van Ginkel, 1995) under rainfed conditions or very low water availability. The selection is based on individual lines rather than on individual plants. The progenies are selected based on such criteria as spike density, biomass/vigour, grains/m^2, and others (Van Ginkel et al., 1995) (Table 6). This index helps identify lines which may adapt to low water situations.

F5, F6. The selected lines from F4 are further evaluated under optimum conditions.

F7, F8. Simultaneous evaluations under optimum and low water environments. Selection of those lines showing outstanding performance under both conditions. Further evaluation in international environments is carried out for purposes of verification.

The proposed breeding methodology is supported in research published in recent years by others, not only on wheat (Ehdaie et al., 1988; Duvick, 1990, 1992; Bramel-Cox et al., 1991; Uddin et al., 1992; Zavala-Garcia et al., 1992; Cooper et al., 1994), where the importance of testing and selecting in a range of environments, including well-irrigated ones, has been shown to identify superior genotypes for stressed conditions. The methodology aims at combining input efficiency with input responsiveness, by alternating selection environments during the breeding process. This approach results in germplasm that is accepted by farmers because it translates improved environmental conditions into yield grains. The traditional methodology of only selecting under drought conditions, and narrowly relying on the landrace

TABLE 6.   Genotypic correlation (rg) between agronomic traits and final grain yield, for optimum environment (full irrigations) and reduced water regime (late drought, Mediterranean type) in wheat.

Trait	Moisture regime	
	Full irrigation	Late drought
Days to heading	0.40	0.19
Days to maturity	0.29	0.27
Grain fill period	−0.32	0.36
Height	−0.39	0.05
Peduncle length	−0.46	0.22
Relative peduncle extrusion	−0.51*	0.25
Spike length	−0.28	−0.50*
Spike m^{-2}	−0.12	0.64**
Grains/spike	0.62*	−0.42
Grains m^{-2}	0.74**	0.68**
Yield/spike	0.55*	−0.64**
1000 grain weight	0.08	−0.45
Test weight	0.13	0.05
Harvest index (HI)	0.83**	−0.39
Biomass	0.90**	0.94**
Straw yield	0.52*	0.86**
Yield / day (planting)	0.99**	0.57*
Yield / day (heading)	0.94**	0.44
Biomass / day (planting)	0.86**	0.69**
Biomass / day (heading)	0.74**	0.63**
Vegetative growth rate	0.32	0.63**
Spike growth rate	0.62**	−0.58*
Grain growth rate	0.17	−0.44

Significant at the 0.05 and 0.01** probability level, respectively.
Source: van Ginkel et al. (1995).

genotypes, does not move yield levels significantly beyond those traditionally obtained, and does not provide the farmer with a bonus yield in the "fat years".

FUTURE INTEGRATION OF RESEARCH

Yield stability and yield potential

Traxler et al. (1995) analyzed grain yield increases and yield stability of bread wheat cultivars released during the last 45 years. In the early period of the Green Revolution, when rapid yield increases occurred, variance for yield concomitantly increased. Since the early 1970's, yield stability has increased at the cost of increases in yield. However,

steady progress was made in developing varieties with improved stability, grain yield or both. For the developing world, yield stability increased since the beginning of the Green Revolution (Smale & McBride, 1996). While price policy, input supplies and environmental variation contribute more to yield stability than the genotype, the increasing yield stability reflects the emphasis given by breeders to development of germplasm with tolerance to a wider range of diseases and abiotic stresses. Sayre *et al.* (1997) concluded that from 1964 to 1990, yield potential in CIMMYT-derived cultivars increased at a rate of 67 kg ha^{-1} yr^{-1} or 0.88% yr^{-1}. The data did not suggest that a yield plateau had been reached and the performance of recently released lines, such as Attilla or Baviacora indicate that yield potential has been further enhanced. Improvements made by breeding for yield stability and adaptation may be illustrated by data for the advanced line Pastor which out-yielded the hallmark check cultivar Seri 82 in 34 out of 50 locations where the 13th Elite Spring Wheat Yield Nursery was grown (Fig. 4). The grain yield of Pastor was significantly less than the highest yielding entry at only 8 locations (Braun *et al.*, 1996). Results from CIMMYT international nurseries do not suggest that plateaus for yield or yield stability are imminent. Discussion on how to increase the yield potential of wheat often still centres around traits which contributed to the success of the Green Revolution varieties more than 30 years ago, e.g. photoperiod and dwarfing genes (Worland *et al.*, 1998; Sears, 1998). This emphasizes the long-term commitment needed to introduce genes that may radically alter the conventional phenotype of a wheat plant. This experience may serve as a reminder for those who believe that introducing new genes through transformation, which may effect the adaptation of wheat, will allow the breeder a "quick fix".

Plant nutrition

Selection for yield potential and yield stability under medium to high levels of nitrogen has indirectly increased efficiency for nutrient uptake. Recently released CIMMYT bread wheat cultivars require less nitrogen to produce a unit amount of grain than cultivars released in the previous decades (Ortiz Monasterio *et al.*, 1997). Under low N levels in the soil, N use efficiency increased mainly due to a higher N uptake efficiency, the ability of plants to absorb N from the soil. Under high N levels, there was an increase in the N utilization efficiency – the capacity of plants to convert the absorbed N into grain yield. In spite of the increased N-use efficiency of recently released wheat cultivars, the response to nitrogen of wheat production systems has been observed to be declining in many areas of Southeast Asia. In Turkey, where zinc-deficient soils are widespread, recently released winter bread cultivars have a higher Zn-uptake and consequently higher grain yield than local landraces (M. Kalayci, pers. comm.).

Physiology

A recent survey of wheat breeders suggested that research in plant physiology has had a limited impact on wheat improvement (Jackson *et al.*, 1996). A strong body of evidence now, however, indicates that physiological traits may have real potential for complementing early generation phenotypic selection in wheat. One of the more promising traits identified is canopy temperature depression (CTD). CTD refers to the cooling effect exhibited by a leaf as transpiration occurs. While soil water status has a major influence on CTD, there are strong genotypic effects under well-watered,

heat-stressed or drought-stressed conditions. CTD gives an indirect estimate of stomatal conductance, and is a highly integrative trait being affected by several major physiological processes including photosynthetic metabolism, evapo-transpiration, and plant nutrition. CTD and stomatal conductance, measured on sunny days during grain filling, showed a strong association with the yield of semi-dwarf wheat lines grown under irrigation, in both temperate (Fischer *et al.*, 1998), and sub-tropical environments (Reynolds *et al.*, 1994). In addition, CTD as measured on large numbers of advanced breeding lines in irrigated yield trials, was a powerful predictor of performance not only at the selection site but also for yield averaged across 15 international sites. CTD has been shown to be associated with yield differences between homozygous lines, indicating a potential for genetic gains in yield, in response to selection for CTD (Reynolds *et al.*, 1998).

Genetic resources

Three quarters of the wheat breeders recently surveyed felt that lack of genetic diversity would limit future breeding advances (Rejesus *et al.*, 1996), though genetic diversity was not considered an immediately limiting factor in most programs. This concern was greater from breeders in developing and former USSR countries (>80%) than from higher income countries (59%). Furthermore, in countries where privatization of wheat breeding programs has occurred, investments have declined in strategic germplasm development which may be risky or have importance only in the long term (McGuire, 1997).

A wide range of opinion has been expressed concerning the abundance of availability of usefully exploitable genetic variability. Allard (1996) emphasized that the most readily useful genetic resource were modern elite cultivars, since these lines possessed relatively high frequencies of favorable alleles. Rasmusson & Phillips (1997) have shown that the assumption that all genetic variability is a result of the inherent exclusive contribution by two parents, *per se*, is not necessarily true considering results from molecular analysis. They discuss mechanisms by which induction of genetic variability may involve altering the expression of genes, the possible mechanisms of single allele change, intragenic recombination, unequal crossing-over, element transpositions, DNA methylation, paramutation or gene amplification. They also stressed the possible importance of epistasis effects which may have been underestimated in the past.

Introduction of genetic variability from distantly related wheat cultivars, or related or alien species, has often been specifically aimed at the introduction of simply inherited traits (e.g. genes for disease resistance), but has appeared to be of limited value in quantitative trait improvement. Cox *et al.* (1997) incorporated genes for leaf rust resistance from *Triticum tauschii* into *Triticum aestivum*. With two back-crosses to the recurrent wheat parent, leaf rust resistant winter wheat advanced lines with acceptable quality and equal in yield to the highest yielding commercially grown cultivars were identified. In addition, it has been postulated that since recombination between the D genomes of *T. aestivum* and *T. tauschii* occurred at a level similar to that in an intraspecific cross (Fritz *et al.*, 1995), *T. tauschii* could be considered another primary source of genes for wheat improvement.

The number of wheat/rye translocations that have had a significant impact on wheat improvement is actually small. The majority of the 1BL.1RS translocations occurring in more than 300 cultivars worldwide can be traced to one German source and all 1AL.1RS translocations, widely present in bread wheat cultivars grown in the Great Plains of the US, trace to one source, "Amigo" (Schlegel, 1997a,b; Rabinovich, 1998). Other translocations carry genes for copper efficiency (4BL.5R) and Hessian fly resistance (2RL.2BS, 6RL.6B, 6RL.4B, 6RL.4A; McIntosh, 1993). Chromosome 2R and 7R enhance zinc efficiency in wheat rye addition lines (Cakmak & Braun, unpublished). Considering the impacts that have come from the use of wheat/rye translocations, it may be warranted to further exploit these translocations.

While there have been reports indicating a positive effect of 1BL.1RS translocations on yield performance and adaptation (Rajaram et al., 1990), Singh et al. (1998) have determined that with Seri 82, replacing the translocation with 1BL from cv. Oasis resulted in a yield increase of 3.4 and 5.0% in irrigated and moisture stress conditions, respectively. A further increase in grain yield in disease free conditions of about 5% was observed in the irrigated trials through the introgression of 7DL.7Ag translocation carrying the Lr19 gene (from Agropyron elongatum). This yield increase was attributed to higher rate of biomass production in the 7DL.7Ag lines. However, under moisture stress condition 7DL.7Ag lines were associated with a 16% yield reduction, possibly due to excessive biomass production in early growth stages. This would suggest that the effect of the 1BL.1RS translocation is genotype specific and 7DL.7Ag could be a useful translocation for enhancing the yield potential at least in irrigated conditions.

Recent efforts to generate newly accessible genetic diversity has involved the reconstitution of hexaploid wheat by producing 'synthetic wheat' by crossing durum wheat (Triticum turgidum), the donor of the A and B genomes, with Ae. tauschi, the donor of the D genome (Mujeeb-Kazi et al., 1996). Villareal (1995) and Villareal et al. (1997) showed that lines, derived after two backcrosses to T. aestivum, showed increased morpho-agronomic variation, and resistance to Karnal bunt (Tilletia indica) and scab (Fusarium graminearum). Under full irrigation in northwestern Mexico, the yield potential of this material was nearly 8 t ha^{-1}. When tested under drought conditions for two years, nearly all of the synthetic derivatives had a significantly higher 1000-kernel weight, with grain yield varying between 84 and 114%, when compared with the bread wheat checks.

It is likely that for no other crop have more crosses been made, or recombinations occurred to break linkages, than with wheat. The more focused a breeding objective may be, the more restricted a breeder may be in the choice of suitable parents. With increased understanding of the inheritance of a trait, selection strategies may be better targeted. With yield, a complex trait still not well understood genetically or physiologically, the use of genetically diverse material will continue to be a prime genetic source for increasing yield potential. As long as breeders have no other readily accessible tools, genetic diversity and the opportunity for its recombination through crossing will be important to break undesired linkages and increase the frequency of desirable alleles. Future breakthroughs in yield potential will likely come from such genetically diverse crosses.

Hybrid wheat

When farmers or breeders discuss strategies for increasing wheat yields, hybrid wheat is often mentioned as an alternative. Pickett (1993) and Pickett & Galwey (1997), however, evaluating 40 years of wheat hybrid development concluded that hybrid wheat production is not economically feasible because of (a) limited heterotic advantage, (b) lack of advantage in terms of agronomic, quality or disease resistance traits, (c) higher seed costs and, probably most importantly, (d) heterosis could be "fixed" in polyploid plants and consequently hybrids would have no advantage over inbred lines. The use of hybrid crops are usually targeted to higher yield potential environments. Results from South Africa (Jordaan, 1996), however, show that hybrids out-yield inbred lines by 15% at a 2 t ha^{-1} mean production potential when narrow row spacing and low seeding rates (<25 kg ha^{-1}) are used. Mean grain yield of hybrids tested in the Southern Regional Performance Nursery (SRPN), across locations in the southern Great Plains, were significantly higher than for inbred lines (Peterson et al., 1997). Bruns & Peterson (1998) calculated a yield advantage of hybrid wheat at between 10 to 13% and attributed this advantage, in part, to better temporal and spatial stability and improved tolerance to heat. In contrast, recent reports of hybrid performance in Europe indicate lower levels of heterosis (5 to 12%) (Eavis et al., 1996). Gallais (1989) stated that provided overdominance is of little importance in wheat, in the long term, inbred line development will be more effective than F$_1$ hybrids. If biotechnological methods can identify increased expression of heterosis by more effective selection of favorable alleles, this impact will likely have equal advantage to inbred and hybrid development. Whether hybrids have a higher absolute yield potential than inbred lines has to be seen in light of inbred bread wheat cultivars with an observed grain yield of 17 t ha^{-1} (Hewstone, 1997).

Biotechnology

Techniques such as doubled haploids were considered "biotechnology" ten years ago, but have become an applied routine in many programs. The potential of biotechnology has been discussed elsewhere (Sorrells & Wilson, 1997; Snape, 1998) and will be part of many presentations at this symposium. We will rather look at the application of biotechnology in today's breeding programs. Lack of genetic polymorphism in crops like wheat and soybeans and the consequent problems to identify molecular markers have been a major limitation to the impact of marker assisted selection (MAS) in wheat breeding. The identification of a high number of polymorphisms in single sequence repeats (SSR) should therefore greatly enhance the potential to find molecular markers in wheat.

Conventional plant breeders adopt breeding methods which increase their breeding efficiency but are conservative when making methodological changes. In a small survey of wheat programs having unrestricted access to new biotechnological methods, few research programs, and no main-line wheat breeding programs, routinely use MAS or quantitatively inherited trait loci (QTL). Limitation in use is due to lack of markers for traits of interest, population specificity of a given marker, or their relatively high costs when compared with conventional selection techniques. These limitations may lessen in the next decade.

Modern cultivars are the product of recombinations among the high number of landraces in their pedigrees (Smale & McBride, 1996). Direct use of landraces in contemporary breeding programs, however, is often considered only as a source for qualitatively inherited traits. Tanksley & McCouch (1997) argue that the lack of success from crosses involving landraces for the improvement of grain yield, was mainly due to evaluation on a phenotypic basis, an imprecise indicator of genetic potential. Analysis of QTL have revealed that loci controlling a quantitative inherited trait do not equally contribute to the observed variation for the trait and often few QTL explain most of the observed variation. In rice, QTL for yield were identified in a wild, low yielding relative. After introgression into modern hybrid rice cultivars, yield increases of 17% compared to the original hybrid were observed. Based on the observed gains, Tanksley & McCouch (1997) identify the need to more thoroughly evaluate exotic germplasm. Those accessions most distinct from modern cultivars may contain the highest number of unexploited, potentially useful alleles.

The comparative genetic mapping of cereal genomes has identified a vast amount of conserved linearity of gene order (Devos & Gale, 1997). This observation will likely accelerate the application of QTL in wheat, as well as aid in the identification of genes required for introgression from alien species. Considering the low number of loci tagged today in wheat, the problems related to developing a high-density map for wheat (Snape, 1998) and consequently the limited progress to identify QTL in wheat for yield, we believe that the impact from this linearity on wheat improvement will be significant.

Wheat has been successfully transformed for herbicide resistance and high molecular weight (HMW) glutenins, using both the ballistic and *Agrobacterium tumefaciens* systems (Cheng *et al.*, 1997). Barro *et al.* (1997) inserted two additional HMW glutenin subunits, 1Ax1 and 1Dx5, and observed a stepwise improvement of dough strength. Altpeter *et al.* (1996) introduced 1Ax1 into Bobwhite and increased total HMW glutenin subunit protein by 71% over Bobwhite. However, the affects of transformation are not necessarily additive as was shown by Blechl *et al.* (1998) who identified trangenics for HMW glutenins that also exhibited decreased accumulation due to transgene-mediated suppression.

Conclusion

The challenge to produce 1 billion tons of wheat annually within the next 25 years is formidable and can only be met by a concerted action of scientists involved in diverse disciplines – agronomy, pathology, physiology, biotechnology, breeding, as well as economics and politics. We are optimistic that this target will be met. Today, funds are often directed from breeding towards biotechnology, often due simply to the novelty required for publication. Eventually, transformation may be a valuable technique to alter the performance of a genotype. However, at least during the next decade, the simple decision of a breeder in the field to "keep or discard" will contribute more to yield increase than any other approach. In conclusion, we agree with Ruttan (1993) who stated that "at least for the next two decades to come, progress through conventional breeding will remain the primary source of growth in crop and animal production".

REFERENCES

Allard RW. 1996. Genetic basis of the evolution of adaptedness in plants. *Euphytica* **92**: 1–11.

Altpeter FV, Vasil V, Srivastava V, Vasil IK. 1996. Integration and expression of the high-molecular-weight glutenin subunit 1Ax1 gene into wheat. *Nature Biotechnology* **14**: 1155–1159.

Barro F, Rooke L, Bekes F, Gras P, Tatham AS, Fido R, Lazzeri PA, Shewry PR, Barcelo P. 1997. Transformation of wheat with high molecular weight subunit genes results in improved functional properties. *Nature Biotechnology* **15**: 1295–1299.

Blechl AE, Altenbach BSB, Le HQ, Gras PW, Bekes F, Anderson OD. 1998. Genetic transformation can be used to either increase or decrease levels of wheat HMW-glutenin subunits. Abstracts of 21st HRWWWW, Jan. 28–30, Denver, CO. USDA-ARS, University of Nebraska, Lincoln, NE.

Borlaug NE. 1995. Wheat Breeding at CIMMYT. Commemorating 50 years of research in Mexico for global wheat improvement. *Wheat Special Report* **29**: IV–VI.

Borlaug NE. 1966. Basic concepts which influence the choice of methods for use in breeding for diverse resistance in cross pollinated and self pollinated crop plants. In: HD Gerold *et al.* (eds). *Breeding Pest Resistant Trees*. Pergamon Press, Oxford.

Bramel-Cox PJ, Barker T, Zavala-Garcia F, Eastin JD. 1991. Selection and testing environments for improved performance under reduced-input conditions. In: *Plant breeding and sustainable agriculture: considerations for objectives and methods. CSSA Special Publication* No. 18. CSSA and ASA, Madison, USA, 29–56.

Braun H-J, Pfeiffer WH, Pollmer WG. 1992. Environments for selecting widely adapted spring wheat. *Crop Science* **32**: 1420–1427.

Braun H-J, Rajaram S, van Ginkel M. 1996. CIMMYT's approach to breeding for wide adaptation. *Euphytica* **92**: 147–153.

Braun H-J, Ekiz H, Eser V, Keser M, Ketata H, Marcucci G, Morgounov AI, Zencirci N. 1998. Breeding priorities of winter wheat programs. In: Braun H-J, Altay F, Kronstad WE, Beniwal SPS, McNab A (eds). *Wheat: Prospects for Global Improvement. Proc. of the 5th Int. Wheat Conf., Ankara, Turkey. Developments in Plant Breeding, Vol.* **6**. Dordrecht: Kluwer.

Brown LR. 1997. Can we raise grain yields fast enough? *World Watch* **Jul/Aug 1997**: 8–18.

Bruns R, Peterson CJ. 1998. Yield and stability factors associated with hybrid wheat. *Euphytica* **100**: 1–5.

Bull JK, Cooper M, Basford KE. 1994. A procedure for investigating the number of genotypes required to provide a stable classification of environments. *Field Crops Research* **38**: 47–56.

Byerlee D, Moya P. 1993. *Impacts of international wheat breeding research in the developing world, 1969 – 90.* Mexico: CIMMYT.

Caldwell RM, 1968. Breeding for general and/or specific plant disease resistance. In: *Proceedings of the 3rd International Wheat Genetics Symposium,* Canberra, Australia.

Calhoun DS, Gebeyehu G, Miranda A, Rajaram S, van Ginkel M. 1994. Choosing evaluation environments to increase wheat grain yield under drought conditions. *Crop Science* **34**: 73–678.

Ceccarelli S, Nachit MM, Ferrara GO, Mekni MS, Tahir M, Van Leur J, Srivastava JP. 1987. Breeding strategies for improving cereal yield and stability under drought. In: Srivastava JP, Porceddu E, Acevedo E, Varma S (eds). *Drought tolerance in winter cereals.* New York: Wiley, 101–104.

Ceccarelli S. 1989. Wide adaptation: How wide? *Euphytica* **40**: 197–205.

Cheng M, Fry JE, Pang S, Zhou H, Hironaka CM, Duncan DR, Conner TW, Wan Y. 1997. Genetic transformation of wheat mediated by *Agrobacterium tumefaciens*. *Plant Physiology* **115**: 971–980.

CIMMYT. 1996. *CIMMYT 1995/96 World Wheat Facts and Trends.* Mexico: CIMMYT.

Cooper M, Byth DE, Woodruff DR. 1994. An investigation of the grain yield adaptation of CIMMYT wheat lines to water stress environments in Queensland. II. Classification analysis. *Agriculture Research* **45**: 985–1002.

Cox TS, Bequette RK, Bowden RL, Sears RG. 1997. Grain yield and bread making quality of wheat lines with the leaf rust resistance gene Lr41. *Crop Science* 37: 154–161.

Devos KM, Gale MD. 1997. Comparative genetics in the grasses. *Plant Molecular Biology* 35: 3–15.

Duvick DN. 1990. Ideotype evolution of hybrid maize in the USA, 1930–1990. In: *ATTI Proceedings, Vol. II, National maize conference; research, economy, environment. Grado (GO)- Italy September 19-20-21, 1990*. Bologna, Italy: Centro regionale per la sperimentazione agraria, pozzuolo del friuli edagrocole s.p.a., 557–570.

Duvick DN. 1992. Genetic contributions to advances in yield of U.S. maize. *Maydica* 37: 69–79.

Duvick D N. 1996. Plant breeding, an evolutionary concept. *Crop Science* 36: 539–548.

Eavis RM, Batchelor SE, Murray F, Walker KC. 1996. Hybrid breeding of wheat, barley and rye: Development to date and future prospects. *Research Review*, No. 35. London: Home-Grown Cereals Authority.

Edmeades GO, Bolanos J, Lafitte HR, Rajaram S, Pfeiffer W, Fischer R A. 1989. Traditional approaches to breeding for drought resistance in cereals. In: Baker FWG (ed.). *Drought resistance in cereals*. Paris: ICSU and Wallingford, England: CAB International, 27–52.

Ehdaie B, Waines JG, Hall AE. 1988. Differential responses of landrace and improved spring wheat genotypes to stress environments. *Crop Science* 28: 838–842.

Fischer RA, Rees D, Sayre KD, Lu Z, Condon AG, Larque-Saavedra A, Zeiger E. 1998. Wheat yield progress is associated with higher stomatal conductance, higher photosynthetic rate and cooler canopies. *Crop Science* (In Press).

Fritz AK, Cox TS, Gill BS, Sears RG. 1995. Molecular marker-facilitated analysis of introgression in winter wheat x *Triticum tauschii* populations. *Crop Science* 35: 1691–1695.

Gallais A. 1989. Lines versus hybrids – The choice for the optimum type of variety. *Vorträge fur Pflanzenzuchtung* 16, Berlin: Paul Parey, 69–80.

Hewstone MC. 1997. Los cambios geneticos y agronomicos que incrementaron el rendimiento de trigo en Chile. *Explorando altos rendimientos de trigo. Oct. 20–23, 1997*. La Estanzuela, Uruguay: INIA and CIMMYT.

ICARDA. 1993. *Cereal Program. Annual Report for 1992*. Aleppo: ICARDA.

Jackson P, Robertson M, Cooper M, Hammer G. 1996. The role of physiological understanding in plant breeding: from a breeding perspective. *Field Crops Research* 49: 11–37.

Jlibene M, Gustafson JP, Rajaram S. 1992. A field disease evaluation method for selecting wheat resistant to *Mycosphaerella graminicola*. *Plant Breeding* 108: 26–32.

Jordaan JP. 1996. Hybrid wheat. Advances and challenges. In: Reynolds MP, Rajaram S, McNab A (eds). *Increasing Yield Potential in Wheat: Breaking the barriers*. Mexico: CIMMYT, 66–75.

Kronstad WE. 1998. Agricultural development and wheat breeding in the 20th century. In: Braun H-J, Altay F, Kronstad WE, Beniwal SPS, McNab A (eds). *Wheat: Prospects for Global Improvement. Proceedings of the 5th International Wheat Conference, Ankara, Turkey. Developments in Plant Breeding*, vol. 6. Dordrecht: Kluwer, 1–10

Matus-Tejos IA. 1993. Genetica de la resistencia a *Septoria tritici* en trigos harineros. Tesis de Maestria en Ciencia (M.Sc Thesis), Montecillo, Mexico.

McGuire S. 1997. The effects of privatization on winter-wheat breeding in the UK. *Biotechnology and Development Monitor* 33 (Dec.): 8–11.

McIntosh R. 1993. Catalogue of gene symbols for wheat. In: Li ZS, Xin ZY (eds). *Proceedings of the 8th International Wheat Genetics Symposium, Beijing*. Beijing: China Agric. Scientech Press, 1333–1500.

Mitchell DO, Onco MD, Duncan RD. 1997. *The world food outlook*. Cambridge: Cambridge University Press.

Morris M.L, Belaid A, Byrelee D. 1991. Wheat and barley production in rainfed marginal environments of the developing world. *Part I of 1990–91 CIMMYT world wheat facts and trends*. Mexico: CIMMYT.

Mujeeb-Kazi A, Rosas V, Roldan S. 1996. Conservation of the genetic variation of *Triticum tauschii* (Coss.) Schmalh. (*Aegilops squarrosa* auct. non L.) in synthetic hexaploid wheats (*T.*

turgidum L. s. lat. X *T. tauschii*; 2n=6x=42, AABBDD) and its potential utilization for wheat improvement. *Genetic Resources and Crop Evolution* **43**: 129–134.

Niederhauser JS, Servantes J, Servin L. 1954. Late blight in Mexico and its implications. *Phytopathology* **44**: 406–408.

Ortiz-Monasterio JI, Sayre KD, Rajaram S, McMahon M. 1995. Genetic progress of CIMMYT's bread wheat germplasm under different levels of nitrogen. I. Grain yield and nitrogen use efficiency.

Ortiz-Monasterio JI, Sayre K.D, Rajaram S, McMahon M. 1997. Genetic progress in wheat yield and nitrogen use efficiency under four nitrogen rates. *Crop Science* **37**: 898–904.

Peterson CJ, Moffatt JM, Erickson JR. 1997. Yield stability of hybrid vs. pureline hard red winter wheats in regional performance trials. *Crop Science* **37**: 116–120.

Pickett AA. 1993. Hybrid wheat – results and problems. *Advances in Plant Breeding*. No. 15. Berlin: Paul Parey.

Pickett AA, Galwey NW. 1997. A further evaluation of hybrid wheat. *Plant Varieties and Seeds* **10**: 15–32.

Pingali PL, Heisey PW. 1997. Cereal crop productivity in developing countries: Past trends and future prospects. In: *Global Agricultural Science Policy for the 21st Century*. 26–28 August, 1996. Melbourne, Australia.

Rabinovich SV. 1998. Importance of wheat-rye translocations for breeding modern cultivars of *Triticum aestivum* L. *Euphytica* **100**: 323–340.

Rajaram S, Singh RP, Torres E. 1988. Current CIMMYT approaches in breeding wheat for rust resistance. In: Rajaram S, Simmonds NW (eds). *Breeding strategies for resistance to the rusts of wheat*. Mexico: CIMMYT, 101–118.

Rajaram S, Villareal R, Mujeeb-Kazi A. 1990. Global impact of 1B/1R spring wheats. *Agronomy Abstracts*, ASA, Madison, USA.

Rajaram S, van Ginkel M, Fischer RA. 1994. CIMMYT's wheat breeding mega-environments (ME). In: *Proceedings of the 8th International Wheat Genetics Symposium, July 19–24, 1993*. Beijing, China.

Rajaram S, van Ginkel M. 1995. Wheat breeding methodology: international perspectives. *Proceedings of the 20th Hard Red Winter Wheat Workers Workshop*. Oklahoma City, USA. In press.

Rajaram S. 1995. Yield Stability and avoiding genetic vulnerability in bread wheat. In: Rajaram S, Hettel G (eds).Wheat Breeding at CIMMYT. Commemorating 50 years of research in Mexico for global wheat improvement. *Wheat Special Report* No. 29. Mexico: CIMMYT, 11–15.

Rasmusson DC. 1996. Germplasm is paramount. In: Reynolds MP, Rajaram S, McNab A (eds). *Increasing Yield Potential in Wheat: Breaking the barriers*. Mexico: CIMMYT, 28–35.

Rasmusson DC, Phillips RL. 1997. Plant breeding progress and genetic diversity from de novo variation and elevated epistasis. *Crop Science* **37**: 303–310.

Rees D, Sayre K, Acevedo E, Sanchez TN, Lu Z, Zeiger E, Limon L. 1993. Canopy temperatures of wheat: Relationship with yield and potential as a technique for early generation selection. *Wheat Special Report* No. 10. Mexico: CIMMYT.

Rejesus RM, van Ginkel M, Smale M. 1996. Wheat Breeder's Perspectives of Genetic Diversity and Germplasm Use. *Wheat Special Report* No. 40. Mexico: CIMMYT.

Reynolds MP, Balota M, Delgado MIB, Amani I, Fischer RA. 1994. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Australian Journal of Plant Physiology* **21**: 717–730.

Reynolds MP, Singh RP, Ibrahim A, Ageeb OAA, Larque-Saavedra A, Quick JS. 1998. Evaluating physiological traits to complement empirical selection for wheat in warm environments. *Euphytica* **100**: 85–94.

Rosegrant MW, Agcaoili-Sombilla A, Perez N. 1995. *Global Food Projections to 2020. Discussion paper 5*. Washington, DC: IFPRI.

Ruttan VW. 1993. Research to meet crop production needs: Into the 21st century. In: Buxton DR *et al.* (eds). *International Crop Science Congress I*. Madison, WI: CSSA, 3–10.

Sayre KD, Rajaram S, Fischer RA. 1997. Yield potential progress in short bread wheat in Northwest Mexico. *Crop Science* **37:** 36–42.

Schlegel R. 1997a. Current list of wheats with rye introgressions of homoeologous group 1. *Wheat Information Service* **84:** 64–69.

Schlegel R. 1997b. About the origin of 1RS.1BL wheat rye chromosome translocations from Germany. *Plant Breeding* **116:** 537–540.

Sears RG. 1998. Strategies for improving wheat grain yield. In: Braun H-J, Altay F, Kronstad WE, Beniwal SPS, McNab A (eds). *Wheat: Prospects for Global Improvement. Proc. of the 5th International Wheat Conference, Ankara, Turkey. Developments in Plant Breeding,* vol. 6. Dordrecht: Kluwer. 17–22.

Singh RP, Rajaram S. 1992. Genetics of adult plant resistance to leaf rust in "Frontana" and three CIMMYT wheats. *Genome* **35:** 24–31.

Singh RP. 1992a. Association between gene *Lr34* for leaf rust resistance and leaf tip necrosis in wheat. *Crop Science* **32:** 874–878.

Singh RP. 1992b. Genetic association of leaf rust resistance gene *Lr34* with adult plant resistance to stripe rust in bread wheat. *Phytopathology* **82:** 835–838.

Singh G, Rajaram S, Montaya J, Fuentes-Davila G. 1995. Genetic analysis of resistance to Karnal bunt (*Tilletia indica mitra*) in bread wheat. *Euphytica* **81:** 117–120.

Singh RP, Huerta-Espino J, Rajaram S, Crossa J. 1998. Agronomic effects from chromosome translocations 7DL.7Ag and 1BL.1RS in spring wheat. *Crop Science* **38:** 27–33.

Smale M, McBride T. 1996. *Understanding global trends in the use of wheat diversity and international flows of wheat genetic resources. Part 1: CIMMYT 1995/96 World Wheat Facts and Trends.* Mexico: CIMMYT.

Snape JW. 1998. Golden calves or white elephants? Biotechnology for wheat improvement. *Euphytica* **100:** 207–217.

Sorrells ME, Wilson WA. 1997. Direct classification and selection of superior alleles for crop improvement. *Crop Science* **37:** 691–697.

Tanksley SD, McCouch SR. 1997. Seed banks and molecular maps: Unlocking genetic potential for the wild. *Science* **277:** 1063–1066.

Traxler G, Falck-Zepeda J, Ortiz Monasterio JI, Sayre K. 1995. Production risk and the evolution of varietal technology. *American Journal of Agricultural Economics* **77:** 1–7.

Uddin N, Carver BF, Clutter AC. 1992. Genetic analysis and selection for wheat yield in drought-stressed and irrigated environments. *Euphytica* **62:** 89–96.

Van Ginkel M, Calhoun DS, Gebeyehou G, Miranda A, Tian-you C, Pargas Lara R, Trethowan RM, Sayre K, Crossa J, Rajaram S. 1995. Plant traits related to yield of wheat in early, late, or continuous drought conditions. *Euphytica* **100:** 109–121.

Villareal RL, Fuentes-Davila G, Mujeeb-Kazi A. 1995. Synthetic hexaploids x *Triticum aestivum* advanced derivatives resistant to Karnal bunt (*Tilletia indica* Mitra). *Cereal Research Communications* **23:** 127–132.

Villareal RL. 1995. Expanding the genetic base of CIMMYT bread wheat germplasm. In: Rajaram S, Hettel G (eds). *Wheat Breeding at CIMMYT. Commemorating 50 years of research in Mexico for global wheat improvement.* Wheat Special Report No 29. Mexico: CIMMYT, 16–21.

Villareal RL, Bañuelos O, Borja J, Mujeeb-Kazi A, Rajaram S. 1997. Agronomic performance of some advanced derivatives of synthetic hexaploids (*Triticum turgidum* x *T. tauschii*). *Annual Wheat Newsletter* **43:** 175–176.

Villareal RL, Del Toro E, Mujeeb-Kazi A, Rajaram S. 1995. The 1BL/1RS chromosome translocation effect on yield characterization in a *Triticum aestivum* L. cross. *Plant Breeding* **114:** 497–500.

Worland AJ, Appendino ML, Sayers EJ. 1994 The distribution, in European winter wheats, of genes that influence ecoclimatic adaptability whilst determining photoperiodic intensitivity and plant height. *Euphytica,* In press.

Worland AJ, Börner A, Koyrun V, Li WM, Petrovic S, Sayers EJ. 1998. The influence of photoperiod genes on the adaptability of European winter wheats. *Euphytica* **100:** 385–394.

Young C, Frey J. 1994. Grain-yield characteristics of oat lines surviving uniform and shuttle selection strategies. *Euphytica* **76**: 63–71.

Zavala-Garcia F, Bramel-Cox PJ, Eastin JD, Witt MD, Andrews DJ. 1992. Increasing the efficiency of crop selection for unpredictable environments. *Crop Science* **32**: 51–57.

Russian Links

Wheat classification
– John Percival's contribution and
the approach of the Russian school

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Abstract

J. Percival, Professor of the University of Reading, selected wheat as the object of his research. His *magnum opus The Wheat Plant*, published in 1921, was the most complete compilation of information on wheat of its time. Its special value lies in the inclusion of Percival's own research results. The first successful attempts at a more natural classification of soft wheats were made by K. Flaksberger in 1915 and J. Percival in 1921. These two independent classifications are compared. They are similar to each other in many respects, and this indicates the correctness of the system, representing significant progress in the taxonomy of soft wheat. At present, systematic sciences should also focus on the infraspecific level (genetic diversity). The study of variation has led to a more detailed insight, and has allowed the description of the complete geographical-botanical structure by an eco-geographical system of classification. The paper illustrates how these independent classifications became the basis for the contemporary classification of soft wheat. The close scientific relations between Percival and N.I. Vavilov, with respect to wheat, are documented through reproductions of their correspondence.

INTRODUCTION

John Percival's *magnum opus The Wheat Plant* (Percival, 1921) was, according to Vavilov (1923), the most complete synthesis of botanical knowledge on wheat accumulated until that time (cf. Appendix 1). Its particular value lies in the presentation of his own research results. Taking the wheat classifications of F. Körnicke (1885) and K. Flaksberger (1915) as bases, Percival added several new species. Proceeding from studies of the large diversity of soft wheat from different parts of the world that had been inaccessible to his predecessors, Percival made a successful attempt towards a natural classification of this species. For the first time in the taxonomy of wheat, not only morphological spike attributes, but also vegetative and anatomical characters were taken into account. Percival made an especially large contribution to the knowledge of Ethiopian wheats. Modern genetic research is still directed towards the search for the donors of the B and D genomes of bread wheat, which have contributed to the genetic constitution of modern bread wheat. In fact, this task was formulated by Percival. His work has stimulated many subsequent systematic and genetic studies of wheat. Letters from N.I. Vavilov to his colleagues and his scientific correspondence with Percival have been preserved in the archives of the Commission for the Conservation and Development of the Works of N.I. Vavilov in Moscow and published in several volumes (Vavilov, 1980, 1987, 1994, 1997). They are partly reproduced in Appendix 2.

INFRASPECIFIC CLASSIFICATION OF CULTIVATED PLANTS

Infraspecific classifications of cultivated plant species may be formal or informal (Hanelt & Hammer, 1995). They allow one to identify with ease areas in which particular morphological forms of a species can be found. The basic taxonomic category, however, is the species. For geobotanical investigations in wild plants, the use of infraspecific taxa is not essential. In the early days of the science of systematics the researchers concentrated on the genus level. Later on the species level was elaborated. At present, systematic sciences should also focus on the infraspecific level, which reflects the genetic diversity. The study of variation leads to a more detailed insight, and allows one to describe the complete geographical-botanical structure by an eco-geographical system of classification.

We discuss here the principles of classification of wheat, which has its peculiarities due to the anthropogenic nature of cultivated plants. So far, no comprehensive criteria for the delimitation of such species have been proposed. The reliability of such criteria may be improved only by perceiving the variability of a genus as a whole, involving also genetic studies and molecular methods.

The most recent systematic treatment of the genus *Triticum* L., which was considerably influenced by Percival's views, was provided by Dorofeev *et al.* (1979) (Table 1). This system reveals the main geographically inherent laws of the distribution of species and infraspecific taxa of wheat in the original area of development of the genus *Triticum*. The distribution of wheat species in the Ancient Mediterranean area of origin of cultivated plants is presented in Table 2 (see also Filatenko, Diederichsen & Hammer, 1999).

TABLE 1. Number of infraspecific taxa in species of the genus *Triticum*, according to the classification of Dorofeev *et al.* (1979). Adapted from Filatenko *et al.* (1998).

Species	Sub spec.	Convar.	Sub convar.	Var.	Formae	Eco-geographical groups
T. aestivum	2	3	4	194	15	23
T. aethiopicum	3	5		203		
T. araraticum	2			13		
T. baeoticum	2			61		
T. carthlicum				18	3	
T. compactum	2	3	4	96	2	9
T. dicoccoides		3		25		
T. dicoccon	4	4		64	2	12
T. durum	2	6	3	120	30	
T. ispahanicum				2		
T. jakubzineri				1		
T. karamyschevii				2		
T. macha		2	2	14		
T. monococcum				14	6	7
T. petropavlovskyi				4		
T. polonicum	2	2		41	1	3
T. sinskajae				1		
T. spelta	2	2		55		2
T. sphaerococcum				17		
T. timopheevii				4		
T. turanicum				20		2
T. turgidum		2		71		5
T. urartu				6		
T. vavilovii				7		
T. zhukovskyi				1		
Total 25	21	32	13	1054	59	63

WHEAT CLASSIFICATION BEFORE PERCIVAL (1921)

Metzger (1824), Séringe (1841) and Alefeld (1866) proposed the first infra- specific classifications of bread wheat, on the basis of which Körnicke (1885) developed his more detailed classification. The first successful attempts at a natural classification of *T. aestivum* were made by Flaksberger (1915) and Percival (1921).

It is interesting to compare these two obviously independent classifications (Table 3). Some "groups" (Percival) or "types" (Flaksberger) were insufficiently characterised, and their exact identification is not possible. However, both scientists

TABLE 2. Distribution of the species of wheat in the Ancient Mediterranean area of origin of cultivated plants (after Dorofeev et al., 1979). Adapted fromFilatenko et al. (1998).

Mediterranean (147)[†]	Sub-area		Dependent area
	Southwest Asia		Ethiopia (250)[‡]
	Anterior Asia (412)	Middle Asia (260)	
T. baeoticum (16)[§]	T. baeoticum (57) T. urartu (6) T. araraticum (13) T. dicoccoides (25)		
T. Monococcum (13)	T. monococcum (14) T. sinskajae (1)		
T. dicoccon (7)	T. dicoccon (15) T. ispahanicum (2) T. karamyschevii (3) T. timopheevii (4) T. militinae (2) T. zhukovskyi (1) T. macha (14) T. vavilovii (7)		T. dicoccon (8)[§]
T. spelta (14)	T. spelta (14)	T. spelta (19)	
T. durum (80)	T. durum (75)	T. durum (8)	
T. turanicum (4)	T. turanicum (34)	T. turanicum (7)	
T. turgidum (34)	T. turgidum (54)	T. turgidum (3) T. jakubzineri (1)	
	T. carthlicum (18)		
T. polonicum (11)	T. polonicum (14) T. sphaerococcum (17)	T. polonicum (3)	T. polonicum (6)
T. compactum (13)	T. compactum (40)	T. compactum (64)	
T. aestivum (25)	T. aestivum (59)	T. aestivum (142) T. petropavlovskyi (4)	T. aestivum (33)
			T. aethiopicum (203)

Number of taxa occuring in the given sub-area
  † number of botanical varieties per area
  §number of botanical varieties per species
  ‡Species of wheat, e.g. Ancient Mediterranean elements of northeast African flora.

used a similar approach to classify the varieties. They preferred different attributes, but nevertheless four "types" of Flaksberger correspond to four "groups" of Percival, as is explained in the heading of Table 3. Thus, for the first time, groups of soft wheat attributes described by complexes connected to geographical distribution, were allocated. This represented significant progress in the taxonomy of soft wheat. Later, these yet insufficiently clearly characterised groups or types of wheat were transferred into convarieties (Dorofeev *et al.* 1979).

VAVILOV AND THE CONTEMPORARY RUSSIAN APPROACH TO WHEAT TAXONOMY

A new grouping was proposed in N.I. Vavilov's "On the knowledge of soft wheats" (Vavilov, 1923), where he defined a programme for future classifications of wheat (cf. Appendix 1). Vavilov esteemed Percival's work highly, as can be seen from his enthusiastic letters to colleagues (Appendix 2). Vavilov's correspondence with Percival touches a broad spectrum of questions on taxonomy, genetics and phylogeny (Appendix 2). Percival donated his type samples of *T. aestivum* groups to VIR's herbarium. A special storage case was made in which they have been preserved to this day (Fig. 1).

TABLE 3.   Comparison of classifications of *Triticum aestivum* L. by K. Flaksberger (1915) and J. Percival (1921). In contrast to Percival, Flaksberger first sub-divided the species into beardless and bearded forms. The following Types (Flaksberger) and Groups (Percival) are closely related to each other: Type 1 and Group 2; Type 4 and Group 3, partially also Group 1; Types 2 and 5, and Groups 5 and 6; Types 3 and 6, and Group 7. Percival's Group 4 does not have any correspondence in Flaksberger's classifications, since these forms were not known to Flaksberger. Characteristics occurring across Groups and Types are highlighted in bold.

K. Flaksberger (1915)

Type 1. Spikes beardless, almost not tapering towards the apex. Empty glumes wide, **inflated,** closely connected with paleas (this is the reason why the seeds do not fall out). Dents of paleas crooked or simply bent. Spring and winter forms found in Turkestan and Iran.

Type 2. Beardless, not compact spikes, tapering towards the apex. Empty glumes vary from oblong and egg-shaped to narrow oblong egg-shaped (shape of an acute triangle also occurs).

Type 3. Beardless square spikes, blunt and more compact at the upper end. Almost all these **"square head"** wheats are cultivated in West Europe.

Type 4. Spikes bearded, not compact, hard; empty glumes spatulate and similar to *T. spelta.* Seeds free-threshing. Winter and spring forms grown in Turkestan and Iran. These forms are **most closely approaching to the real spelt.**

Type 5. Spikes bearded. They are absolutely identical to the beardless spikes of Type 1 with regard to their construction.

Type 6. Spikes bearded, compact, square, blunt to the upper end and more dense. They (**square head type**) are of late maturity and absolutely out of use in Russia.

TABLE 3. *Continued*

J. Percival (1921)

Group 1. Ears often quadrate, short or of medium length (6–10 cm), usually lax and **rigid**, with a somewhat brittle rachis. Spikelets, 12–20, sometimes arranged irregularly on the rachis. **Empty glumes rigid,** scabrid, often **keeled to near the base**; in bearded forms the awns of flowering glumes are short (4–6 cm), scabrid, brittle, and divergent. Grains flinty or semi-flinty, very soft (held somewhat firmly in the glumes). Endemic forms from India, Iran and Turkestan.

Group 2. Lax quadrate ears and characteristic **swollen** spikelets. Ears stiff, 9–12 cm long; awns of bearded forms stout, brittle, and scabrid; spikelets 16–20, elongated, often irregularly arranged on the rachis; grains large and generally soft. Endemic wheats of Iran and Central Asia.

Group 3. Ears 9–12 cm long, narrow, quadrate, 8–10 mm across the face and side, lax, with narrow elongated spikelets. Empty **glumes rigid and frequently keeled to the base,** lateral nerve prominent. Awns of flowering glumes 6–10 mm long, scabrid. Grains long, narrow, semi-flinty, and **firmly invested by the glumes. Rachis breaks readily, but not as brittle as in typical bearded forms of *T. spelta*.** Endemic in Iran, Bokhara, and Turkestan, and occasionally among wheats from Portugal, Spain, and Argentina.

Group 4. In several forms some of the ears of a plant are clubbed while the rest are uniformly dense throughout. Empty glumes frequently keeled to base, awns of flowering glumes of bearded forms slender and comparatively short (4–6 cm). Glumes thin and very easily separated from the rachis, grain often visible between them and readily shed. Endemic to Japanese and Chinese wheats.

Group 5. Ears lax and compressed, face considerably wider than 2-rowed side, usual density 17–21, spikelets 2–3-grained, glumes somewhat thin, grain often visible between glumes, generally flinty and of good milling quality. Group includes a large series of spring wheats, among which bearded forms are most prevalent. Very extensively cultivated in Spain, Portugal, Italy, United States, Canada, and Argentina.

Group 6. Ears similar to those of previous group, lax and compressed, 9–13 cm long, usual density 17–21; spikelets broad, 2–3-grained, with thin glumes frequently not covering the grain. Young shoots prostrate, young leaves narrow, and in many Russian forms strikingly pubescent, straw somewhat tall and slender. Bearded forms very widely distributed in Eastern Europe, also in United States and Canada, and occasionally in Western Europe.

Group 7. Young shoots prostrate or semi-prostrate, straw short and stiff, ears dense, "squarehead". Long growing period, very prolific. The majority are beardless forms. Cultivated in Western Europe.

The enormous diversity of wheat encountered in Central and Southwest Asia prompted Vavilov to revise the relative taxonomic importance of individual characters. He noticed that, despite the large diversity of varieties (as described by Körnicke), wheats endemic to a particular region show common trait complexes, characteristic for distinct areas. For example, endemic forms from the Pamir can be distinguished by the ligule and the degree of ear inflation. There are *eligulatum* forms (first found by Vavilov on Pamir in 1916), and forms with more or less inflated ears. The characters are linked. Vavilov determined the hierarchy of characters according to their taxonomic importance. In *T. aestivum* L., a complex of characters is connected, with difficult

Figure 1. Storage case for Percival's type specimens of *Triticum aestivum* groups in the N.I. Vavilov Institute of Plant Industry, St. Petersburg, Russia.

threshing and stiff ears always accompanied by, for example, rough stalks and ears, drought adaptation. This wheat, subsp. *hadropyrum* (Flaksb.) Tzvel. (Tzvelev, 1976), is typical of Southwest Asia. Types with tender ears, easy threshing ability, on the other hand, are peculiar to Europe and areas of Asia with less continental climates (subsp. *aestivum,* syn. subsp. *indoeuropaeum* Vav.). The results of such a classification for *T. aestivum* are shown in Figs 2 and 3. The Asian subspecies. *hadropyrum* contains three groups of different geographical origin:
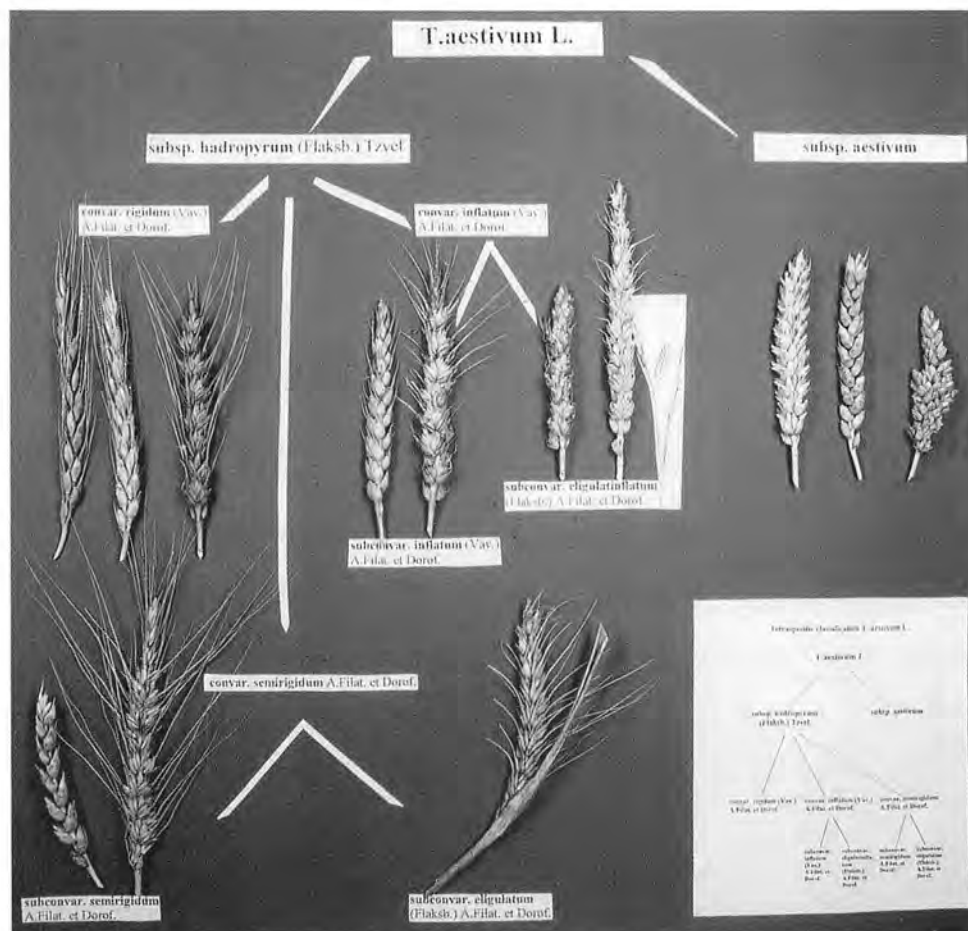
Figure 2. Infraspecific classification of *Triticum aestivum* L., according to Dorofeev *et al.* (1979). See also Fig. 3. The convarieties and subconvarieties are represented by spike samples.

1. convar. *rigidum* (Vav.) A. Filat. et Dorof. corresponds to Group 3 of Percival and Type 4 of Flaksberger;

2. convar. *inflatum* (Vav.) A. Filat. et Dorof. accordingly, to Group 2 and Type 1;

3. convar. *semirigidum* A. Filat. et Dorof. to Percival's Groups 5 and 6 and Flaksberger's Types 2 and 5, partially.

An analysis of the European (subsp. *aestivum*) and the Asian subspecies revealed that the awned varieties of *T. aestivum* mostly belong to the semi- rough-eared type of wheat.

The Asian subspecies shows a greater polymorphism. Southwest Asia is particularly an area of intense evolution of different types. The subspecies *aestivum* is phylogenetically younger, consisting of fewer, but very contrasting, eco-geographical groups.

T. aestivum L. (194)*

    subsp. *aestivum* (38)

    subsp. *hadropyrum* (Flaksb.) Tzvel. (156)

    convar *rigidum* (Vav.) A. Filat. et Dorof. (24)

    convar *inflatum*

            subconvar. *inflatum* (Vav.) A. Filat. et Dorof. (42)

            subconvar. *eligulatinflatum* (Flaksb.) A. Filat. et Dorof. (14)

    convar. *semirigidum*

            subconvar *semirigidum* A. Filat. et Dorof. (59)

            subconvar. *eligulatum* (Vav.) A. Filat. et Dorof. (17)

*Number of botanical varieties in parentheses.

Figure 3. Infraspecific classification of *Triticum aestivum* L., according to Dorofeev *et al.* (1979).

T. compactum Host has much in common with *T. aestivum* and is often included in the latter, e.g. by Mansfeld (1951) and Sinskaya (1955). It was widely cultivated in the past, it has evolved in environments similar to those of bread wheat, and it thus mirrors the polymorphism of *T. aestivum* (Fig. 4).

The development of *Triticum* L., like many other genera comprising both cultivated and wild species, took place historically in the area of the Ancient Mediterranean. Systematic studies confirmed that the greatest number of endemic taxa, and an extraordinary diversity of the variety composition, is connected with Anterior Asia (Table 2). An intensive development took place also in other sub-areas of the Ancient Mediterranean (i.e. the Mediterranean itself and Middle-Southwest Asia).

A detailed study of the botanical and genetic diversity of cultivated plants, like those of Flaksberger (1935), Percival (1926, 1927a, 1927b, 1934, 1936), Vavilov (1935) and Sinskaya (1969), allows one to characterise their areas of origin with high degree of accuracy, and to counteract the loss of biological diversity both in nature and in collections.

CONCLUSIONS

Without doubt, there are many rich genebank collections in the world, but very often the diversity of their accessions is estimated only by the number of plant samples collected. Hence, the qualitative aspect is often neglected. Through infraspecific classifications, traditional botanical taxonomy provides a scientific approach for the evaluation and maintenance of a collection, reduces the threat of genetic erosion of valuable plant properties and plant samples, and makes it possible to develop a well-grounded interpretation of the newest data of molecular biology (see Korzun *et al.*, in press).

T. compactum Host (96)

      convar. *rigidicompactum* (Kudr.) A. Filat. et Dorof. (41)

            subconvar. *rigidicompactum* A. Filat. et Dorof. (37)

            subconvar. *eligulatum* Flaksb. (4)

      convar. *inflatum* Vav. et Kob. (32)

            subconvar. *roshanum* (Korzh.) A. Filat. et Dorof. (28)

            subconvar. *bartangiense* A. Filat. et Dorof. (4)

      convar. *compactum* (23)

* Number of botanical varieties in parentheses

Figure 4. Infraspecific classification of *Triticum compactum* Host, according to Dorofeev *et al.* (1979).

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REFERENCES

Alefeld F. 1866. *Landwirtschaftliche Flora.* Berlin.

Dorofeev VF, Filatenko AA, Migushova EF, Udachin RA, Yakubtsiner MM. 1979. *Flora of cultivated plants. Vol. 1. Wheat.* Leningrad. [in Russian].

Flaksberger KA. 1915. *Determination of wheats.* Petrograd. [in Russian].

Flaksberger KA. 1935. *Wheat. Flora of Cultivated Plants.* Leningrad. [in Russian].

Filatenko AA, Diederichsen A, Hammer K. 1999. Vavilov's work on the theories of domestication of the crop plants in the Old Mediterranean Area. *Proc. Sympos. The Origins of Agriculture and the Domestication of Crop Plants in the Near East*, Aleppo: ICARDA, 9–24.

Hanelt P, Hammer K. 1995. Classifications of intraspecific variation in crop plants. In: Guarino L, Ramanatha Rao V, Reid R (eds). *Collecting Plant Genetic Diversity. Technical Guidelines.* Wallingford: CAB International, 113–120.

Körnicke F, Werner H. 1885. *Handbuch des Getreidebaues.* Vol. 1. Berlin.

Korzun V, Filatenko A, Röder M, Ganal M, Hammer K. 1999. Genetic diversity among the diploid wheats *Triticum urartu, T. baeoticum* and *T. monococcum* as revealed by microsatellite markers. *Theoretical and Applied Genetics* (in press).

Mansfeld R. 1951. Das morphologische System des Saatweizens, *Triticum aestivum* L. s.l. *Der Züchter* 21: 41-60.

Metzger J. 1824. *Europäische Cerealien.* Heidelberg.

Percival J. 1921. *The Wheat Plant: A Monograph.* London: Duckworth (photographic reprint, 1974).

Percival J. 1926. Some new varieties of wheat. *Journal of Botany.* (August.)

Percival J. 1927a. The coleoptile bundles of Indo-Abyssinian emmer wheat. *Annals of Botany* 41: No. 159.

Percival J. 1927b. The beginning of agriculture. *Nature* **2987**.

Percival J. 1934. *Wheat in Great Britain*. 1st edn. Shinfield: the author, 2nd. edn 1948. London: Duckworth.

Percival J. 1936. Cereals of Ancient Egypt and Mesopotamia. *Nature* **138**: No. 3485.

Séringe NC. 1841. *Céréales européennes*. Paris-Lyon.

Sinskaya EN. 1955. *The origin of wheat. Problems of Botany, vol. 2*. Moscow, Leningrad. [in Russian].

Sinskaya EN. 1969. *Historical geography of cultivated floras (at the dawn of agriculture)*. Leningrad: Kolos. [in Russian].

Tzvelev NN. 1976. *Cereals of USSR*. Leningrad. [in Russian].

Vavilov NI. 1923. On the knowledge of soft wheats (systematic-geographical study). *Trudy po prikladnoy botanike i selektsii* **13**: 149–257. [in Russian].

Vavilov NI. 1935. The phyto-geographical basis for plant breeding. In: *Theoretical Basis for Plant Breeding* **1**: 17-75. Moscow-Leningrad. [in Russian].

Vavilov NI. 1980. *Nikolay Ivanovich Vavilov – Scientific heritage. From the epistolary heritage (1911-1928)*. Vol. 5. M, Moscow: Nauka. [in Russian].

Vavilov NI. 1987. *Nikolay Ivanovich Vavilov – Scientific heritage. From the epistolary heritage (1929–1940)*. *1987*. Vol. 10. Moscow: Nauka. [in Russian].

Vavilov NI. 1994. *Nikolay Ivanovich Vavilov – Scientific heritage in letters (International correspondence)*. *1994*. Vol. 1. *The Petrograd period (1921–1927)*. Moscow: Nauka, 556 pp. [in Russian].

Vavilov NI. 1997. *Nikolay Ivanovich Vavilov - Scientific heritage in letters (International correspondence)*. *1997*. Vol. 2. *(1928–1930)*. Moscow: Nauka. [in Russian].

APPENDIX 1.

Excerpts from the Introduction to Vavilov's work "On the knowledge of soft wheats – a systematic-geographical study" (1923).

> "It is hardly possible to recall another plant investigated in as much detail, as the wheat species most widely distributed in cultivation, namely, *Triticum vulgare* Vill. Hundreds of separate articles and books have been written about wheats. In front of us, we have the recently published, most complete (by 1922) study of wheats by the English botanist Percival, a world monograph of wheats, the result of more than 20 years of persistent work...
>
> Nevertheless, despite all the great work done during the last two centuries, it seems that this plant demonstrates how far our knowledge is, even for the main cultivated plant species, from the complete revelation of their botanical structure...
>
> Truly, we are in a period when the old Linnean species, with closer exact studies, break down into a number of independent forms; when these same old Linnean species have to be understood as complex compound systematic units, as a genus or even a whole family, if one takes into account the large number of diverse forms embraced by the Linnean species. It is not without justification to try to really establish systems of forms within the limits of Linnean species."

APPENDIX 2.

From letters of N.I. Vavilov to his colleagues:

Vavilov, 1980, page 43. To Olga Vjacheslavovna Jakushkina[1]

England, 30. 11. 1921.

... "I visited Percival. Saw Abyssinian wheats and I hope to receive about 200 Afghani, Spanish and Portuguese wheats. If everything I collected will arrive, perhaps our cereals collection will become the best in the world.

I have learned about one extremely important fact: *T. persicum* anatomically belongs to the group of Abyssinian *dicoccum* (4–6 vascular bundles). This is a fact of major importance. Perhaps it is "African" also by origin.

A trip to Africa becomes inevitable. The book of J. Percival is, perhaps, the best thing that I shall bring along with me..."

Yours, Vavilov

Vavilov, 1987,
 page 124. To Olga Konstantinovna Fortunatova[2]

July 21, 1931

.... "I just returned from London, where I visited Percival. He also persistently continues to work. It is a pleasure to see how people at the age of 70 still go forward persistently and go on the defined ways. He carries out many crosses with *Aegilops*.

In our crossings it is now necessary to consider parallelism between *durum* and soft wheats and, in particular, in awn characters. Further on, great attention should be paid to "*sphaerococcum*". Please, finish [the work on] density of inflorescences by all means, this is prime business; these characters are too important..."

Nikolay Ivanovich Vavilov – Scientific Heritage in Letters. The international correspondence. Volume 1. The Petrograd period. 1921–1927. Moscow, Nauka, 1994.

---

1   Jakushkina, Olga Vjacheslavovna. Agronomist, worked with N.I. Vavilov in the Saratov Agricultural Institute during these years.
2   Fortunatova, Olga Konstantinova (1898–1941). Employee of VIR from 1923, worked in the Central Asian branch of VIR, in the Department of Geography.

Page 71. To D.N. Borodin[1]

March 2, 1923

"The wheat material received from Algeria and from Abyssinia revealed a mass of things of paramount importance for us, that did not come in mind neither to Martin, nor to Clark, not even to Percival, who recently published a wonderful monograph on wheat."

Letter of N.I. Vavilov to J. Percival

Vavilov, 1994, page 178. To J. Percival

October 24, 1927

Dear doctor Percival,

"....request to send us samples of wheat from Cashmere and Indostan[2]...

...also thanks for the samples of *Vicia faba*..."

Letters of J. Percival to N. Vavilov (Vavilov, 1994).

Original letter reproduced in Fig. 5

Reading, England, February 16, 1924

Dear Professor Vavilov,

I was very pleased to have your paper on the Soft Wheats which came a day or two ago. It is excellent and extends our knowledge of them considerably.

I am interested to see that you consider Black Persian as a separate species. I have no doubt that it is very closely allied to *T. dicoccum*. The chromosome number, the peculiar character of the hairs on its leaves exactly like those of *dicoccum*; the form of its grain; 3–4 nerved coleoptiles (readily seen in cross sections of germinating grains) exactly like the Abyssinian and Indian *dicoccum*s all point to this conclusion.

Please thank Mr. Popoff for so kindly sending his paper on the *Durum* Wheats. It is very interesting, but I am sorry to disagree with his views on *T. pyramidale*. This wheat has nothing to do with *T. durum*. It is somewhat

1 Borodin, Dmitriy Nikolaevich. Florist, entomologist. Head of the New York Bureau of Applied Botany of the [Soviet] State Institute of Experimental Agronomy from 1922 to 1927. Supported Vavilov in introducing useful plants to Russia, in establishing contacts with foreign scientists, and in providing foreign literature to Russia.
2 Receipt of these samples was acknowledged in Vavilov's letter of December 3, 1927.

5]

Faculty of Agriculture and Horticulture,

Prof. JOHN PERCIVAL, Sc.D.   UNIVERSITY COLLEGE, READING.
(Professor of Agricultural Botany).

.Feb.-16 .th._____1924

- Dear Professor Vavilov.
                I was very pleased to have your paper on the
Soft Wheats which came a day or two ago. It is excellent and extends
our knowledge of them considerably.
                I should be very grateful if you would be so good as send
me a few grains and ears if possible of the varieties which I name on
the accompanying sheet. I am very anxious to see and study these and
grow them.

                I am interested to see that you consider Black Persian an a separat
species. I have no doubt that it is very closely allied to T. dicoocum:
The chromosome number,; the peculiar character of the hairs on its leaves
exactly like those of dicoccum; the form of its grain; 3-4 nerved coleop
(readily seen in cross setions of germinating grains) exactly like the
Abyssinean and Indian dicoccums all point to this conclusion.

                Please thank Mr. Popoff for so kindly sending his paper on the
Durum Wheats. It is very interesting , but I am sorry to disagree
with his views on T. pyramidale. This wheat has nothing to do with
T. durum. It is somewhat allied to dicoccum- the Abyssinean form-
but I thought nearer to Turgidum in some of its characters. It might
without much error be grouped as a compactum form of turgidum.
separate it at once from durum (which always has glabrous leaves, except
when hybridised) and a very different form and texture of grain.
                The placing of Arraseita in durums is certainly an error.
It belongs to pubescent leaved dicoccum group, with others from Abyss
                I have been busy with the cytology of the wheats and
species of Aegilops and their hybrids.
Aegilops cylindrica has 7 (haploid) chromosomes, A. ventricosa and
A. ovata 14 (haploid) . These I feel have in some way contributed
to the origin of the Soft Wheats.
                I often think of you and wish you were nearer. I hope that
you and your wife and son are well.
                Your s very sincerely

Figure 5. Original letter of Percival to Vavilov, February 16, 1924. See also Appendix 2.

The following notes were translated from the Russian edition of Vavilov's scientific correspondence by H. Knüpffer:
The numbers correspond to those shown encircled in the figure above.

2. *Triticum persicum* Vav. (comment A. A. Filatenko, Wheat Department, VIR)

3. In the "Trudy po prikladnoy botanike" (Papers on Applied Botany), vol. 13, No. 1 (1922–1923), besides the paper of N. I. Vavilov "On the knowledge of soft wheats", the following papers were also printed: A.A. Orlov's "Geographical centre of origin and area of cultivation of hard wheat" and G. Popova's "Species of Aegilops and their mass hybridisation with wheat in Turkestan".

4. The differences between Percival, on one side, and Vavilov, Flaksberger and Orlov on the other, with respect to the species status of wheats with pyramid-type ears can be explained by the limited knowledge of the character at that time and amount of diversity of the tetraploid species *Triticum durum* Desf., *T. turgidum* L., as well as *T. aethiopicum* Vav. The latter species, which was delimited as result of long-term study of the material collected by N.I. Vavilov in Ethiopia, differs from other species by a specific complex of traits, to which the pyramidate form and density of ears do not belong. These characters occur in all species mentioned, and they serve as examples of their homologous diversity (pers. comm. A.A. Filatenko, Wheat Department, VIR).

5. *Triticum arraseita*, which was formerly grouped into *T. dicoccum*, is considered a variety of *T. aethiopicum* nowadays (pers. comm. A.A. Filatenko, Wheat Department, VIR).

6. The first indication of J. Percival's idea of hybrid origin of soft wheats (see letter no. 172, part II, and comment 3 to this letter) (pers. comm. A.A. Filatenko, Wheat Department, VIR).

allied to *dicoccum* – the Abyssinian form – but I thought nearer to *Turgidum* in some of its characters. It might without much error be grouped as *compactum* form of *turgidum,* as *T. compactum.*

The form of glumes, the densely pubescent leaves; the mealy, dorsally-humped grain, separate it at once from *durum* (which always has glabrous leaves except when hybridised and a very different form and texture of grain).

The placing of *Arraseita* in *durum*s is certainly an error. It belongs to pubescent leaved *dicoccum* group, with others from Abyssinia.

I have been busy with the cytology of the wheats and species of *Aegilops* and their hybrids.

Aegilops cylindrica has 7 (haploid) chromosomes, *A. ventricosa* and *A. ovata* 14 (haploid). These I feel have in some way contributed to the origin of the Soft Wheats.

I often think of you and wish you were nearer. I hope that you and your wife and son are well.

Yours very sincerely

John Percival

[(hand-written): Can you tell me where to obtain the Bulletin of Applied Botany. The parts to complete my set?]

Page 306. [Original letter reproduced in Fig. 6]

Reading, England, February 18, 1924

...Could you possibly send me specimens of the *Aegilops crassa, squarrosa, triuncialis.*

I am particularly interested in these plants, and feel sure that some day we shall find that they are connected with the origin of the *vulgare* wheats by crossing with the *dicoccoides* group.

Your opportunities are so much better than mine that I hope you will work at this subject, ...

(Reproduction of handwritten/typed letter)

(Ivanovich...)   *52*

Faculty of Agriculture and Horticulture,

Prof. JOHN PERCIVAL, Sc.D.   UNIVERSITY COLLEGE, READING.
(Professor of Agricultural Botany).

                                                        Feb 18th.   192

            Dear Professor Vavilov,

                        Since writing my letter on the 16 th
                                    vol 13
            No 1 of the Bulletin of Applied Botany has come. Thank you very

            much for it. I should still be very glad to have the others

            mentioned in the other letter.

                        Could you possibly send me specimens of the

            ①
                        Aegilops crassa
                                Squarrosa
                                triuncialis
            I am particularly interested in these plants, and feel sure

            that some day we shall find that they are connected with the origin

            of the vulgare wheats by crossing with the dicoccoides group. *②*

                        Your opportunities are so much better than mine that I hope

            you will work at this subject ,

                        With very kind regards and many thanks for the Bulletin

                        Yours very sincerely,

                                    (signature)

            ○ I should like to have the Supplements issued in
            1922-1923   *③*   *④*
                No. 1 by Regel ; No. 2 by Vavilov ; No.3 by Tchingo- Tchingas
                No. 4 by Flaksberger; No. 5 by Butler.
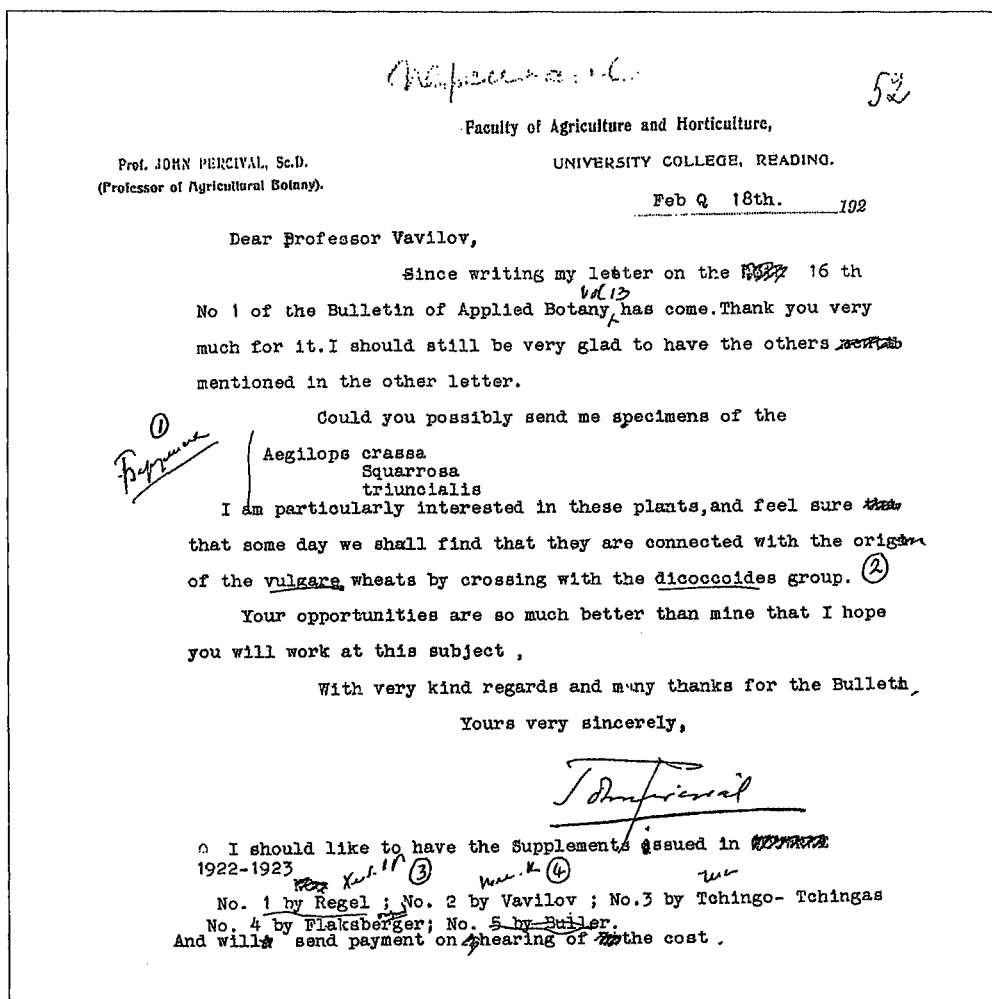   And will send payment on hearing of the cost .

Figure 6. Original letter of J. Percival to N. Vavilov, February 18, 1924. See also Appendix 2. The following
      notes were translated from the Russian edition of Vavilov's scientific correspondence by H. Knüpffer:

The numbers correspond to those shown encircled in the figure above
1. On the right side there is a handwritten remark by Vavilov: "To Barulina"
2. The question of the origin of T. vulgare (aestivum) is still open (pers. comm. A.A. Filatenko, Wheat Dept., VIR).
3. On the side there is a handwritten remark of N. I Vavilov about which books should be sent to Prof. Percival, namely
"Bread cereals in Russia", i.e. R.E. Regel, "Bread cereals in Russia", Petrograd, Sabashnikov Publishers. Materials for
the Study of Natural Productive Powers in Russia. 1922, No. 9, 56 pp.
4. Remark from Vavilov's hand: 2 Field crops of the South-East" (see remark 3 to letter no. 6, part I); "Tchingo-Tchingas"
(see remark 2 to letter 56, part I). From Vavilov's hand: "Opredelitel", i.e. K.A. Flaksberger's "Key to the determination of
bread cereals", 2nd revised edition. Petersburg, Novaya Derevnya Publishers, 1922. 119 pp.

From Percival to Vavilov [Original letter reproduced in Fig. 7a, b]

Reading, England, February 18, 1924

...I have also a very fine collection of Egyptian wheats. Extremely interesting. They will help in settling the classification of relationships of wheat races which I hope to clear up some day...
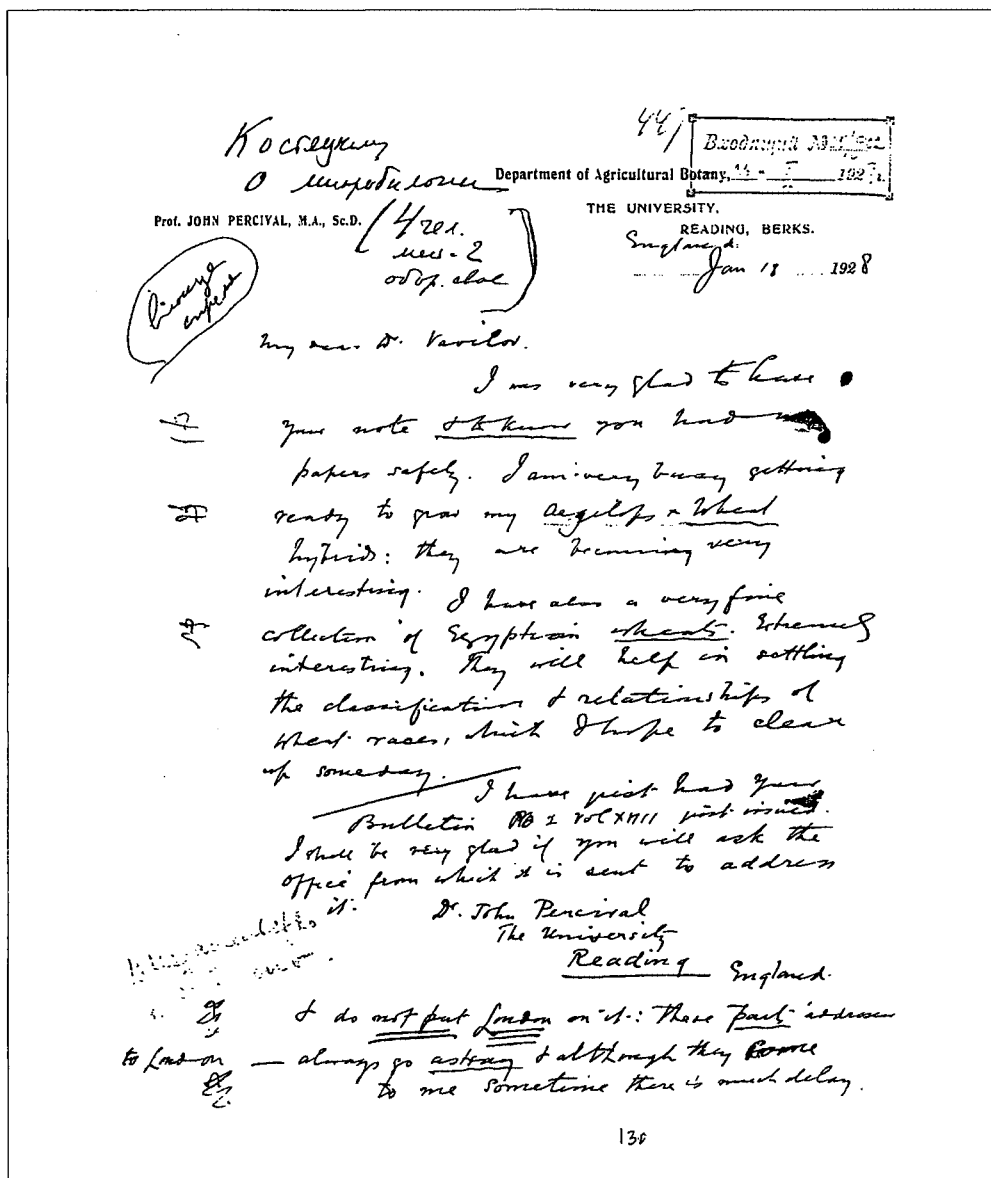

Figure 7a, b. Original letter from J. Percival to N. Vavilov, January 18, 1928. cf. also Appendix 2.

I enclose the cover of the
last No. sent. you see London
is on it & after going to me
or two Places in London it came
to me ~~here~~ here.

In your last letter you mentioned that
you could send me or let me see
a written copy of Mattei monograph on
Vicia Faba —

with kindest regard
in which Dr Leith joins.

Yours very truly

Sch{signature}

Figure 7b.

Figure 8a, b. Original letter from J. Percival to N. Vavilov, February 27, 1928.

clearing up relationships
among the 14 chr. wheats: & I
hope some day to deal
exhaustively with wheat again.
Time flies however, & one cannot
expand one hour into 2 - or four
which would be better.

With kind regards from
all of us at Reading.

Yours very sincerely

John Percival

Figure 8b.

Aegilops species: A monograph

Foreword to John Percival's
Aegilops species

PETER D. S. CALIGARI

Department of Agricultural Botany, The University of Reading,
Whiteknights, Reading RG6 6AS, UK

The six pages following this Foreword are examples of the pages that were "found" in the Department of Agricultural Botany at the University of Reading, comprising an unfinished piece of Percival's prolific work. It is the unpublished part of what Percival himself had titled *Aegilops species: A Monograph*, a publication that would have gone alongside his masterly *The Wheat Plant: A Monograph*. The date that John Percival last carried out his preparations to publish his accumulated knowledge on *Aegilops* is unclear. The last date evidenced, among the material that was found with the pages of the unfinished *Aegilops* monograph, is an envelope dated 1937. This, with other pieces of information, clearly indicates that he was still working on completing the manuscript after his official retirement in 1932, but we do not know when he last worked on it between then and his death in 1949.

The exact history of the Monograph is thus shrouded in the mist and dust of past events within a typical, dynamic academic department with its changes and developments – including its physical relocation. The first hint that I personally had of its existence was in 1992 while I was in Pakistan. I was invited to present the opening address at the "2nd International Symposium on New Genetical Approaches to Crop Improvement" by the organiser, Professor Khushnood A. Siddiqui. He innocently asked me during the Conference Dinner (during which he surprised me with the news that I was giving the after-dinner address!) if I knew what had become of the unpublished monograph by Percival that he had seen in a cupboard when he was a PhD student (graduated 1965) under Dr John K. Jones' supervision. On my return to Reading I made enquiries and a brief search but found no trace of the supposed manuscript.

However, it was two years later, while we were once again trying to create more space for our research activities, that a dusty black herbarium box was found on the very top shelf of the darkest storage cupboard. It contained the rough draft of the monograph; some associated herbarium specimens and sheets of descriptions related to interspecific crosses were all safely inside, if a little yellow and brittle.

Clearly, Percival had not managed to complete the monograph and so it is not certain how conclusively he had sorted out the taxonomic relationships in his own mind. Nevertheless it was clear that, despite the more likely possibility of the Russian scientists of the time publishing on *Aegilops*, he felt the need to take on the task himself.

We have decided to make his unfinished monograph available in the form he left it, with his hand-written amendments, on:

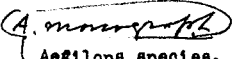http://www.herbarium.reading.ac.uk/percival/

There are also 76 pages of descriptions of inter-specific hybrids and their parents which are matched by herbarium sheets. A few examples are presented here (Figs 1–6) to illustrate what can be found in full on the website.

The 50th anniversary of Percival's death was a suitable occasion to celebrate his contribution, particularly in the field of wheat taxonomy. The preceding papers bear testament to his life and work and so it seemed a very appropriate opportunity finally to put into the literature his monograph on *Aegilops*, as a historical document and as an inspiration for those that followed, and will follow, after him.

Professor Peter D. S. Caligari
August 1999

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                    Aegilops species.

                    A Monograph.

                    By John Percival.
                                                      Page.
          1. A. umbellulata     Zhuk.                  1
          2. A.ovata  L.                                3
          3. A. triaristata     Willd.                  5
          4. A. biuncialis      Visiana.                7
          5. A. variabilis      Eig.                    9.
          6. A. columnaris      Zhuk.                   11
          7. A. triuncialis     L.                      13
          8. A. Kotschyi        Boiss.                  16
          9. A. caudata         L.                      18
         10. A. cylindrica      Host.                   20
         11. A. comosa          Sibth.et Sm.            22
         12. A. Heldreichii     Holzm.                  24
         13. A. uniaristata     Vis.                    26
         14. A. ventircosa      Tausch.                 28
         15  A. squarrosa       L.                      30
         16. A. crassa          Boiss.                  32
         17. A. ligustica       Cosson.                 35
         18. A. speltoides      Tausch.                 37
         19. A. bicornis        (Forsk)
                         Jaub.et Spach.                 39
         20. A. longissima      Schweinf. et
                                       Muschl.          41
         21. A. sharonensis     Eig.                    43
         22. A. mutica          Boiss.                  45.
```

Figure 1. The unpublished *Aegilops* Monograph. Title page.

(A. ~~~~~~)

Aegilops species.

By John Percival.

I. Aegilops umbellulata Zhuk. Bull. Applied Bot.(Leningad) p.483 (1928).

(= A. ovata var. anatolisa Eig.).

Chromosomes number; 2n = 14.

Seminal roots; 3 - 7

Coleoptile;

First leaf; blade,6-8 cm. long,3.5 - 4 mm. broad, ridges 10-14, with a row
    of long hairs on each ridge; margins hairy; sheath ,hairy.

Shoots of the young plants,prostrate; leaves galucous, blades, 4 mm.
    broad, ridges 11-14, on each of which is a single line of long hairs;
    leaf-sheaths, green.

Culms; decumbent below, erect above,25-30 cm. long, glabrous, upper
    internode solid,or hollow,with thick walls, straw -coloured when ripe.

Leaves of the culm; glaucous, blades up to 7 cm.lomg,5 mm.broad with
    soft long hairs on all ridges, margins scabrid; lower sheaths, pubescent,
    with ciliate overlapping margins, upper sheaths glabrous; upper leaf-
    blade 5-7 cm.long, 4-5 mm.broad; auricleds,. fringed with many long hairs
    ; ligule very short.

Inflorescence; yellowish-green when unripe, ovate-lanceolate, the
    upper part very attenuated,3-4 cm.long falling as a whole when ripe,
    disarticulating at the base of the intermode-below the lowest fertile
    spikelet; rachis tough, the lower internodes shorter, the upper
    longer than the spikelets.

Spikelets; 7 - 8, the three lowest , rudimentary; lateral fertile
    spikelets crowded, about 10 mm.long,5-6 mm.broad, urceolate, con-
    stricted above and tapering below the widest ventricose part, which
    is above the mid dle of the empty glume, 4- flowered, 2 flowers usuall
    fertile , the two upper spikelets vefy thin and sterile, or ripening
    only ja single small grain; anthers 3 mm.lomg.

Empty glumes of the lateral fertile spikelets; ventricose above the middle,
    constricted above and tapering downwards from the inflated part,
    7-9 mm.long,5 mm.broad, with 8-9 chief, scabrid nerves; apex oblique.
    broad, with 4-7 scabrid awns,2.5 - 4 cm.long, purple when ripe and
    often brittle at the base, the margins of the awns are smooth near the
    base.

                                                                        2
Flowering glume; oblong or ovate in the first and second flowers of the
    spikelet, 7-8-nerved, with 3-4 awns, two of them 2-3 cm.long, the
    others much shorter.

Palea; ovate, membranous, 8 mm.by////   long, 2 mm.broad,bicarinate ,
    keels ciliate; apex or emarginate.

Terminal spikelet; small, oblong,6-7 mm.long, 1.5 mm.broad,2-3-flowered,
    sterile; empty glumes,oblong, 3 mm.long, each with 4-5 awns,2-5 cm.
    long, long and short awns alternating; flowering glume of the lowest
    flower with three awns,2.5-3 cm.long.

Caryopsis; free, plano-convex, narrowly ovoid or ellipsoid,pale or dark
    brown.6-8 mm.long, 2 - 2.5 mm.broad.

    A somewhat less robust and shorter plant than the common form of

A. ovata.   Immune to Yellow Rust (Puccinia glumarum).

        Found on the Islands of Chios and Samos, and in Syria, Asia Minor,

Iraq and Persia.

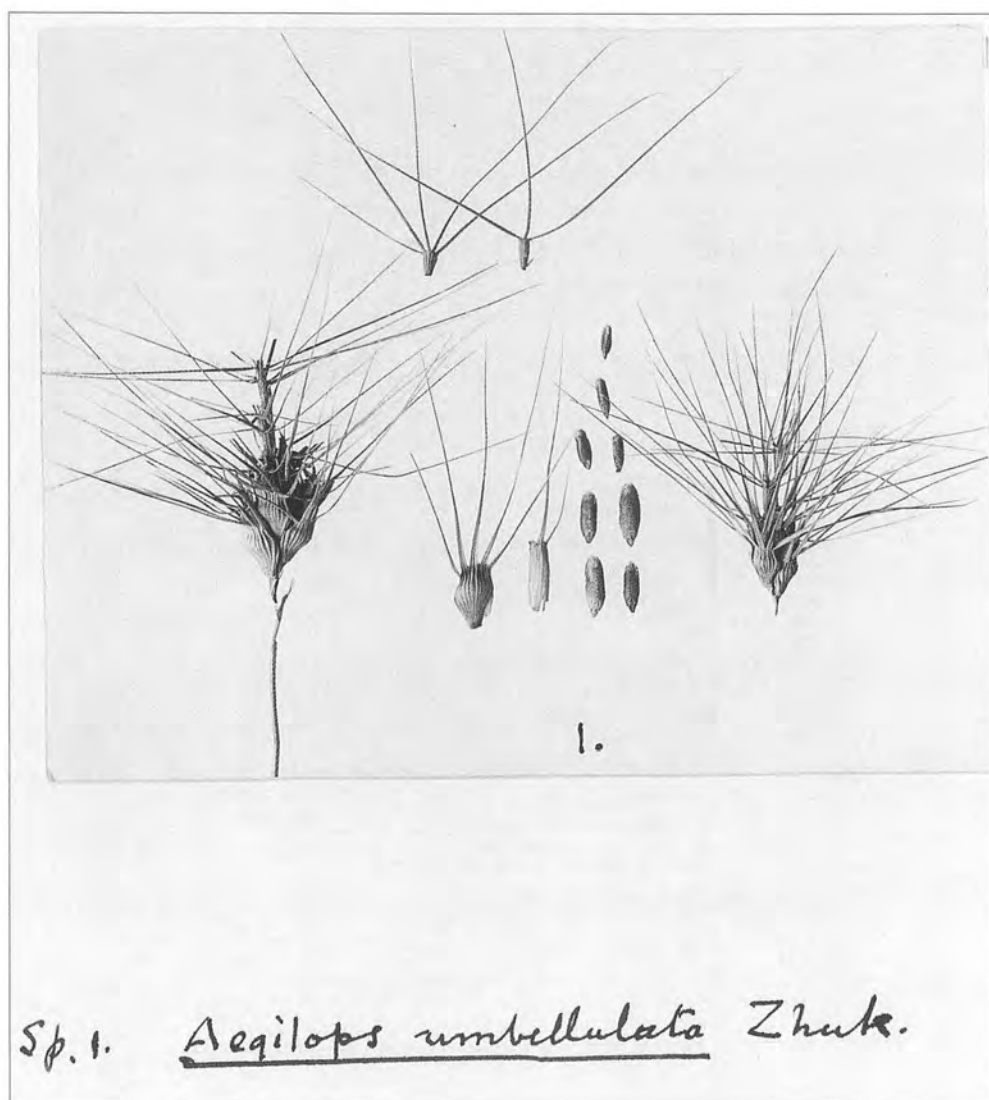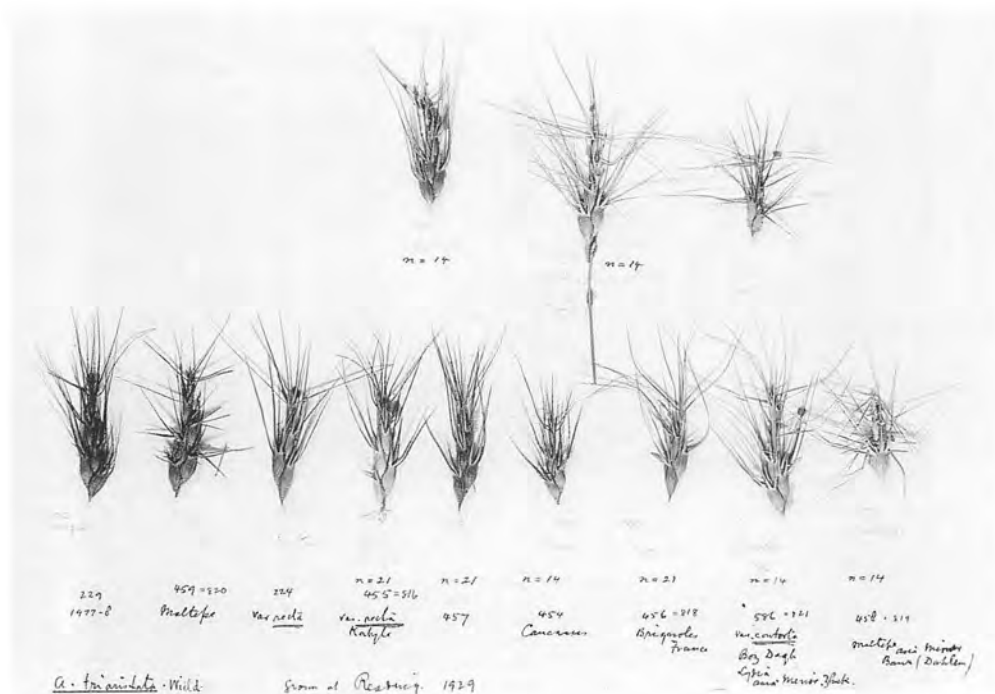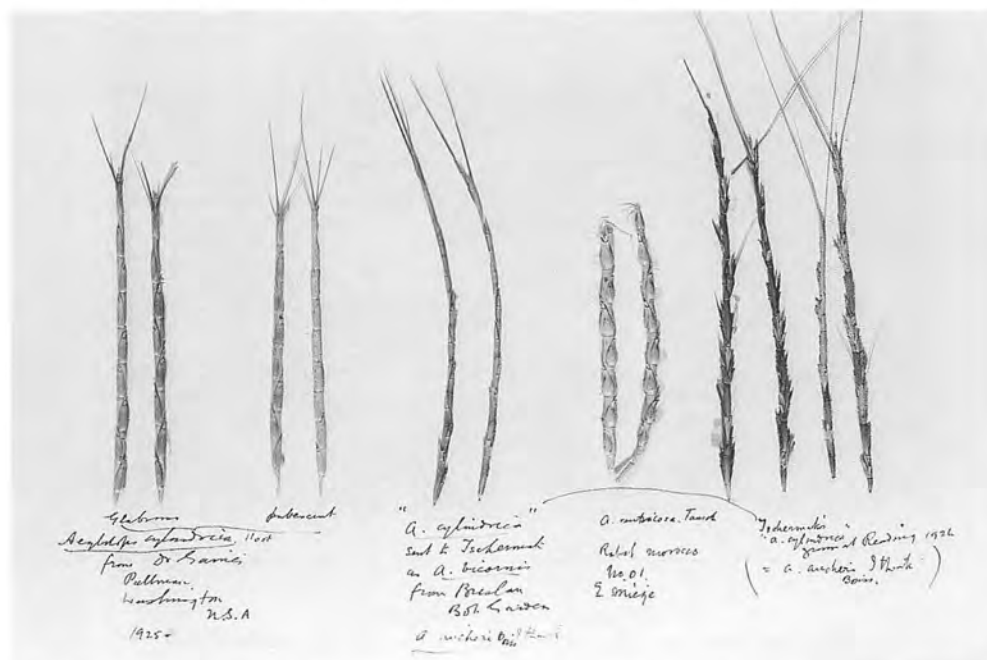Figure 2. The *Aegilops* Monograph. Description of *Ae. umbellulata*.

Figure 3. *Aegilops* Monograph. Fruiting heads and seeds of *Ae. umbellulata*.

Figure 4. *Aegilops* Monograph: fruiting heads and seeds of tetraploid and hexaploid *Ae. triaristata*.

Figure 5. The unpublished *Aegilops* monograph: Fruiting heads of *Ae. cylindrica* and *Ae. ventricosa*.

	♀ *A. cylindrica*	Hybrid 22, 1928 cylind: × ventricosa	♂ *A. ventricosa* 860
		* (1929 hybrid 12-15 cm long with 19 spikelets)	
Inflorescence	6-12 cm long. Rachis fragile, breaking below each node so as to leave spikelet attached to internode next above it. Internode 10-12 mm long wedge-shaped 3mm across top 2 mm at base, scabrid.	10-13 cm long. Rachis tough each internode 7-8 mm long wedge shaped 3mm across top, 2mm at base, smooth with fringe of hairs at margins	8-9cm long. Rachis very fragile disarticulating at each node except at base clean where 1 perfect or 1-2 abortive spikelets remain attached to culm Internodes 9-12 mm long wedge shaped 3mm across top 2·5mm at base, scabrid
Spikelets	5-12, 1.0-1.2 cm long 3 flowered 2 fertile lowest spikelet sometimes abortive. Rachilla very hairy	16-19, 1.2 cm long a lowest abortive, Upper spikelets 4-5 flowered none fertile Rachilla hairy.	8-10, ·9-1·1 cm long 1 or 2 lowest spikelets sometimes abortive 4-5 flowered 3 only fertile. Rachilla hairy.
Empty glume	pale straw colour 8-9 mm long 3 mm across, hairy, rigid rounded with 5-6 well marked ridges the glume bears a sharp keel tooth and a blunt lateral tooth or shoulder, keel tooth scabrid 2-4 mm long >(3cm long in terminal spikelet.	Straw colour - grey 9mm long 4mm across rigid rounded with a few stiff hairs and a distinct scabrid heel ending in a short tooth 1mm long. The indistinct lateral ridge ends in a very blunt tooth or shoulder.	pale straw colour 9-10 mm long, 5 mm across, rigid rounded scabrid with a prominent keel-like ridge and 5 other less prominent scabrid ridges, one scabrid heel tooth an awn <2 or 3 mm in length and 1 very blunt tooth or shoulder.
Flowering glume	9 mm long, thin smooth & attached to the grain except at the apex which bears two small teeth one of which is prolonged to an awn <4 or 5 cm long in terminal spikelet.	10 mm long, thin rounded smooth with hairs at tip and a slight median scabrid tooth which is prolonged into an awn 2-4 cm long in terminal spikelets.	10 mm long thin smooth with hairs at margins and bearing a median scabrid awn and 1 or 2 short lateral teeth. Awn ·5-2 cm long, <4 cm long in terminal spikelet. glume fused to grain
Palea.	pale thin awnless bicarinate attached to grain & divided at tip, keels hairy	pale thin awnless bicarinate, keels hairy.	pale thin awnless bicarinate hairy closely fused to grain when ripe.

Figure 6. *Aegilops* Monograph.
Comparison of the morphology of *Ae. cylindrica*, *Ae. ventricosa* and their hybrid.

CONTENTS