CORN AND CORN IMPROVEMENT

AGRONOMY

A Series of Monographs Published by the
AMERICAN SOCIETY OF AGRONOMY

General Editor Monographs 1 to 6, A.G. NORMAN

1. C. EDMUND MARSHALL: The Colloid Chemistry of the Silicate Minerals, 1949
2. BYRON T. SHAW, *Editor:* Soil Physical Conditions and Plant Growth, 1952
3. K.D. JACOB: Fertilizer Technology and Resources in the United States, 1953
4. W.H. PIERRE and A.G. NORMAN, *Editors:* Soil and Fertilizer Phosphate in Crop Nutrition, 1953
5. GEORGE F. SPRAGUE, *Editor:* Corn and Corn Improvement, 1955
6. J. LEVITT: The Hardiness of Plants, 1956

---

7. JAMES N. LUTHIN, *Editor:* Drainage of Agricultural Lands, 1957
General Editor, D.E. GREGG

8. FRANKLIN A. COFFMAN, *Editor:* Oats and Oat Improvement, 1961
Managing Editor, H.L. Hamilton

9. C.A. BLACK, *Editor-in-Chief,* and D.D. EVANS, J.L. WHITE, L.E. ENSMINGER, and F.E. CLARK, *Associate Editors:* Methods of Soil Analysis, 1965.
Part 1 — Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling
Part 2 — Chemical and Microbiological Properties
Managing Editor, R.C. DINAUER

10. W.V. BARTHOLOMEW and F.E. CLARK, *Editors:* Soil Nitrogen, 1965
Managing Editor, H.L. HAMILTON

11. R.M. HAGAN, H.R. HAISE, and T.W. EDMINSTER, *Editors:* Irrigation of Agricultural Lands, 1967
Managing Editor, R.C. DINAUER

12. R.W. PEARSON and FRED ADAMS, *Editors:* Soil Acidity and Liming, 1967
Managing Editor, R.C. DINAUER

13. K.S. QUISENBERRY and L.P. REITZ, *Editors:* Wheat and Wheat Improvement, 1967
Managing Editor, H.L. HAMILTON

14. A.A. HANSON and F.V. JUSKA, *Editors:* Turfgrass Science, 1969
Managing Editor, H.L. HAMILTON

15. CLARENCE H. HANSON, *Editor:* Alfalfa Science and Technology, 1972
Managing Editor, H.L. HAMILTON

16. B.E. CALDWELL, *Editor:* Soybeans: Improvement, Production, and Use, 1973
Managing Editor, H.L. HAMILTON

17. JAN VAN SCHILFGAARDE, *Editor:* Drainage for Agriculture, 1974
Managing Editor, R.C. DINAUER

18. GEORGE F. SPRAGUE, *Editor:* Corn and Corn Improvement, 1977
Managing Editor, D.A. FUCCILLO

Monographs 1-6, published by Academic Press, Inc., should be ordered from: Academic Press, Inc., 111 Fifth Avenue, New York, New York 10003

Monographs 7-18 should be ordered from: American Society of Agronomy, 677 South Segoe Road, Madison, Wisconsin, USA 53711

CORN AND CORN IMPROVEMENT

EDITOR:

G.F. SPRAGUE

Professor of Plant Breeding and Genetics,
University of Illinois,
Urbana, Illinois

Managing Editor:
D.A. FUCCILLO

Assistant Editor:
L.S. PERELMAN

Editor-in-Chief, ASA Publications:
MATTHIAS STELLY

Number 18 in the series
AGRONOMY

American Society of Agronomy, Inc., Publisher
Madison, Wisconsin, USA
1977

Library of Congress Cataloging in Publication Data

Sprague, George Frederick, 1902 -
Corn and Corn improvement.

(Agronomy; no. 18)
Includes bibliographies and index.
1. Corn. 2. Corn — Breeding. I. Title.
II. Series: Agronomy, a series of monographs; 18. SB191.M2S6254 1976 633'.15'3
76-29528 ISBN 0-89118-043-5

The American Society of Agronomy, Inc.
677 S. Segoe Rd., Madison, Wisconsin, USA 53711

Printed in the United States of America

FOREWORD

Could any American alive in the year our nation was founded have possibly imagined that 200 years later corn would achieve its present importance to the nation and the world? Could the editor and authors of the first edition of this monograph have envisioned at that time the improvement in yields, in nutritional value and overall efficiency in production of calories, oil, and protein which would take place between then and now? Perhaps the best answer is given in the Editor's preface to the First Edition: "The limits of further improvement are not yet definable by corn breeders."

Certainly we are now a long way from seeing the end to the improvement and to the increasing importance of this marvelous American crop. Continuing improvement in yield, quality, and value of this crop will be limited only by the talent and effort devoted to it. It is, indeed, most appropriate that the second edition of this Monograph entitled *Corn and Corn Improvement* is published by the American Society of Agronomy as our nation finishes its bicentennial celebration.

Dr. George F. Sprague, Editor of both the First and the Second Editions, has been a distinguished leader of corn research for decades. His leadership is recognized wherever corn research is in progress. After serving with distinction as a scientist and program leader for the Agricultural Research Service of the U.S. Department of Agriculture, he has "retired" to a University faculty position where he can be found in office, field, or laboratory almost any working day.

Dr. Sprague, the first recipient of the Crop Science Award of the American Society of Agronomy, has been a Fellow of the Society for 30 years and has also served as President. He has had numerous honors and awards. He has been elected a member of the National Academy of Sciences, America's most distinguished scientific body.

Urbana, Illinois
February, 1977

MARLOWE D. THORNE, *President*
American Society of Agronomy

GENERAL FOREWORD

Interest in corn as food, feedstuff, and various products has continued at an unabated pace over the two decades since the first edition of the Corn Monograph. Recognizing this fact, the American Society of Agronomy Executive Committee in 1972 asked the Monographs Committee to proceed with the preparation of another Corn Monograph. Like the first Corn Monograph, this publication is largely a new contribution. The society was fortunate in obtaining the services of the previous Editor, George F. Sprague, who remains an active worker in corn research now with many more years of accumulated experience. Dr. Sprague and members of his committee circulated a Table of Contents of the new Corn Monograph widely among researchers and other scientists knowledgeable on the subject. The authors contributed several years of effort, and the result of their cooperation is this volume.

Corn and Corn Improvement is the 18th monograph in the series prepared by the American Society of Agronomy since 1949. Publication of the first six volumes was by the Academic Press, Inc., of New York but since 1957 the society has become the publisher. A complete list of the titles in the series may be found among these first pages. These publications represent a significant and continuing activity of the American Society of Agronomy, its officers, and its more than 9,000 members located in more than 100 countries around the world.

The American Society of Agronomy is associated with the Crop Science Society of America and the Soil Science Society of America. The three societies share many objectives and activities in promoting these branches of agriculture and scientific disciplines. Members of these three educational and scientific societies contribute generously of their time and talents in producing various publications, including monographs, and in pursuing other activities of an educational nature for public use.

This book should be of great interest and benefit to corn scientists, producers, and users. The American Society of Agronomy considers it as one of its major contributions to human welfare because of the worldwide importance of corn as a field crop. Through the presentation of this up-to-date scientific and practical material on corn, the society believes that this effort will help to make corn an even more useful crop to mankind.

In behalf of society members and myself in particular, I sincerely thank Dr. Sprague for his repeated performance as editor, and many authors, the managing editor, and all others who have contributed directly or indirectly to the accomplishment of this worthy project.

Madison, Wisconsin
June, 1977

MATTHIAS STELLY
Editor-in-Chief
ASA Publications

PREFACE TO FIRST EDITION

Corn was indigenous in the Americas at the time of their discovery. Its production and utilization played an important role in successful colonization. In fact one historian has stated "The maize plant was the bridge over which English civilization crept, tremblingly and uncertainly, at first, then boldly and surely to a foothold and permanent occupation of America."

Tremendous developments have been made in agricultural methods since the first colonization, and throughout this whole period corn has remained one of the major crops grown in the New World. In the beginning the only corn available was the type or types being grown by the natives. Although the early history of corn domestication is still largely shrouded in mystery, by 1800 a large number of varieties were in existence. Through the efforts of private and public agencies intensive work was done on mass selection followed in order by varietal hybridization and ear-to-row breeding. Finally the present method of inbreeding and hybridization emerged from the early studies of Shull, East, Jones, and others. This present method is continuing to show progress as evidenced by the rapid replacement of the first commercial hybrids by newer and better combinations. The limits of further improvement are not yet definable by corn breeders.

Concomitant with the development of improvements in breeding methods has been the acquisition of increased knowledge of plant morphology, of mode of pollination, and most recently of the genetics and cytology of corn. At the present time more is known concerning the genetics and cytology of the corn plant than of any other plant species.

Although the most spectacular improvement in corn yields have come from plant breeding, marked progress also has been made in production practices. Fertilization of the crop has changed from the use of one or two fish per hill in certain restricted areas to the extensive use of balanced starter and supplemental commercial fertilizers. Production practices also have changed from a laborious hand culture to a high degree of mechanization.

Utilization has evolved from the various types of hand grinding used by the Indians through the water powered grist mill to present day types of milling which produce a bewildering array of products and by-products. Even the use of corn as a feed has undergone change; from reliance on exclusive use of corn in a fattening ration, practices have become diverse through adoption of extensive supplementation and have resulted in decreasing by at least one half the pounds of feed required per 100 pounds of gain.

Obviously the present Monograph cannot hope to cover all of these developments in any detail. In fact many of them will be largely ignored, and emphasis will be placed primarily upon the present status of our knowledge. Even with this limitation the preparation of this Monograph has posed many problems. It has been assumed that the particular agronomic audience to be served is the research worker and advanced student interested in corn. Even within this limited group interests are so varied that no choice of topics could be universally satisfactory.

The subject matter covered in the Monograph may be divided in three broad divisions; breeding, production, and utilization. Under the broad classification of breeding are included such topics as history and origin, morphology, cytogenetics, and breeding. The chapters included under the general topic of production treat with climatic requirements, mineral nutrition, culture, production of hybrid seed, the special crops, sweet corn and popcorn, and diseases and insect pests. Utilization is treated under the headings of industrial utilization and corn as a livestock feed.

Any bias which is apparent in the choice of the various sub-topics and in the relative space assigned is to be charged primarily to the editor although some contributors did not use all of the space and others exceeded the space allocations originally made. In any volume involving multiple authorship it is extremely difficult to obtain uniformity of treatment among chapters. This is particularly true where all coordination must be done by correspondence. Certainly others serving in an editorial capacity might well have chosen a somewhat different array of topics and made quite different space allocations than were used here.

The volume includes a rather large number of illustrations. The general policy was followed of using adequate illustrations where this was felt to be an essential part of the presentation, and limiting illustration in other chapters where they did not serve an equally important function.

The editor wishes to express his sincere appreciation to the authors of the several chapters who were persuaded to take the necessary time, often against their better judgment, from their already full research and teaching schedules to prepare their separate contributions.

Ames, Iowa
May, 1955

G.F. SPRAGUE

PREFACE TO SECOND EDITION

The first edition of *Corn and Corn Improvement* was published in 1955 and has been out of print for many years. Possibly the acceptance and usefulness of the first edition can best be judged by the fact that it was translated into several languages. The prime justification for the preparation of a new edition of any book is to provide an updating of information and thereby increase its overall usefulness.

Since 1955 major advances have been achieved in breeding and genetics, in production techniques, and in utilization. The new edition has been rewritten to cover these developments.

The origin of corn has received renewed attention and concepts have been materially modified in the last 20 years. The race concept has been developed and much of the world germplasm has been collected and classified. New chapters on each of these topics should provide information which will facilitate a more intelligent use of the great wealth of genetic diversity available within the species.

The new chapter on genetics provides the first comprehensive review in many years. The chapter on cytogenetics has been extensively revised.

Since publication of the first edition, average yields of corn have more than doubled. This increase has been achieved through a combination of improved cultivars and management practices. New breeding procedures have been devised, evaluated, and are being incorporated into standard breeding practice. The changes in techniques of hybrid seed production are also detailed.

A new chapter has been added covering the development and use of special corn types arising from genetic modification of the carbohydrate, oil, and protein reserves of the corn kernel.

With increased intensity of production, diseases and insects and their control have assumed an increased importance. The more common pests are described as are the most effective means of control.

Improved management practices involving simplified systems of planting, weed control, and harvesting have come into general use. There has been a continuing trend toward heavier plant populations and increased fertilizer applications.

Improvements have also occurred in the utilization of corn in livestock feeding and in industrial processing.

The current revision attempts to provide an interpretive overview of the current situation in each of the major areas mentioned.

The current volume was prepared for the research worker, graduate and advanced undergraduate students and others interested in any or all aspects of genetics, breeding, production, or utilization. Adequate illustrations and extensive literature citations should enhance usefulness.

The editor expresses his sincere appreciation to the several contributors for their respective chapters and to the many others who have provided assistance in this effort.

Urbana, Illinois G.F. SPRAGUE
November 25, 1976

CONTRIBUTORS

D.E. ALEXANDER, *Department of Agronomy, University of Illinois, Urbana, IL 61801.*

WILLIAM L. BROWN, *Pioneer H-Bred International, Inc., 1206 Mulberry Street, Des Moines, IA 50308.*

WAYNE CARLSON, *Department of Botany, University of Iowa, Iowa City, IA 52240.*

E.H. COE, JR., *Agricultural Research Service, U.S. Department of Agriculture, University of Missouri, Columbia, MO 65201.*

WILLIAM F. CRAIG, *Funk Seeds International, Inc., 1300 W. Washington Street, Bloomington, IL 61701.*

ROY G. CREECH, *Department of Agronomy, Mississippi State University, State College, MS 39762.*

F.F. DICKE, *Pioneer Hi-Bred International, Inc., Johnston, IA 50131.*

S.A. EBERHART, *Agricultural Research Service, U.S. Department of Agriculture, Iowa State University, Ames, IA 50010; now with Funk Seeds International, Inc., 1300 W. Washington Street, Bloomington, IL 61701.*

WALTON C. GALINAT, *Suburban Experiment Station, University of Massachusetts, Waltham, MA 02164.*

MAJOR GOODMAN, *Department of Statistics, North Carolina State University, Raleigh, NC 27607*

J.J. HANWAY, *Department of Agronomy, Iowa State University, Ames, IA 50010.*

W.E. LARSON, *Agricultural Research Service, U.S. Department of Agriculture, University of Minnesota, St. Paul, MN 55101.*

M.G. NEUFFER, *Department of Genetics Research, University of Missouri, Columbia, MO 65201.*

JOHN E. SASS *(deceased), Iowa State University, Ames, IA 50010.*

ROBERT H. SHAW, *Department of Climatology and Meteorology, Iowa State University, Ames, IA 50010.*

G.F. SPRAGUE, *Department of Agronomy, University of Illinois, Urbana, IL 61801.*

ARNOLD J. ULLSTRUP, *Department of Botany and Plant Pathology, Purdue University, W. Lafayette, IN 47907.*

STANLEY A. WATSON, CPC *International, Inc., Moffett Laboratories, Argo, IL 60501.*

CONTENTS

Chapter 2 Races of Corn

WILLIAM L. BROWN
Pioneer Hi-Bred International, Inc.
Des Moines, Iowa
MAJOR M. GOODMAN
North Carolina State University
Raleigh, North Carolina

It was about 30 years ago that Anderson and Cutler (1942) pointed up the need for a more natural classification of the variability known then to exist among the varieties of corn, *Zea mays* L. In the late 1800's, Sturtevant (1899) separated corn into six main groups, five of which were based upon the composition of the endosperm. Anderson and Cutler recognized the artificial nature of Sturtevant's system and suggested that knowledge from archaeology and genetics, accumulated since Sturtevant's work, should make possible a more natural classification. They indicated that variability in maize was comparable to that found in mankind and proposed the use of a racial classification based to the extent then possible on natural relationships.

The first thorough assessment of the variation present in corn had been attempted more than a decade prior to Anderson and Cutler's proposal by Vavilov's associates (Kuleshov, 1929, 1930). Although those studies were partly completed before the downfall of Vavilov, the published results are not easily accessible. More limited studies by Girola (1919), Parodi (1932, 1935), and Marino (1934) also received limited distribution and little recognition.

Anderson and Cutler defined race "as a group of related individuals with enough characteristics in common to permit their recognition as a group." In genetic terms, a race according to Anderson and Cutler, "is a group of individuals with a significant number of genes in common, major races having a smaller number in common than do sub-races."

In a series of publications, Anderson (1943, 1944a, 1945, 1946, 1947), Anderson and Cutler (1942), Carter and Anderson (1945), Cutler (1946), Brown and Anderson (1947, 1948), and Anderson and Brown (1952) defined further the racial concept, described the morphological characters thought to be most useful in delimiting races, and classified in a preliminary way the corn of Mexico, Central and South America, and parts of the United States. At about the same time the cytological variation of corn and its relationships to varietal and regional diversity were being described by Longley (1938, 1941), Mangelsdorf and Cameron (1942), and Brown (1949).

While much progress has been achieved toward a natural system of classification of maize since that time, relatively little progress has been made in determining which characters are the most definitive for the study of racial differences in corn. Anderson and Cutler (1942) suggested a number of useful tassel, ear, and kernel characters, many of which were used by Wellhausen et al. (1951); more recently Goodman and Paterniani (1969) presented data suggesting that several ear and kernel characters were superior. However, the latter study was based on a narrow sample of germplasm and may not be representative of the species as a whole. Essentially none of the archaeologically important cob characters (Nickerson, 1953, 1954) have been tested to determine the relative importance of the genotype, the environment, their interaction, and sampling error on the expression of the characters.

Wellhausen et al. (1951) published the results of a comprehensive study of an extensive collection of Mexican corn made in order to organize the variation for use in a corn breeding program initiated in Mexico in 1943 and sponsored jointly by the Rockefeller Foundation and the Mexican government. This report, *Razas de Maiz en Mexico,* enlarged upon previous studies and set the stage for a series of race studies which followed over the next 12 years. The procedures followed in each of these studies were similar, although they varied considerably in emphasis and detail. First the corn grown in the region under study was sampled by collectors who usually obtained from 5 to 15 ears from each farm visited. Usually several thousand collections were made per study. These ear collections were then assembled, spread out on laboratory benches, and similar collections were tentatively assigned to the same race. Emphasis was placed upon such characters as ear shape, row number, kernel denting, etc., which were thought to be polygenic, rather than simply inherited ones such as pericarp and aleurone colors or endosperm differences such as flint vs. floury. The collections tentatively assigned to a given race were then grown together and those collections which differed in plant and tassel characters were removed from the set. Usually three to five collections were chosen on the basis of ear and plant characteristics (and sometimes as a result of breeding true to type) as being most typical of each race. Several ears from each of the most typical collections were saved as museum specimens, while the others were shelled and later increased. Descriptions of the races, including photographs and racial averages for many plant, tassel, ear, kernel, and sometimes physiological characters, as well as chromosome morphology, were published for Mexico and Central America (Wellhausen et al., 1952, 1957); Cuba (Hatheway, 1957); the West Indies (Brown, 1960); Venezuela (Grant et al., 1963); Colombia (Roberts et al., 1957); Ecuador (Timothy et al., 1963); Peru (Grobman et al., 1961); Bolivia (Ramírez et al., 1960); Chile (Timothy et al., 1961); and eastern South America (Brieger et al., 1958). This series of "race bulletins" was followed or accompanied by similar studies on European corn races (Sanchez-Monge, 1962; Leng et al., 1962; Edwards and Leng, 1965; Paviličić and Trifunovic, 1966; Brandolini and Mariani, 1968; Brandolini, 1969, 1970b, 1971; Costa-Rodrígues, 1969; Paviličić, 1971; Covor, 1972) and on Asian corn(Stonor and Anderson, 1949; Anderson and Brown, 1953; Suto and Yoshida, 1956; Mochizuki, 1968), and further studies on the races of Chile (Parker and Paratori, 1965); Bolivia (Rodriguez et al., 1968; Brandolini and Avila, 1971); Mexico (Hernandez and Alanis, 1970); and Brazil and adjacent areas (Blumenschein and Deuber, 1968; Paterniani and Goodman, in press).

The series of "race bulletins," which followed *Razas de Maiz en Mexico,* stemmed from the interest and concern of the late Ralph Cleland of Indiana University. Cleland was, at that time, Director of the Division of Biology and Agriculture of the National Academy of Sciences-National Research Council (NAS-NRC). Under his leadership, the Committee on the Preservation of Indigenous Strains of Maize (1954, 1955) was established within NAS-NRC. The committee was charged with the responsibility for collecting, classifying, and preserving the corn germplasm of the Western Hemisphere, a formidable task when viewed in retrospect. The committee, nonetheless, was unusually successful. Over a period of years, it provided stimulus, guidance, and direction, and obtained sufficient financial support to collect, classify, and publish the results of studies of most of the corn of the Western Hemisphere. In addition, and in cooperation with many USA and Latin American agencies, it helped to organize seed storage centers in Mexico, Colombia, and Brazil.

The classification of Western Hemisphere corn as reported in the NAS-NRC bulletins was considered by many of the authors of these reports to be of a preliminary nature. It was looked upon as a starting point and a basis for more definitive studies which it was hoped would follow. So far, this has occurred to a limited extent only. Goodman (1967, 1968, 1972) and Goodman and Bird (in press) have restudied many of the Latin American collections and have attempted, through the use of numerical taxonomy, to determine more precisely racial relationships between the previously described races.

A study of the chromosome knobs of Latin American races was initiated in the late 1950's by McClintock, Kato, and Blumenschein. This work is now nearing completion and should add much to our knowledge of the origin and relationships of the major races of maize of the Western Hemisphere. Preliminary reports of the results of these studies, (McClintock, 1959, 1960; Longley and Kato, 1965; Kato and Blumenschein, 1967; Blumenschein, 1973; Kato, 1975), indicate the presence of well-defined knob patterns associated with specific geographical areas and maize races. More importantly, these studies reveal the migration patterns of certain definitive knobs and knob complexes and apparently provide the best information to date on the movement of races from one geographic area to another.

Mangelsdorf (1974) has attempted to survey the variability found among the various Latin American corn races. Rather than delineating racial groups, complexes, or "super races," he assigned races to lineages, lineage being used in the sense of "descent in a line from a common progenitor." He described six such lineages, each of which he postulates was derived from a wild race of corn. "From north to south, the still-living ancestral races of these lineages are:

1. Palomero Toluqueño, the Mexican pointed-seeded popcorn.
2. The Chapalote-Nal-Tel complex of Mexico.
3. Pira Naranja of Colombia, the progenitor of the tropical flint corns with orange-endosperm color.
4. Confite Morocho of Peru, the progenitor of eight-rowed corns.
5. Chullpi of Peru, the progenitor of all sweet corns and related starchy-seeded forms with globular ears.

6. Kculli, the Peruvian dye corn, the progenitor of all races with complexes of pericarp and aleurone colors."

The only other recent attempt at comprehensive description of the maize races is that of Brandolini (1970a), who lists a number of primary and secondary centers of differentiation and races associated with such centers.

An understanding of the variability of corn is important for several reasons. It should shed light on the history and relationships of the peoples whose lives are closely associated with corn. Corn breeding should benefit from a better understanding of the evolutionary history and genetic variability within the genus. Finally, and perhaps more importantly, increased knowledge of the racial composition of corn should point the direction to the most efficient and effective ways of minimizing the genetic vulnerability of the commercial corn of the Americas. As indicated in a recent study by the Committee on Genetic Vulnerability of Major Crops (1972) of the National Academy of Sciences, corn has undergone a gradual but continual decrease in genetic diversity over the past 50 years. The decrease in genetic diversity has been accompanied by an increase in genetic vulnerability. As the genetic base of corn germplasm used in commerce is diminished, the risk of economic loss of the crop due to diseases, insects, or unusual stress conditions increases correspondingly. The most recent example of the hazards associated with the widespread use of uniform genetic material is that of the southern corn leaf blight epidemic of 1970 (Sprague, 1971). That experience has brought to the fore again the realization of the hazards associated with the erosion of genetic diversity in any widely grown crop species.

Most of the corn germplasm in use in the USA today is derived from mixtures of only two major races (Wallace and Brown, 1956). The simplest means of correcting this situation and of increasing the genetic diversity in this important crop is to introduce unrelated sources of germplasm, most of which are found in the tropics and subtropics. To do this intelligently and efficiently is a formidable task. There is a vast store of corn germplasm outside the USA which differs greatly in its potential usefulness within the USA. Though our knowledge of the races of corn found in the tropics and subtropics is still incomplete, the knowledge which is available should, if used, simplify the task of reducing the genetic vulnerability of our most important feed grain.

In the discussion which follows, no attempt is made to provide detailed descriptions of the races. This information is already available in the various publications cited earlier. Our objective, rather, is to recognize those earlier described races which seem still to be valid and to shed some light on apparent relationships between them. Many of these relationships are most simply indicated in the text figures. Readers interested in detailed descriptions are referred to earlier cited papers.

This report contains no reference to corn found outside the Western Hemisphere. There are many reasons for this, the foremost of which is the limited information available on the variability of corn of Europe, Africa, and Asia. In our opinion, much more information is needed before a complete and orderly classification of the corn of the Old World is possible. Supposedly, corn had its origin in the Western Hemisphere, yet it is apparent that distinct races have evolved in many areas excluded from this report.

Table 1—Races for which relationships are uncertain

Race	Country	Reference
Conejo	Mexico	Wellhausen et al. (1952)
Mushito	Mexico	
Complejo Serrano de Jalisco	Mexico	
Zamorano Amarillo	Mexico	
Maíz Blando de Sonora	Mexico	
Onaveño	Mexico	
Dulcillo del Noroeste	Mexico	
Apachito	Mexico	Hernandez and Alanis (1970)
Rosita	Mexico	
Gordo	Mexico	
Azul	Mexico	
Bofo	Mexico	
Tablilla de Ocho	Mexico	
White Pop	Cuba	Hatheway (1957)
Yellow Pop	Cuba	
White Dent	Cuba	
Nal-Tel Ocho	Guatemala	Wellhausen et al. (1957)
Huesillo	Costa Rica	
Maiz Dulce	Colombia	Roberts et al. (1957)
Maiz Harinoso Dentado	Colombia	
Mishca	Ecuador	Timothy et al. (1963)
Chillo	Ecuador	
Cónico Dentado	Ecuador	
Uchima	Ecuador	
Gallina	Ecuador	
Cholito	Ecuador	
Yunga	Ecuador	
Enano Gigante	Ecuador	
Yungeño	Ecuador	
Rabo de Zorro	Peru	Grobman et al. (1961)
Chancayano	Peru	
Marañón	Peru	
Chuncho	Peru	
Jora	Peru	
Coruca	Peru	
Sarco	Peru	
Ajaleado	Peru	
San Gerónimo	Peru	
Perlilla	Peru	
Tumbesino	Peru	
Colorado	Peru	
Chancayano Amarillo	Peru	
Polulo	Chile	Timothy et al. (1961)
Chutucuno Grande	Chile	
Choclero	Chile	
Morotí Guapí	Paraguay	Paterniani and Goodman (in press)
Cristal Semi-Dentado	Paraguay	
Achilli	Argentina	Brieger et al. (1958)
Culli	Argentina	
Oke	Argentina	
Bola Blanca	Argentina	
Brachytic Popcorn	Argentina	
Avati Moroti Mitá	Paraguay	
Avati Djakaira	Paraguay	
Chavantes White Soft	Brazil	

RACES OF MEXICO, CENTRAL AMERICA, AND THE WEST INDIES

With the exception of the races described by Rodriguez et al. (1968) for which no representative collections were cited, all the named Latin American corn races are included in this survey. For a number of races, the authors lack sufficient knowledge to accurately circumscribe the racial boundaries or to correctly describe their relationships to other races. Such races are listed in Table 1, although such a listing does not preclude mentioning such a race elsewhere.

Mexican Races

Most of the 25 recognized races of corn in Mexico (Wellhausen et al., 1952) can be reasonably assigned to what appear to be well-defined racial groups (Goodman, 1972). Figure 1 gives a general view of the apparent racial relationships. Only a single race, Maíz Dulce, appears not to have any close relatives among the other Mexican races.

The long, narrow-eared corns typical of northwestern Mexico, whether popcorns, flints, or flours, are all similar to the Indian corns of the southwestern USA (Anderson, 1944b, 1946; Brown et al., 1952; Carter and Anderson, 1945). These races include Chapalote, Reventador, Harinoso de

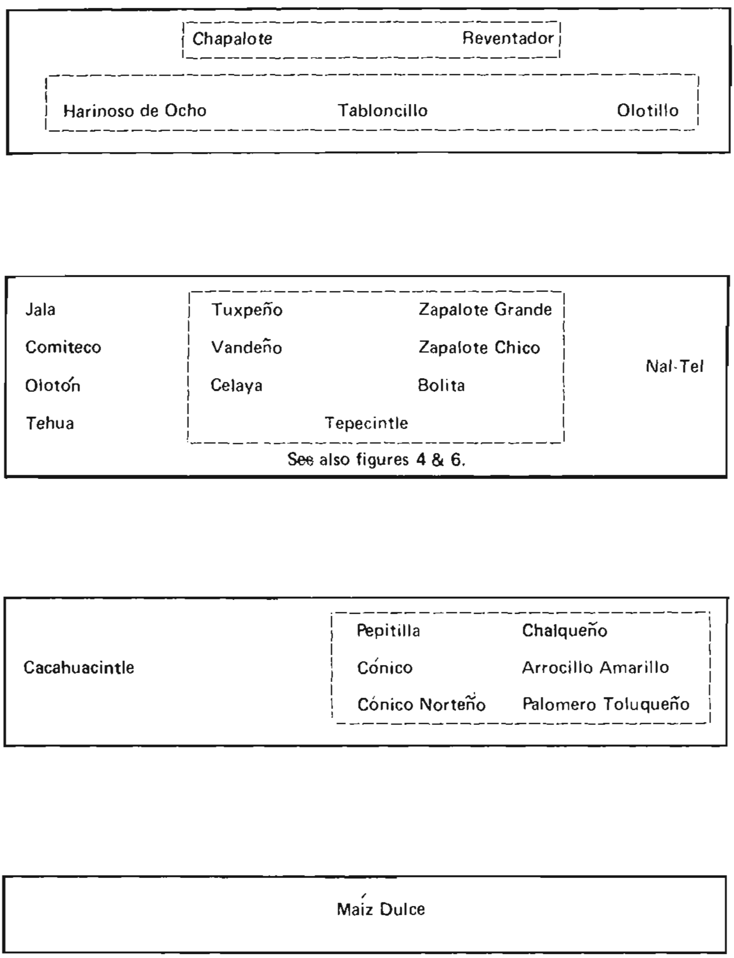

Fig. 1. Racial relationships of the corn of Mexico. Those races within cells outlined by solid lines are thought to be more closely related than races found in different cells. Similarly, races outlined by broken lines are assumed to be more closely related to each other than to races found outside the sub-cells. This method of depicting racial relationships is used in all text figures (Fig. 1 through Fig. 10).

Ocho, Tabloncillo, and Olotillo (the latter from southern rather than northwestern Mexico) as well as several more recently described races (Hernandez and Alanis, 1970). It appears (Nelson, 1952, 1960) that Harinoso de Ocho is one of only two Mexican races which shared the ga_1/ga_1 genotype with the most prevalent USA corn types (Northern Flints, Southern Dents, and Corn Belt Dents).

A second distinctive racial group consists of the conically-eared corns with pointed kernels mostly found at relatively high elevations in central Mexico. Endosperm varies from dented floury to pop, but the plant type — pubescent leaves; sparsely branched, thick tassels; weak roots — is consistent. Cónico, Cónico Norteño, Chalqueño, Arrocillo Amarillo, and Palomero Toluqueño each fall into this category. Pepitilla seems to be related to these races, but it may include sources of germplasm from lower altitude races. Cacahuacintle seems to be related more closely to the Guatemalan race Salpor than to any Mexican race, yet it shares both ear shape and the general aspect of the plant with the Cónico group. It differs most by its very large floury kernels. Kato and Blumenschein (1967) suggested that Cónico, Chalqueño, Palomero Toluqueño, Cacahuacintle, and Arrocillo Amarillo share an essentially knobless karyotype whose influence they have traced to the southern USA. More recently Blumenschein (1973) has suggested that Palomero Toluqueño is distinct from the other members in this group in its chromosome knob morphology. He gave no details, but this view is supported by the report by Nelson (1960) that Palomero Toluqueño, unlike most Mexican corn, possesses the ga_1/ga_1 genotype at the gametophyte locus on chromosome four. Palomero Toluqueño is the ancestral race for one of the six lineages described by Mangelsdorf (1974). He traces its influence as far as the Andean pointed popcorns and their relatives.

The remaining well-defined Mexican races fall into a set of clines or gradients between large-eared races (Jala, Olotón) and small-eared races (Zapalote Chico, Bolita, Nal-Tel). These appear to include the widest assortment of dent races found in a single area. Included are the widely used Tuxpeño, Vandeño, and Celaya dents, as well as races such as Comiteco, Tehua, Tepecintle, and Zapalote Grande, which appear to be closely related to them. Nal-Tel appears to be related to both the small-eared dents and to Chapalote, a popcorn from northwestern Mexico. Within this group, Kato and Blumenschein (1967) found two distinct chromosome knob complexes. The Tuxpeño knob complex of many medium-sized knobs was found along the east coast of Mexico from Yucatán to the southern USA, in central and northeastern Mexico, and along the southwest coast of Mexico. Its influence reached as far as Panama and Cuba and is found in scattered parts of South America. The Zapalote Chico complex of many knobs of various sizes encompasses the races Zapalote Chico, Zapalote Grande, and Bolita, and is found from the southwest coast of Mexico to western Costa Rica. It is suspected (Blumen schein, 1973) that this complex also reached Venezuela.

Chapalote and Nal-Tel, two races which today appear to be distinct in both ear shape and plant type, are listed as ancestral to one of Mangelsdorf's (1974) lineages. That lineage includes, among others, Reventador, the Mexican dents described above, and the Central American Nal-Tels.

Central American Races

The races from Central America have neither been as carefully collected or described as the races of Mexico. Only for Guatemala (see Fig. 2) are the collections or descriptions reasonably thorough. The Guatemalan races, especially those from higher altitudes, resemble South American types of corn as closely as they resemble Mexican types. Very limited tests of *R* alleles, which condition aleurone color, by Van der Walt and Brink (1969), however, suggest that, at least for those corn races possessing aleurone color, the corn found north of the Andes is distinct from that of the Andes. They found that all tested Andean corn possessed nonparamutable *R* alleles, while all Central and North American corn tested, as well as most non-Andean South American corn, has paramutable *R* alleles. A number of lowland Guatemalan collections resemble Mexican Nal-Tel from Yucatán, although they are phenotypically and apparently genotypically (Nelson, 1960; McClintock, 1960) rather variable. Wellhausen et al. (1957) report that the influence of Nal-Tel extends as far south as Panama.

The Guatemalan Imbricado complex shares many features of both the ear and plant with the pointed Mexican popcorn, Palomero Toluqueño, although having larger kernels, less kernel pointing, and much less uniformity than Palomero Toluqueño. In these respects it more closely resembles the Colombian race Imbricado. As mentioned above, the Guatemalan Salpors seem to be closely related to the Mexican race Cacahuacintle. Both show great similarity in ear and plant characteristics to the Mexican Cónicos and their relatives but have distinctive large, floury, white kernels.

Comiteco, a medium to high altitude, long-eared semident and several low altitude dent races are common to Mexico and Guatemala. These include Tepecintle and Tuxpeño, as well as Dzit-Bacal, an eight-rowed, white dent described as a subrace of Olotillo in Mexico. Guatemalan Dzit-Bacal is much faster maturing and shorter than Olotillo, and appears more closely related to the low altitude collections of Nal-Tel than does Olotillo. Kato and Blumenschein (1967) reported that the southern Guatemala chromosome knob complex with numerous large knobs has influenced lowland corn from Panama to northern Mexico along the west coast, in Yucatán, and in Chiapas and Oaxaca. This complex, found especially in the race Nal-Tel, is reported to have reached Cuba and the Greater Antilles from Costa Rica.

Although the long-eared Guatemalan race Olotón is also found to a minor extent in Mexico, it resembles closely a South American racial complex of medium to high altitude, large-kernelled, long-eared flints (the Montañas, Amagaceño), Two other Guatemalan races, Serrano and Quicheño, also resemble South American races. There seems to be essentially continuous variation between Serrano (a small-eared flint, often with an enlarged base) and Olotón, with Quicheño being intermediate in altitudinal distribution. Olotón, and to a lesser extent, Quicheño, have very long ears borne on tall, late maturing plants. This series of clinal variants corresponds to the Pollo-Sabanero-Montaña complex found in northwestern South America. San Marceño seems to be basically a Serrano with eight rows of partially dented kernels, while Nal-Tel de Tierra Alta appears to have some Quicheño ancestry. A complex of small chromosome knobs is reported to be typical of high altitude collections from Guatemala (Kato and Blumenschein, 1967).

The influence of this complex extends to high elevations from southwestern Mexico to Panama. There is also an indication in Nelson's (1960) data that highland Guatemalan corn carries the ga_1 allele rather than the alleles common to the tropical races. Finally, Negro de Chimaltenango, a fairly long, slender, tapering-eared, flinty flour corn with rounded kernels having deep blue aleurone, appears to be similar to Güirua and Negrito from northwestern South America. Wellhausen et al. (1957) suggest that this medium altitude race has introgressed into both high altitude Serrano and several lowland races to form the subraces Negro de Tierra Fría and Negro de Tierra

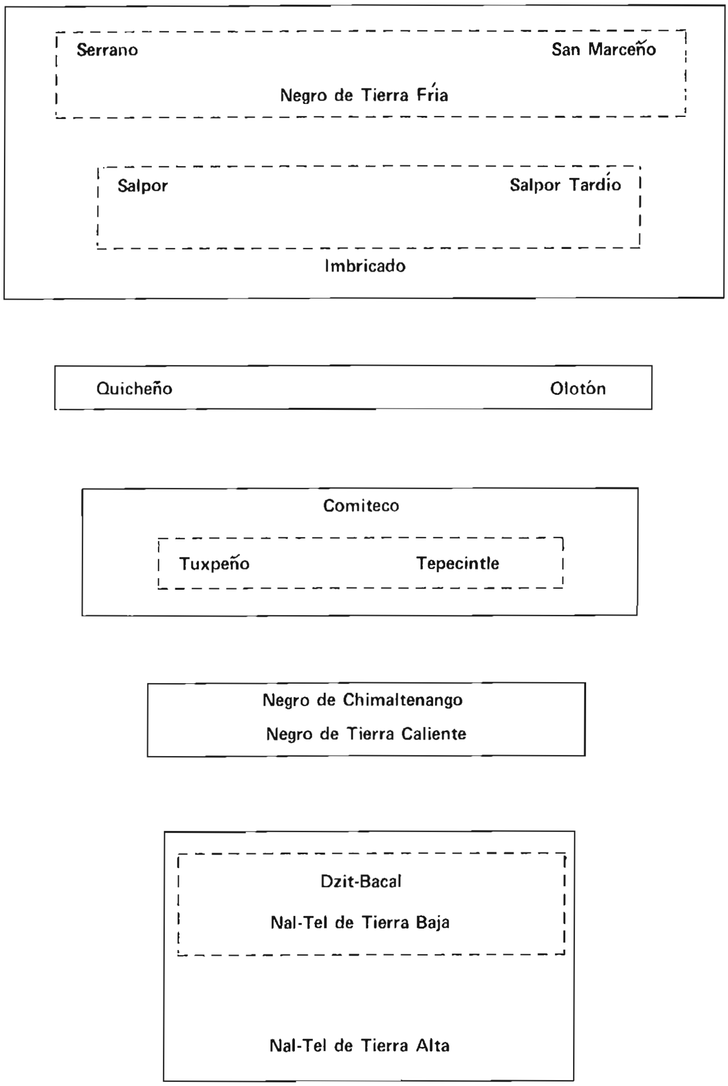

Fig. 2. Racial relationships of the corn of Guatemala.

Caliente, respectively.

The principal commercial corn from El Salvador, Honduras, Nicaragua, and Costa Rica is a low altitude, early maturing, flinty dent with tapering ears called Salvadoreño. In Costa Rica and Panama, a slender-eared white flint, called Clavillo by Wellhausen et al. (1957), resembles the Colombian race Clavo. Huesillo, an 8 to 10-rowed, white-capped flint resembling the Tabloncillos of Mexico, is also found in Costa Rica. Two Colombian races, Chococeño (Nickerson and Covich, 1966) and Cariaco, are found in southern Panama.

West Indian Races

The classification of West Indian corn into clearly defined races is difficult for several reasons. The area is lacking in natural barriers; because of the close proximity of the islands, one to the other, there has long been free migration of peoples between the islands. Likewise, the geographic position of certain of the islands relative to the South American mainland has encouraged the movement of peoples from the mainland to the islands since the days of the Arawak. The free movement of peoples in the area has apparently been accompanied by transport of corn varieties. As a result, there has been much mongrelization of varieties and a masking of racial differences. Despite these difficulties, it has been possible to identify several reasonably well-defined races in the West Indies. The validity of certain of these races has been confirmed through the subsequent discovery of similar counterparts in other areas of Latin America.

The first study of West Indian corn was that of Hernandez (1949), who described six provisional races from collections made primarily in Cuba. This was followed by a preliminary study by Brown (1953) of collections from 11 Caribbean islands. Brown recognized eight provisional races. Hatheway (1957) reported on a detailed analysis of Cuban corn and described seven races existing in Cuba at the time of his study. Brown (1960) did a more detailed study of West Indian maize in which he attempted to correlate his earlier findings with those of other authors. This work included the progenies of 135 collections which were grown and studied in Trinidad. He concluded that West Indian corn consisted essentially of seven distinct races plus a number of intermediate types which presumably were the products of interracial hybridization. The races recognized by Brown were Cuban Flint, Haitian Yellow, Coastal Tropical Flint, Chandelle, Early Caribbean, Tusón, and St. Croix.

This classification seems as valid today as when it was made in 1960. To our knowledge, no new, indigenous races have been reported from the West Indies since that date. On the contrary, many of the varieties formerly used as commercial corn have recently been replaced by modern hybrids. In Jamaica, for example, we estimate that 90% or more of the corn now grown consists of hybrid varieties.

The two most prominent races occupying the West Indies are Coastal Tropical Flint and Tusón. Both are widely distributed throughout the islands from Cuba to Trinidad. The two are also probably closely related. Brown (1953, 1960) postulated that Tusón arose as a hybrid between Coastal Tropical Flint and some unidentified dent maize. Even though related, the two races are distinct. Coastal Tropical Flint is more flint-like than Tusón, has a lower number of kernel rows, and has shorter and somewhat narrower kernels. The ears of Coastal Tropical Flint are distinctly tapered, whereas the ears of Tusón are cylindrical. The name Tusón, meaning "large cob," seems particularly appropriate for this race, since it has distinctly larger cobs than found in any other West Indian race. Tusón is slightly earlier in maturity than Coastal Tropical Flint and has somewhat fewer primary and secondary tassel branches. Both races are tall, without tillers, and have ears placed high on the culm.

Haitian Yellow seems to be more closely related to Coastal Tropical Flint than to other West Indian races. Its ears are characteristically pyramidal with conspicuously enlarged bases and with 8 to 14 rows of kernels. The pointed kernels vary from flint to slightly dented. Plants are tall and late maturing; they usually exhibit purple anthocyanin coloration. The plants possess more extensively developed husk leaf blades, "flag leaves," than do other West Indian races. The distribution of Haitian Yellow, apparently limited to Haiti, suggests relatively recent origin. Its similarity to Coastal Tropical Flint indicates it may have originated from crosses of that race with other Haitian corn.

The four remaining races found in the West Indies, Cuban Flint, Chandelle, Early Caribbean, and St. Croix, are well defined and appear not to be closely related to each other or to the three races referred to previously.

Cuban Flint is the only true flint found in the West Indies. Its distribution is limited to Cuba and the evidence is fairly clear that it was introduced from Argentina in the early 1900's (Hatheway, 1957). The ears of Cuban Flint are relatively short (17 cm), are slightly compressed at the base, and are gently tapered from the base to the tip. Row numbers vary from 12 to 16, with 14 being the most frequently found number. Kernels are short and deep orange yellow in color. Tassel branches are also short in comparison with those of other West Indian races. The plants are usually without tillers, are frequently two-eared, and the leaf sheaths are usually strongly pubescent in contrast with the glabrous leaves of other races.

Although the similarity between Cuban Flint and the Cateto and Cateto Sulino flints of eastern South America [described by Brieger et al. (1958) and Paterniani and Goodman (in press)] is obvious, Hatheway (1957) has suggested that Cuban Flint may be the result of accidental crossing of Argentine flint with local Cuban varieties. He feels that Argentine flints are poorly adapted to Cuba and that Cuban Flint is more similar to other Cuban varieties in plant type than to Argentine flints. Some introgression has undoubtedly occurred between introduced Argentine flint and Cuban varieties, yet the relationship between Cuban Flint and Cateto (and Camelia of Chile as well) appears to be still quite strong. Blumenschein (1973) suggested, on the basis of chromosome knob mapping, that the Cateto flints of eastern South America originated in the Antilles as a result of crosses between representatives of the Tuxpeño knob complex and the two Guatemalan knob complexes.

Chandelle is found in Cuba, Haiti, the Dominican Republic, Trinidad, and the Caicos Islands. It is a dominant race in the Dominican Republic. Two forms of Chandelle occur in Cuba and the Dominican Republic — a flint and a dent. In Haiti, Trinidad, and the Caicos Islands, it occurs only as a flint. Because of the nature of the ear, Chandelle is never confused with other races. The ears are long, slender, strongly compressed at the base, and gently tapered to the tip. Kernel rows range from 10 to 16, and the kernels are long in relation to the diameter of the cob resulting in a high shelling percentage. The cob is slender and flexible even when mature and dry, a trait which occurs infrequently in corn and in none of the other West Indian races. Chandelle is of late maturity, and the plants are taller than those of other West Indian races; however, some early maturing tropical lines have been extracted from the race. Considerable red anthocyanin color is usually present in the leaf sheaths.

Because of its early maturity, short stature, and distinctive internode pattern, Early Caribbean is unique among West Indian corns. When grown in the lowland tropics, it flowers 46 to 48 days after planting, which is 10 days to 2 weeks earlier than other West Indian races. It is sensitive to changes in photoperiod, however, requiring about 95 days to flower in Raleigh, North Carolina. Early Caribbean has few condensed internodes above the ear, resulting in an internode pattern more typical of early USA varieties than of those from the tropics. The ears are relatively short (18 cm) and slightly tapered with 10 to 12 rows of relatively wide, semi-flint kernels. Pericarp color is frequently red or reddish, although colorless pericarp is not unusual. The husks are quite loose compared with other races of the area. Insofar as is known, the distribution of Early Caribbean is limited to Martinique and St. Kitts. Its characteristics are such as to suggest relationship to some of the early flint corns of North America or Europe. Introgression with introduced early flints from North America or Europe could have occurred, yet in the absence of any supporting evidence for such we are inclined instead to consider Early Caribbean a relic of an old, indigenous race.

St. Croix apparently arose from introgression between local varieties and introductions from southeastern USA. Since many of the characteristics of St. Croix are similar to those of the old white endosperm variety, Hickory King, and because of the political connection between the USA and certain of the Virgin Islands, it seems likely that Hickory King is involved in the ancestry of St. Croix. Ears of St. Croix are the longest found in the West Indies; they are cylindrical to slightly tapered and consist of 10 to 14 rows of wide, well dented, flat-topped kernels. Endosperm is light yellow in color, suggesting again the possibility of some white endosperm parentage. The plants of St. Croix also suggest relationships to temperate zone corn. Ear placement is low compared to other races, and the husks are relatively short and loose. The tassels have relatively few branches which are arranged more or less at right angles to the primary axis. Except for Early Caribbean, St. Croix is of earlier maturity than other West Indian races. To our knowledge, the race is limited in its distribution to the island of St. Croix. Brown (1960) suggested that St. Croix might have arisen from the introgression of local varieties with Hickory King of the USA or Olotillo of Mexico. While one cannot completely rule out the possibility of relationship to Olotillo, the phenotype of St. Croix is that which one would more reasonably expect to result from introgression with temperate varieties.

Four of the seven races found in the West Indies have similar counterparts in South America (Fig. 3). These are Cuban Flint, Coastal Tropical Flint, Chandelle, and Tusón. Their relationships are discussed further in the next section. The three remaining races, Haitian Yellow, Early Caribbean, and St. Croix, have not been collected from other areas and are apparently limited in their distribution to the Caribbean islands.

Cuban Flint – West Indies

Cuba Yellow Flint -- Venezuela and Central America
Camelia -- Chile   Cateto -- Bolivia
Cateto & Cateto Sulino -- Argentina, Uruguay & Brazil

Coastal Tropical Flint -- *West Indies*

Común -- Venezuela & Colombia
Costeño -- Venezuela & Colombia
Perla -- Peru   Andaquí -- Colombia
Yunquillano -- Ecuador
Cateto Nortista -- The Guianas

Tusón -- West Indies, Venezuela, & Brazil

Maíz Cubano -- Ecuador
Cubano Dentado -- Bolivia
Cuban Yellow Dent -- Peru
Salvadoreno -- Central America

Haitian Yellow

Chandelle -- West Indies & Venezuela

Clavo -- Colombia
Puya -- Colombia & Venezuela
Puya Grande -- Colombia
Clavillo -- Costa Rica
Canilla -- Venezuela

Early Caribbean

St. Croix

Fig. 3. Relationships of the races of corn of the West Indies and their Central and South American counterparts. (See also Fig. 4).

Kato and Blumenschein (1967) report that the corn of the West Indies appears to be influenced by three sources of chromosome knob variation. They suggest that the Tuxpeño complex of medium-sized knobs from the eastern coast of Mexico and the southern Guatemalan, mostly large-knobbed complex were introduced to the Greater Antilles. These introductions combined to form a secondary knob complex which they labelled Northwest Caribbean. This new, secondary complex spread southward through the Lesser Antilles to South America, then spread along the coast to Uruguay and northeastern Argentina, and inland to Paraguay and southwestern Brazil. The third chromosome knob complex found in the West Indies is Kato and Blumenschein's Venezuelan complex. This complex of large knobs apparently spread through the Lesser Antilles and along the coast of South America to Panama, Ecuador, Brazil, and Uruguay.

RACES OF SOUTH AMERICA

Much of the corn variation in South America can also be discussed on a regional basis. There are, of course, races which do not fit regional patterns closely, but several racial complexes, each largely confined to one of the four regions below, appear to encompass the realm of corn variation in South America. Detailed results of one set of numerical analyses of most of these races have been presented elsewhere (Goodman and Bird, in press). Other analyses are currently in preparation (Bird and Goodman, unpublished data). The summary presented here is largely based upon the results of these analyses tempered somewhat by field experience with the materials. We have also attempted to consider the sometimes extensive reviews of the histories and geographical distributions of the races which are included in the various "race bulletins." Nevertheless, we would like to emphasize that the racial groupings presented here are, at best, working hypotheses which need much further study.

Lowland Northern South America

Many of the flint and semi-flint races of northern South America were discussed in the section on West Indian corn, and their relationships are presented diagrammatically in Fig. 3. Cuban Yellow Flint of Venezuela (Grant et al., 1963), the Catetos and Cateto Sulinos of eastern South America (Brieger et al., 1958; Paterniani and Goodman, in press), and Camelia of Chile (Timothy et al., 1961) appear to be mainland counterparts of Cuban Flint. The currently available typical collections of Cuban Flint from Venezuela are phenotypically rather variable and appear to include some Tusón and Chandelle influence.

Coastal Tropical Flint (Fig. 3) occurs under the names of Perla in Peru (Grobman et al., 1961), Cateto Nortista in the Guianas (Paterniani and Goodman, in press), and Costeño and Común, both in Venezuela and Colombia (Grant et al., 1963; Roberts et al., 1957). However, the range of variation described for the latter two races seems to encompass both Coastal Tropical Flint and Tusón. The Costeño collections from Colombia are quite variable in ear shape, while the Común collections from that country have a much larger kernel size than those from Venezuela. This would appear to be the result of a higher percentage of high altitude germplasm in Colombian Común. The Colombian race Andaquí and the very similar Ecuadorian race Yunquillano, (Roberts et al., 1957; Timothy et al., 1963), also appear to belong to this racial group. Andaquí is a small-eared, white, semi-flint with many chromosome knobs. It is found at low elevations in the southern interior of Colombia.

Tusón is widespread in South America (see Fig. 3). It has been described from Ecuador as Maíz Cubano (Timothy et al., 1963), from Venezuela and Brazil as Tusón (Grant et al., 1963; Paterniani and Goodman, in press), from Bolivia as Cubano Dentado (Ramirez et al., 1960), and from Peru as Cuban Yellow Dent (Grobman et al., 1961). Salvadoreño from Central America (Wellhausen et al., 1957) and many of the collections of Tuxpeño from Venezuela and Puya Grande from Venezuela could also be classified as Tusóns. Because of its productivity, Tusón has undoubtedly been widely dispersed as a commercial corn in recent times. Whether the initial migration of Tusón was from the mainland to the islands or vice versa is still unknown. Yet, the antiquity of corn in South America suggests that Tusón probably reached the West Indies from the mainland.

Races very similar to Chandelle are found in Venezuela (Grant et al., 1963), Colombia (Roberts et al., 1957), and Central America (Wellhausen et al., 1957) — see Fig. 3. The collections from Venezuela have been given the names Canilla, Puya, and Chandelle, whereas in Colombia they are known as Clavo and Puya. Clavo seems to be very close to Chandelle, whereas Puya is probably less closely related. Venezuelan Canilla has somewhat smaller, more flinty kernels than Chandelle. Clavillo from Costa Rica (Wellhausen et al., 1957) is apparently also a member of the same racial complex. Puya Grande from Colombia appears also to be fairly closely related to Chandelle, whereas the Puya Grande collections from Venezuela seem more closely related to the Tusóns, described above.

There is also a group of dents and semidents (Tuxpeño of Ecuador and Venezuela; Yucatán from Colombia; Alazán and Arizona from Peru; Puya Grande from Venezuela) which presumably trace back to Mexican dents of the Tuxpeño-Vandeño type (see Fig. 4). Several Peruvian (Alemán, Chuncho, Jora) and Ecuadorian (Uchima, Gallina) races have apparently arisen as a result of admixture between Caribbean flint or dent races and lower altitude Andean races. The source of denting in all of these races presumably traces to Mexico.

The narrow-eared characteristics of Puya (see discussion above) and Chandelle appear to trace to the Canilla-Clavo-Tusilla-Clavito group of narrow-eared flints (Fig. 4). The latter appear to be related to Rienda, Chimlos, and Pagaladroga (and perhaps Rabo de Zorro) of Peru and Güirua of Colombia. Güirua has elongate ears similar to the Chandelles but with blue aleurone; it is an Indian corn collected from non-Spanish speaking Indians.

The relationships, if any, between the narrow-eared flints and flours discussed above and the phenotypically similar popcorns, such as Pira (Fig. 4) from Venezuela and Colombia (a white, cigar-shaped popcorn with a very thin, often almost disarticulating, cob) and Pira Naranja (a yellow, cigar-shaped popcorn from Colombia, which is quite late maturing and very tall), are unclear. Mangelsdorf (1974) suggests that Pira Naranja was ancestral to a lineage leading to the Cateto flints of eastern South America. Since Pira Naranja is not only extremely sensitive to photoperiod (Stevenson and Goodman, 1972) but also is quite late maturing even under short day conditions, it, unlike Mangelsdorf's other postulated ancestral races, would appear to be quite resistant to successful adaptation to new environments, particularly those with longer days and shorter growing seasons. Both of the latter are characteristic of the environments wherein the Catetos are found.

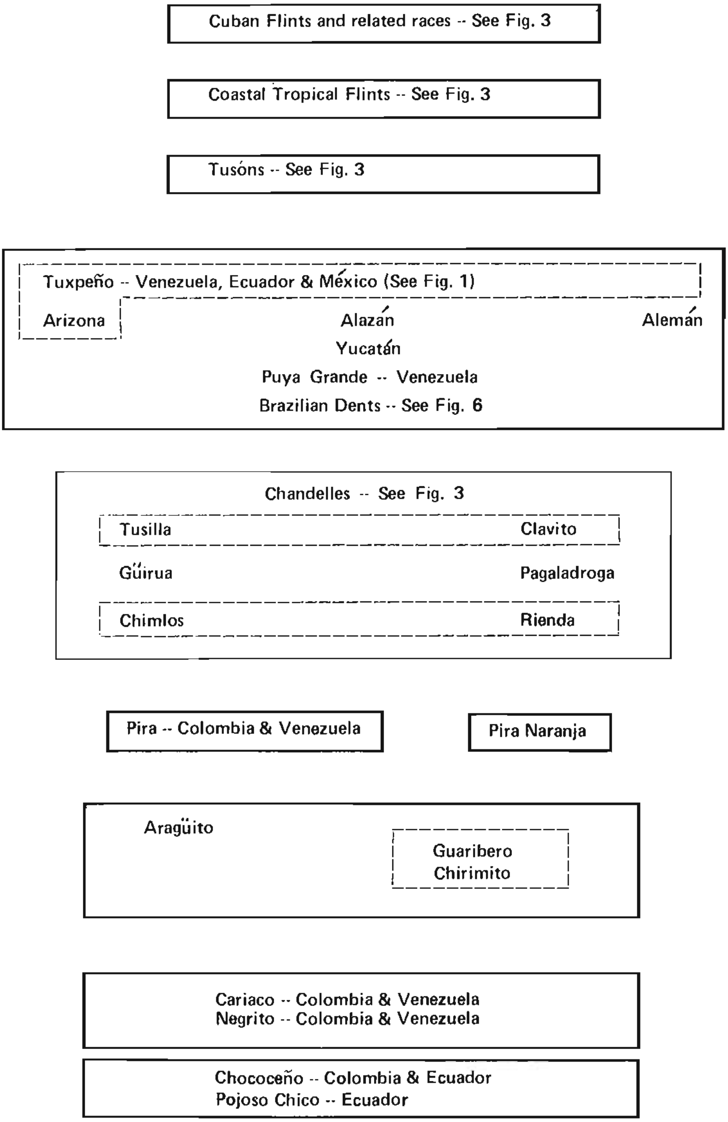

Fig. 4. Racial relationships of the corn of lowland northern South America.

Whether the Chirimito, Aragüito, and Guaribero small flints or popcorns (Fig. 4) from Venezuela are related to larger-eared races such as Pira (see above) is not yet known. The former (especially Araguito) are quite short and very early, but lack the brittleness and upright leaf and tassel branch habit of the somewhat similar collections of Enano (see next section and Fig. 5) from Bolivia and Peru. In plant type they more closely resemble two early maturing floury races with short, broad ears, Cariaco and Negrito of Venezuela and Colombia (Fig. 4). The latter especially appears to share its ear shape with the shorter-eared Caribbean tropical flints (discussed above) and both appear to share their kernel coloration with Amazonian races described in the next section. Negrito is often quite flinty.

The Chococeños (Fig. 4) of western Colombia and Ecuador (Patino, 1956) share the same general ear shape with Enano, Chirimito, Guaribero, and Aragüito (described just above), but the plants are tall, heavily tillered, and very late. While there are floury collections of Chococeño, it typically is a popcorn reportedly grown by sowing rather than row planting (Roberts et al., 1957).

The Amazon Basin and Surrounding Lowlands

Throughout the interior lowland area east of the Central Andes, a single racial complex predominates. First described by Cutler (1946) under the name Coroico (Fig. 5), it has also been called Piricinco and Pojoso (Grobman et al., 1961) as well as Entrelaçado (Brieger et al., 1958). The characteristic features of this racial complex are its long, narrow ears, often with bulging butts, interlocked rows of kernels instead of the customary paired-kernel rowing, and strongly attached shanks. The very low condensation, especially near the ear tip, which is a distinctive feature of these races, has been described by Galinat (1970). The kernels are usually floury with bronze or orange-colored aleurone, although lemon yellow aleurone is often found; there are collections with white, flinty kernels. Recently Wolf et al. (1972) reported that many collections of this racial complex have multiple aleurone layers.

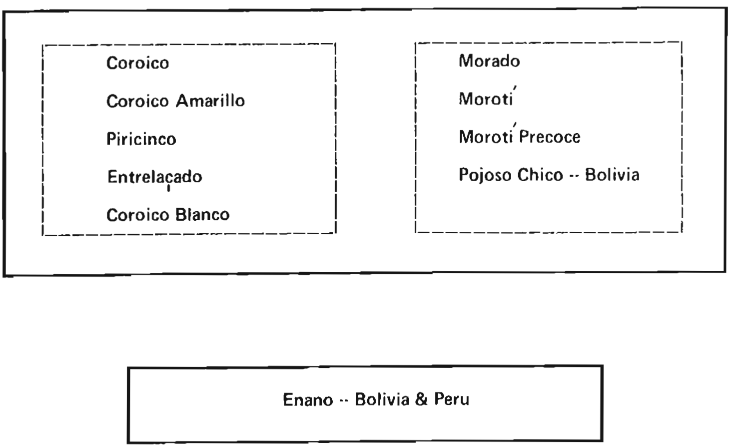

Fig. 5. Racial relationships of the corn of the Amazon basin and surrounding lowlands.

Around the periphery of this region, a number of races share similar kernel coloring and/or ear shape with the Coroico types described just above. Whether these features indicate genetic relationships remains to be ascertained, but the combination of geographic proximity and phenotypic similarity is suggestive. Several of these peripheral races are grouped together in the upper right of Fig. 5. The following races all appear to share their kernel coloring and texture with the Coroicos: Cacao and Cariaco from Colombia and Venezuela, Candela from Ecuador, Cabuya from Colombia, Moroti and Pojoso Chico from Brazil, Bolivia, and Paraguay, and perhaps Marañon from Peru. The ear shape of the Coroico types described above seems to be shared with the Montañas from Colombia and Ecuador, Amagaceño from Colombia, Morado from Bolivia, and Rienda, Chimlos, Pagaladroga, and Rabo de Zorro from Peru, as well as with most of the former (Cariaco and Marañon are exceptions).

Sympatric with the Coroicos, but apparently much more limited in distribution is Enano (Fig. 5), a dull, ivory-kernelled popcorn with short, tapering ears, very strongly attached shanks, and very stiff plants with erect leaves and tassel branches. The relationship between the two racial types is uncertain, but some collections of Enano approach the smaller collections of Coroico Blanco in ear size and shape.

The two types of genetic markers studied in these materials (chromosome knobs and presence of paramutable *R* alleles) present somewhat conflicting evidence for these races. With a few exceptions (Cacao, Rienda, possibly Cariaco, Montaña, and Amagaceño), these races basically have an "Andean" knob pattern with a medium to small knob in the long arm of chromosome 7 and a small or no knob at the lower position on the long arm of chromosome 6 (Roberts et al., 1957; Grobman et al., 1961). Other knobs are rare (McClintock, 1959). On the other hand, the limited evidence accumulated by Van der Walt and Brink (1969) suggests that at least some of these materials (Entrelaçado, possibly Cariaco) have paramutable *R* alleles rather than the nonparamutable *R* alleles typical of Andean maize.

Lowland Southern South America

Eastern and southern South America is characterized by a group of white (Cristal and Cristal Sulino from Brazil, Paraguay, Uruguay, and Argentina; Perola from Bolivia; Curagua Grande from Chile) and yellow or orange (Cateto and Cateto Sulino from Brazil, Bolivia, Uruguay, and Argentina; Cristalino and Camelia from Chile) flints with cylindrical to tapering, medium-sized ears (see Fig. 6). In addition, floury variants of the Coroico complex (Morotí from Brazil and Paraguay; Pojoso Chico from Bolivia) discussed above were spread as far south as northern Argentina by the Guaraní Indians.

In recent years, introduction of USA, Mexican, and Caribbean dents has resulted in a number of dent and semident races (Fig. 6) of hybrid origin (the dents of southern Brazil; Cubano Dentado and Argentino from Bolivia; Dentado Comercial from Chile). It also appears that flints from the northern part of the USA were introduced into both Chile (Cristalino Norteño, Araucano) and Argentina (Canario de Ocho). Similarly, USA sweet corns were collected and described in Chile (Timothy et al., 1961).

Several distinct floury races (Camba, a large, tapering white dent from Bolivia; Caingang, a long-eared, cylindrical, white dent from Brazil; Cholito, a short-eared, cylindrical to tapering, predominantly white dent segregating for purple or dotted aleurone, from Bolivia; Lenha, a stubby-eared, white-kernelled race with soft cobs, from Brazil; Harinoso Tarapaqueño, a wide-kernelled Chilean race) are found along the northern edge of the region (Fig. 6). Cateto Sulino Grosso from Uruguay is quite unlike most of the Catetos. It has thick ears with high row numbers, sharing its ear shape with Lenha and Cravo, both found in southern Brazil.

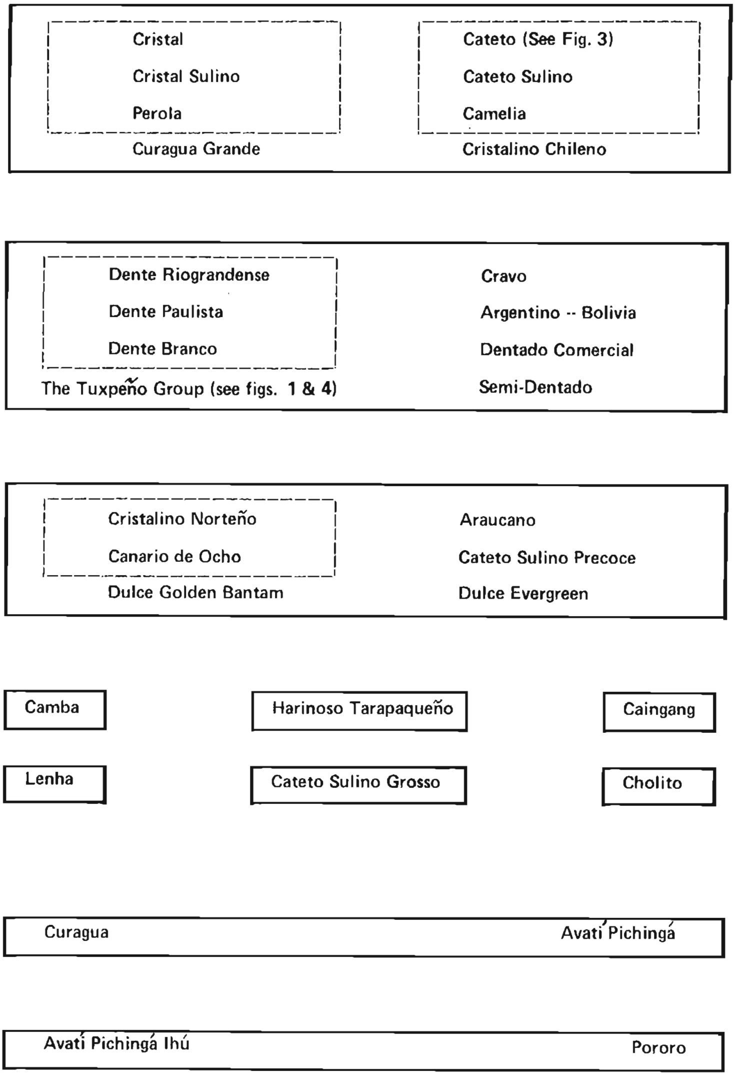

Fig. 6. Racial relationships of the corn of lowland southern South America.

Several cigar-shaped popcorn (Fig. 6) races (Avatí Pichingá Ihú from Brazil and Paraguay; Pororo from Bolivia) with predominantly white, rounded kernels (sometimes with red pericarp) are scattered throughout the region. Neighboring races with predominantly white, pointed kernels and more conical ear shape (Avatí Pichingá from Brazil and Paraguay; Curagua from Chile) may be related to higher altitude Andean pointed popcorns (see next section). These races tend to have multiple ears, flag leaves, and several tillers.

The Andean Region

The geographic diversity found in the region and the isolation imposed by the terrain has, in conjunction with trading and migration, resulted in a diverse set of mostly interrelated maize races. Figure 7 illustrates the sort of

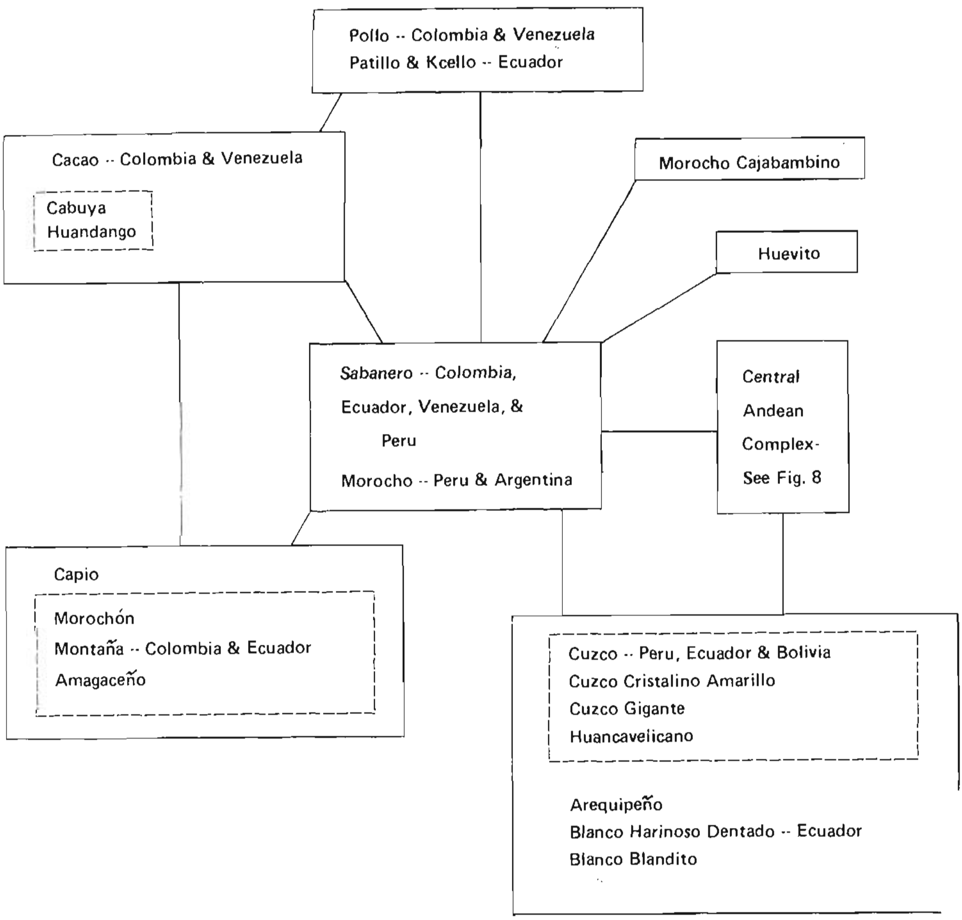

Fig. 7. Racial relationships of the major portion of the corn of Andean South America. Lines joining cells indicate closer relationships (often essentially continuous gradients) between racial groups.

variation that is most commonly encountered in mid to high altitude Andean corn. Sabanero from Venezuela, Colombia, Ecuador, and Peru and, to a lesser extent, Morocho from Peru are races which are central to a number of clines of variation throughout the north Andean region. Sabanero is a tapering, conical-eared flint or flour race with an enlarged base. It typically has very large yellow kernels, but both white and colored forms are common. Huevito seems to have somewhat smaller ears with narrower butts than has Sabanero, while Morocho Cajabamino has smaller kernels and higher row numbers.

Pollo from Venezuela and Colombia, and Patillo and Kcello from Ecuador (Fig. 7) have smaller ears than does Sabanero (see above). These small-eared flints have relatively large, rounded kernels.

Cacao from Colombia and Venezuela appears to be a brown or bronze variant of floury Sabanero (Fig. 7). Cabuya from Colombia and Huandango from Ecuador tend to have lower row numbers than Sabanero; Huandango especially seems to lack the enlarged ear base and conical shape common to Sabanero. Both Cabuya and Huandango appear to share common aleurone coloration with Cacao [and with the lowland Colombian and Venezuelan race Cariaco (discussed in the section on northern South America) as well (Mangelsdorf, 1974)].

Montaña from Colombia and Ecuador, Morochón from Ecuador, and Amagaceño from Colombia have larger (especially longer) ears than Sabanero. Amagaceño appears to include smaller-kernelled variants resembling Pira Naranja or Clavo (see section on northern South America) from Colombia. Capio from Colombia seems to be essentially a floury form of the Montañas.

In the Central Andes, the Cuzcos from Peru, Ecuador, and Bolivia; Huancavelicano and Arequipeño from Peru; and Blanco Harinoso Dentado and Blanco Blandito from Ecuador (Fig. 7) generally have wider, more floury kernels and lower row numbers than Sabanero. These races appear to have been spread northward as a consequence of the agriculture of the Incas and/or their predecessors. The Huancavelicano kernels are pointed as are the kernels of Chillo and Mishca from Ecuador, which may be yellow, floury variants of the same group.

Most of the races of the Central Andean complex in Fig. 8 basically have grenade-shaped ears, the size of which varies inversely with the altitude to which they are adapted. Plant height follows a similar pattern. Additional distinctions among these races are based upon kernel coloring (Kulli from Bolivia, Racimo de Uva from Ecuador, and Morado Canteño and Kculli from Peru are essentially black; Piscorrunto from Peru and Checchi from Bolivia are speckled), row numbering (the Chulpis, Capia from Argentina, Paro from Peru, etc., tend to have very high row numbers), or combinations of these two features with geographic distribution and kernel shape and texture.

In Fig. 8 the races are divided, perhaps somewhat artificially, into three groups. The upper group consists of races having relatively low row numbers (and often highly colored kernels). The middle group consists largely of those races having very high row numbers. This group includes essentially all of the indigenous South American sweet corns (the various Chulpi, Chullpi, and

Chuspillu races from Ecuador, Chile, and Argentina; Peru; and Bolivia, respectively). The third group consists of the very high altitude races Patillo from Bolivia and Confite Puneño from Bolivia and Peru. The latter are adapted to altitudes of about 3.50 km above sea level. They are probably ecologically specialized relatives of the second group in Fig. 8, having reduced ear and plant size as a result of their adaptation to extremely high elevations. Some of the collections having low row numbers, however, may be more closely related to members of either the first group in Fig. 8 or to the Uchuquilla group of 8 to 10-rowed flints to be described next.

Ancestral races for two of Mangelsdorf's (1974) postulated lineage relationships are included in Fig. 8. Mangelsdorf suggests (based mostly on ear shape, row number, and the deleterious nature of the *su* locus) that most, if not all, sweet corns trace their source of the *su* gene to the Andean Chulpi. While the argument weakens as the distance from the Andes increases, it appears to hold for most of the indigenous South American sweet corns. He also suggests that many of the races possessing dark red pericarp and/or bronze, orange, or brown aleurone in addition to floury endosperm are descended from Kculli of Peru.

A group of 8 to 10-rowed, knobby-kernelled flints (Fig. 9) is found in southern Peru and Bolivia in the east central Andes. Representative races include Uchuquilla from Peru and Bolivia, and Karapampa, Chake-Sara, Patillo Grande, and Kcello from Bolivia. Aysuma, Niñuelo, and some of the Patillo-Confite Puneño types from Bolivia also seem to belong to or intergrade into this group. All tend to have broad, flat flinty kernels which easily shell off the rather narrow cobs.

Two Andean popcorns with white, pointed kernels, Canguil from Ecuador and Confite Puntiagudo from Peru, have ears which are very similar to those of Pisankalla and Pisincho of Bolivia and Argentina (see Fig. 9). The Colombian pointed "popcorn" Imbricado also appears to be related to these

Kulli	Granada	Huilcaparu
Kculli	Checchi	Piscorrunto
Racimo de Uva	San Geronimo -- *Huancavelicano*	
Morado Canteno	Altiplano -- Bolivia and Argentina	

Huayleño	Paro	Capia
Shajatu	Marcame	Capio Chileno
Ancashino	Chullpi -- Peru	Chulpi -- Argentina, Ecuador & *Chile*
Paru	Negrito Chileno	Chuspillu -- Bolivia

Confite Puneño -- Bolivia & Peru
Patillo -- Bolivia

Fig. 8. Racial relationships of the corn of the Central Andean Complex.

races (as does the Chilean popcorn, Curagua), but Imbricado often has large kernels similar in size to the flinty Sabaneros (Fig. 7 and adjacent text). Both McClintock (1960) and Mangelsdorf (1974) present evidence that at least some of these Andean pointed popcorns are related to similar Mexican materials.

A third Andean popcorn, Confite Morocho of central Peru (Fig. 9), has yellow kernels, often arranged in eight rows on a very thin cob. It has been hypothesized to be a primitive ancestor to a number of more productive races (Grobman et al., 1961). In what appears to be Mangelsdorf's (1974) most speculative lineage, Confite Morocho is regarded as the ancestral race of a lineage leading to Harinoso de Ocho of Mexico and the Northern Flints of the United States, the so-called "Maíz de Ocho" of Galinat and Gunnerson (1963). Chutucuno Chico, a small, yellow, pearl popcorn from Chile appears to be distinct.

At lower elevations along the west coast, a series of small-eared, early, mostly white, floury corns (Fig. 9) is often found. These include races such as Mochero, Chaparreño, and Huachano from Peru. Large-eared Chancayano from Peru may also belong with this group, but several collections of this race appear to also have Caribbean flint germplasm. At low to intermediate locations in the eastern Andes are found two morphologically similar races,

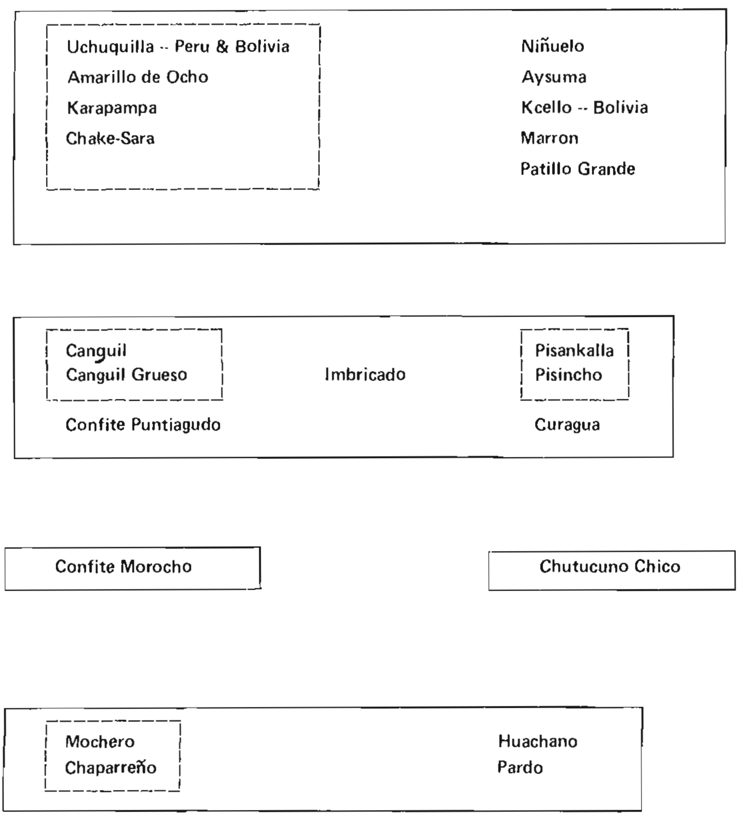

Fig. 9. Racial relationships among some additional Andean races.

Marañon and Chuncho, with dissimilar chromosome knob patterns (Grobman et al., 1961). Both have very tall, late maturing plants with ear types varying from conical, with many rows, usually with rounded to dented kernels, to elongate, often with pointed kernels. Despite their morphological similarity, Chuncho has many chromosome knobs while Marañon has few — it is essentially "Andean" in knob constitution.

With only a few exceptions (the Montañas, Amagaceño, Capio, possibly Pollo, Pisankalla, and Canguil, and especially Cacao) the races included in Figs 7, 8, and 9 basically appear to have the "Andean" chromosome knob pattern described on the basis of McClintock's work (Ramírez et al., 1960). In addition, the results obtained by Van der Walt and Brink (1969) suggest that Andean corn is also unique in possessing nonparamutable *R* alleles.

RACES OF THE USA

Unlike that of most countries of the world, much of the indigenous corn of the USA was replaced by modern hybrids prior to the implementation of an organized program of germplasm preservation.

A significant factor in the success of hybrid corn was the availability of highly selected adapted varieties as sources of the first inbred lines. Many of these varieties had undergone selection for almost a century in the hands of intelligent and ingenious farmers. Progress in population improvement by Robert and James Reid, Isaac Hershey, George Krug, Chester Leaming, and others gave the early USA developers of hybrid corn a source of elite germplasm not duplicated elsewhere in the world.

Unfortunately, after usable inbred lines were developed, these original sources of germplasm were largely ignored. Even less attention was given to the numerous Indian varieties and minor land races found outside the central Corn Belt. Consequently, when, at a later date, interest developed in preserving the corn germplasm of the USA, much of it had long since disappeared.

The literature, beginning with *The History and Present State of Virginia* (Beverly, 1705), contains descriptions of numerous varieties of corn found in specified geographic areas of the USA. Among the more comprehensive treatments are those of Atkinson and Wilson (1914), Will and Hyde (1917), Carter and Anderson (1945), and Brown and Anderson (1947, 1948). Yet, to date, no comprehensive attempts have been made to identify all of the major races of corn known to have existed in this country prior to the advent of hybrid corn. While much of this germplasm has disappeared from cultivation, some of it is still available, albeit frequently in a modified form, in germplasm banks, breeder's collections, etc.

The bulk of USA corn, exclusive of the popcorns and sweet corns, can be assigned to one of the nine broad racial complexes (Fig. 10) as follows:

1. Northern Flints
2. Great Plains Flints and Flours
3. Pima-Papago
4. Southwestern Semidents
5. Southwestern 12 Row
6. Southern Dents
7. Derived Southern Dents

8. Southeastern Flints
9. Corn Belt Dents

There is considerable variation within each of these racial groups, yet to split them into additional entities seems unjustified on the basis of present knowledge.

Northern Flints

The Northern Flints, which also include floury endosperm types, are characterized by ears possessing 8 to 10 rows of crescent-shaped kernels, relatively short, highly tillered, frequently two-eared plants with narrow leaves, well developed husk-leaf blades, and slender culms. The shanks tend to be both long and thick, and the ears are frequently enlarged at the base.

The Northern Flints were, until the early 1800's, the dominant type of corn of eastern North America. Detailed descriptions, illustrations, and the geographic distribution of this racial complex have been given by Brown and Anderson (1947).

The origin of the Northern Flints is still unclear. Galinat and Gunnerson (1963) trace the eight-rowed flint and flour corns of North America to the Mexican race Harinoso de Ocho. Yet, the only important traits the two races seem to have in common are eight rows of kernels and early maturity (the latter is evident only when Harinoso de Ocho is grown under short day conditions). Mangelsdorf and Reeves (1939) suggested the Northern Flints reached eastern North America from the southwestern USA where corns with similar ear types are found. The latter, derived primarily from western

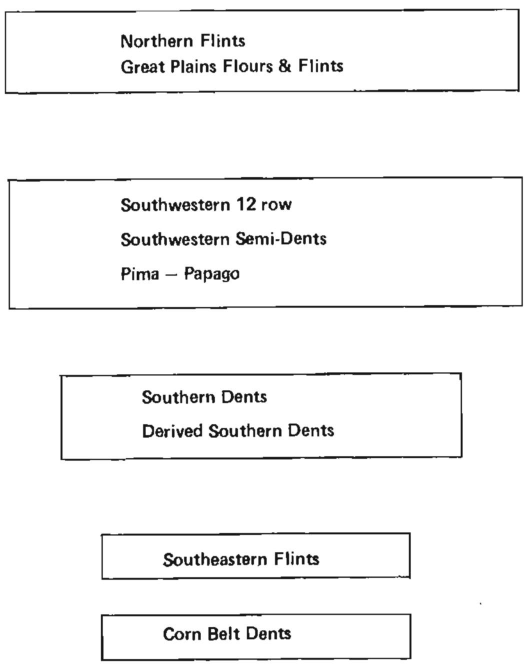

Fig. 10. Racial relationships of USA corn.

Mexico and from the Central Mesa of Mexico, differ from the Northern Flints in several traits including internode and chromosome knob patterns. Most of the southwestern USA corns possess many knobs in contrast to the knobless or nearly knobless Northern Flints (Longley, 1938).

Races which are quite similar in ear morphology to the Northern Flints are found in the highlands of Guatemala (Brown and Anderson, 1947). Within the races San Marceño and Serrano, from highland Guatemala, ear types are found which are quite similar to the Northern Flints. These are eight-rowed ears with crescent-shaped, flint kernels and distinctly enlarged butts. In contrast, Harinoso de Ocho typically possesses flat-topped kernels, distinct husk striations, and compressed butts. However, the route or routes by which these Guatemalan materials may have reached eastern North America is not clear, if indeed they do represent the origin of this race.

The role of the Northern Flints in the evolution of Corn Belt Dents has been described in detail by Anderson and Brown (1952) and Wallace and Brown (1956). The mixing of Northern Flints with the later, higher yielding dents of the South by Colonial farmers resulted in a new race which later completely dominated the corn-producing areas of the USA.

Some of the common varieties of Northern Flints and Flours are Longfellow, Dutton, Smut Nose, Canada Flint, Mammouth Yellow, Wilbur's Flint, Parker's Flint, Thompson Flint, New England Flint, and New York Council Flour Corn.

Great Plains Flints and Flours

Whereas practically all the corn found east of the Mississippi and north of northern Georgia in pre-Colonial times was typical Northern Flint, that found in the Northern Great Plains was much more variable. The flints and flours of this region are obviously related to the Northern Flints. Many of the varieties suggest mixtures between Northern Flints and varieties from the American Southwest. Apparently this mixing is not recent, since specimens from three village sites in South Dakota thought to have been occupied in the mid-1400's also show evidence of similar mixing (Cutler and Agogino, 1960).

Although much of this corn has 8 to 10-rowed ears and wide, crescent-shaped kernels, the frequency of 12 to 14-rowed ears with small, square kernels is much higher than that found east of the Mississippi. Also, the Great Plains Flints and Flours have shorter and more highly tillered plants and shorter tassel branches than do the Northern Flints. They also have a larger number of chromosome knobs than the Northern Flints, although the range of chromosome knob numbers in the two races overlap.

One of the best descriptions of the Great Plains Flints and Flours is that of Will and Hyde (1917). These authors describe a large number of Indian varieties in considerable detail and also give a wealth of information on corn culture by the various tribes, the uses of corn as food, and the place of corn in the Indian ceremonial organization.

Among the more important varieties included in this racial complex are Pawnee White, Mandan Yellow Flour, Arikara Flints, Rhee Flint, Omaha Flour, Otoe White Flour, Ponca Red Flour, Winnebago White, Winnebago Blue, Gehu, Assiniboine, Dakota Squaw, and Santee.

Pima-Papago

Because of the archaeological and ethnological interest in the southwestern USA., corn of the area has been extensively collected. Both prehistoric and modern varieties are reasonably well represented in museum collections, yet only a small part of the historic corn of the area is still available in viable form.

Corn of the southwestern USA has apparently undergone a complicated history and includes germplasm and mixtures of germplasm from at least three geographic areas.

Apparently, one of the earliest types of corn in the area was that of the prehistoric "Basketmakers" (Carter and Anderson, 1945). Some of the modern varieties showing strong Basketmaker influence have been designated Pima-Papago by Anderson and Cutler (1942). This race is characterized by ears which are strongly compressed at the base and which taper gently from a subbasal position to the tip. Row numbers range from 10 to 16, with 10 rows being most common (Carter, 1945), and the tessellate kernels frequently exhibit strong husk striation. The ears are small (about 12 cm in length and 2.5 cm in diameter). The endosperm can be either flinty or floury, with the latter being more frequent. Plants usually possess two or more well developed tillers. Leaves are narrow and the leaf sheaths frequently exhibit purple anthocyanin coloration. The tassels are not particularly distinctive compared with other southwestern USA races. The race is most frequently found among the corn of the Pima, Papago, and Yuma tribes (Carter and Anderson, 1945) and is also represented by the variety Kokoma of the Hopi (Brown et al., 1952).

Pima-Papago or its progenitor probably reached the American Southwest from western Mexico where similar types (Chapalote, Reventador) are still grown. When or how it migrated to southwestern USA is still not clear. Mangelsdorf (1954, 1974) has suggested that Chapalote reached New Mexico (Bat Cave) as early as 1500 B.C. Pima-Papago, while undoubtedly related to prehistoric Chapalote, has apparently undergone considerable introgression with other races (Galinat and Gunnerson, 1963). Cutler and Blake (in press) suggest that a form of Pima-Papago spread eastward through Oklahoma and Arkansas and up the Mississippi River to northern Illinois by 100 A.D., and to the Gulf Coast of Georgia even earlier.

Southwestern Semidents

This race is apparently the product of the introgression of Tuxpeño type dent germplasm from Mexico into the typical 12 to 14-row flint and flour corns of the area. Except for a slight degree of denting, higher number of kernel rows, and more pronounced tassel condensation, the race is quite similar to the Southwestern 12 Row described later. While we have indicated the genes for denting found in Southwestern Semidents probably came from Mexico, the source could have been the Northern Periphery (central and northern Utah, western Colorado) where prehistoric dents have been found (Carter, 1945; Anderson, 1959, n.d.).

Although we feel Southwestern Semidents merit racial recognition, our experience suggests that such material is not recognized as a distinct variety by the tribes who grow it. As an example, typical ears of this race are usually present in collections of Hopi White Flour corn. Yet, to our knowledge, the Hopi, who place considerable emphasis on maintaining varietal purity, make no effort to separate the semident and flour forms of their white corn.

For an excellent illustration of Southwestern Semident, the reader is referred to Plate 3 of Carter and Anderson (1945). Those authors suggest that this race is found at highest frequency near the four corners region of the states of Arizona, New Mexico, Colorado, and Utah.

Southwestern 12 Row

This race of southwestern corn is synonymous with the Eastern Complex of Carter and Anderson (1945). Although these corns are similar morphologically to the Northern Flints of eastern North America, they differ in several important traits. Furthermore, the name Eastern Complex implies an eastern origin, which is questionable.

The plants are short (105 to 120 cm), highly tillered, and the tassels are characterized by long central spikes which average 30+ cm in length. The ears are usually enlarged at the base and are attached to large, indurated shanks. The kernels are wide (though not as strongly crescent-shaped as the Northern Flints) and are arranged in long straight rows. Endosperm is either flinty or floury. Row numbers are usually 12 to 14.

As indicated by Carter and Anderson (1945), Southwestern 12 Row corn is more prevalent among the easternmost Pueblos (mostly east of the Rio Grande River of central New Mexico) than among those in the westernmost part of the area. This lends some credence to the notion that this kind of corn germplasm reached the Southwest from the East, rather than having migrated from the Southwest to the East.

The morphological similarities between Southwestern 12 row and Northern Flints are great, suggesting a common origin or at least a close phylogenetic relationship. Yet, the two races differ markedly in two important traits, that of number of kernel rows and chromosome knob numbers and pattern. The Northern Flints possess few knobs. Many varieties are knobless and only a few varieties are known to possess as many as four to five knobs. In contrast, corn of the southwestern USA, including the Southwestern 12 Row, has many knobs (Longley, 1938; Brown, 1949). Furthermore, the chromosome knob patterns characterizing the Northern Flints and the Southwestern 12 Row are distinctly different (Kato, personal communication).

Southern Dents

This racial complex, prior to its replacement by hybrids, was concentrated in the southeastern USA. In Colonial times, it reached as far north as northern Virginia and Maryland. The western limits of its distribution are not clear, yet it is known to have been present in central Texas.

The Southern Dent complex was described and illustrated by Brown and Anderson (1948). The plants are consistently taller than other USA races. Internodes are condensed above the ear in contrast to the long upper internodes of the Northern and Great Plains Flints. Ears are enveloped in many tight, thick husks, which are usually without husk leaf blades. The plants are usually without tillers. Tassels are highly branched and condensed in contrast to the sparsely branched, non-condensed tassels of the Northern Flints. Numbers of rows of kernels are variable, ranging from 8 to 10 rows in the variety Hickory King to 24 to 26 rows in some selections of Gourdseed. Kernels are usually well dented and the endosperm color is usually white.

Many varieties of Southern Dents appear to be closely related to the dent corns of central Mexico. For example, Tuxpan of the southeastern USA is similar to Tuxpeño; except for cob color, Shoepeg is much like Pepitilla, and Hickory King is quite similar to Tabloncillo and Olotillo. Consequently, certain of the Southern Dents seem simply to be northern counterparts of Mexican races still prevalent in Mexico. The time at which these corns reached the southern USA is still unknown and so are the route or routes by which they migrated northward and eastward from Mexico. We know they were widely grown in the southern and southeastern USA in Colonial times, but little is known of their pre-Colombian history. That they provided at least one-half of the parentage of the more recently evolved Corn Belt Dents is well documented (Brown and Anderson, 1948; Anderson and Brown, 1952).

Some of the better known varieties of Southern Dents are Gourdseed, Shoepeg, Tuxpan, Hickory King, Jellicorse, and Mexican June.

Southeastern Flints

This race seems to represent simply a northern extension of the Caribbean flints from the West Indies and eastern South America. According to the historical record, the race was never an important one in the USA. Yet, it was grown to a limited extent in the southeastern states in Colonial and post-Colonial times. It apparently has also played some role in the evolution of certain of the Derived Southern Dents described below. The name usually applied to this race in the Southeast is Creole Flint. Morphologically, the race is very similar to Cuban Flint or to the Catetos of Argentina, Uruguay, and Brazil. The ears, consisting of 12 to 14 rows of kernels, are slightly compressed at the base and gently tapered toward the tip. Cobs are usually white; the kernels are flinty, and endosperm color varies from deep yellow to orange.

The Southeastern Flints referred to here are limited to historic corns. Prehistoric materials from this area seem to be more closely related to the Northern Flints (Cutler and Blake, in press).

Derived Southern Dents

This complex, although closely related to the Southern Dents, has apparently arisen through the hybridization of the latter with other races. The gross morphology of the ears and plants of the Derived Southern Dents suggests that, in addition to Southern Dents, at least three other races may be involved in the ancestry of this complex. These are the Southeastern Flints, Northern Flints, and Corn Belt Dents.

The Derived Southern Dents tend, on the average, to have somewhat less dented kernels, to have fewer chromosome knobs, and to be more prolific than the Southern Dents. Some varieties have many traits in common with the Southeastern Flints and others suggest admixture with Corn Belt Dents. As a group, the Derived Southern Dents represent the primary source of the genes for prolificacy present in southern corns which has found its way into many modern hybrids grown in that area.

A number of the more prominent varieties of Derived Southern Dents are Caraway's Prolific, Giant Yellow Dent, Horsetooth, Jarvis Golden Prolific, Latham's Double, Mosby's Prolific, Neal's Paymaster, Southern Snowflake, and Whatley's Prolific.

Corn Belt Dents

This racial complex dominated the major areas of corn production in the USA for more than half a century preceding the advent of hybrid corn. Although variable, the race is a well defined entity and easily distinguished from other types of North American corn. The ears are slightly tapered or cylindrical and consist of 14 to 22 straight rows of kernels which are distinctly dented at the tip. Cobs are usually red in color, although white cob varieties are known. Yellow endosperm is predominant, but included in the race are a number of white endosperm varieties. The plant typically has a single stem with strong arching leaves and a heavy, many-branched tassel.

The Corn Belt Dents are of recent origin, having arisen in the 19th century in the eastern part of the USA Corn Belt. They are largely the product of crosses of white Southern Dents with long-eared Northern Flints of the eastern USA. The historical literature is quite clear as to how Corn Belt Dents were developed. Some of the mixing of Southern Dents with Northern Flints was, undoubtedly, accidental and occurred when fields with poor stands of Southern Dents were partially replanted with early flints. However, much of it was the result of deliberate, controlled hybridizing on the part of Colonial farmers who recognized and documented the superior yield of the hybrid populations (Anderson and Brown, 1952; Wallace and Brown, 1956).

Even though Corn Belt Dents did not exist prior to the 19th century, they have provided the basic germplasm for virtually all of the corn now produced in the USA as well as in most other temperate regions of the world. Their contribution, therefore, to total corn production in the world is unparalleled.

Hundreds of varieties of Corn Belt Dents have been described, most of which, unfortunately, have long since disappeared. A few of the more prominent varieties were Reid's Yellow Dent, Lancaster Sure Crop, Krug Yellow Dent, Boone County White, Leaming, Osterland Yellow Dent, and Midland Yellow Dent.

Excluded Races

As indicated earlier, no attempt has been made in this brief treatment of USA corn to include the various sweet corns and popcorns. To date, we have not had an opportunity to study these two types of corn sufficiently to feel confident in assigning them to meaningful racial groups. Many of the sweet corns of the USA are simply sugary counterparts of Northern Flints or higher-row-number dents (Galinat, 1971). These two types, which encompass most of the Bantam and Evergreen varieties, and a third type, Country Gentleman, comprise the bulk of USA sweet corn. Yet, there are other older sorts which do not fit these categories, among which are the sweet corns of the Southwestern Indians.

The popcorns are far more complex and will require much more study before their relationships are understood.

In addition to the popcorns and sweet corns, we have excluded two other corn groups — the existence of which we should at least recognize. These are the corns of the Seminole of Florida and the "tamale" corns of southern California. Some of the Seminole corns are quite distinct from the flints and flours of the northeastern USA. But here again, our experience with these corns does not permit us to attempt to classify them. Neither have the "tamale" corns of the southern West Coast of the USA been studied in detail, yet these appear to represent northern counterparts of western Mexican varieties, which probably reached southern California by way of Arizona.

EFFECTIVE SOURCES OF GERMPLASM AMONG LOWLAND TROPICAL RACES

Among the collections of corn germplasm of the Western Hemisphere now existing in the various seed banks, there is undoubtedly much material which should be useful to the breeder. However, to date, little of this material has been systematically evaluated with respect to its usefulness. It is primarily for this reason that breeders have not made full use of the germplasm that is available. Most breeding programs are operated in such a way as to make impractical for the individual breeder the screening of vast numbers of accessions in order to identify the few genotypes of interest or value at the moment.

A major problem encountered in evaluating tropical materials for possible use in temperate regions is the very late maturity which these materials often exhibit. One reason for this is that almost all corn flowers more rapidly under short day growing conditions given equivalent temperatures. Tropical varieties adapted to 12 to 14-hour daylengths flower much later under the longer days typical of temperate regions. It is for this reason that use of these materials in the USA has generally either been confined to the South or limited to very early (hence inherently low yielding) types such as Zapalote Chico of Mexico.

While extreme response to daylength is probably fairly simply inherited, it effectively blocks most evaluation of tropical materials in temperate regions. For example, most collections of the closely related races Tuxpeño and Vandeño have about equally late maturity under temperate, long day conditions. However, most typical Tuxpeño collections from Mexico are later than Vandeño collections under short day conditions; and thus Tuxpeno is probably less adaptable for use in temperate regions despite its favorable yield potential. The daylength response may totally mask the true maturity of the material. One collection of Pepitilla flowers in less than 65 short days (south Florida, winter) while requiring about 150 long days (North Carolina, summer). (A widely used, adapted commercial hybrid flowers in about 75 and 77 days each, respectively, under the same conditions).

Such responses to daylength suggest that the degrees of *apparent* adaption of tropical materials to a temperate environment are probably negatively correlated (if correlated at all) with their breeding potentials for that region. This conflicts with the conclusions reached by Kramer and Ullstrup (1959), although their data can be interpreted to support this viewpoint. They showed that yields of topcrosses of semiadapted exotics onto adapted materials were closely correlated with maturity. In fact, almost all exotics offering potential yield improvement are very late maturing under USA conditions (regardless of their maturities in the tropics), while a number of low yielding exotics (often popcorns) are much earlier. Thus, such a correlation of exotic topcross yields with maturity would be expected for both developmental and genetic reasons.

Limited published work with synthetics in the USA adds support for the view that "preadapted" tropical materials (i.e., those that are very early in the tropics) are not good candidates for yield improvement in temperate regions. Troyer and Brown (1972) have shown that a synthetic involving the very early maturing Mexican races Zapalote Chico and Zapalote Grande initially outyielded two other synthetics involving other, later Mexican materials and West Indies materials, respectively. (These synthetics also included germplasm from elite USA inbreds). Selection for earliness in all three composites appears to have lowered the yield of the Zapalote Chico synthetic to the point where the other synthetics (involving late Mexican and West Indian materials) have higher yields. In contrast, Hallauer and Sears (1972) have shown that late maturing but variable tropical materials — in this case ETO, a synthetic described later — can effectively be selected for much earlier maturity and lower ear height, using relatively few cycles of mass selection or by a single generation of crossing with early maturing elite lines. In addition, Eberhart (1971) and Hallauer (1972) have shown that several synthetics containing large proportions of tropical germplasm (which in itself would largely be very poorly adapted) do show promise as source materials for breeding programs in the USA.

Much work with exotics has been conducted with composites or synthetics, whose ancestry often cannot be clearly traced. While this work has apparently been successful, we have learned less from it than from earlier corn breeding efforts with open-pollinated varieties. In the earlier work, specific sources (such as the varieties Lancaster and Reid's) of successful inbred lines were fairly quickly identified. Such identification has occurred to a lesser extent with the exotic races, in part due to the emphasis on synthetics.

Despite the lack of a systematic evaluation of the so-called "exotic" corn germplasm, some information has been obtained on the relative usefulness in breeding of a number of races, varieties, composites, etc. We have attempted to summarize the accessible published information below; much, of course, remains unpublished.

Wellhausen (1965) has reported on the yield potential of a number of Mexican and Caribbean races and populations which he feels merit additional use in breeding. Considerable information on yields of Mexican races comes from the results of a yield test of all possible crosses of the 25 recognized races of Mexico. This test was conducted near Celaya in Central Mexico. The inter-racial crosses were compared with an adapted hybrid, H352. Sixteen of the inter-racial crosses yielded more than the check hybrid. More importantly, 15 different races were represented among the 16 highest yielding inter-racial crosses. Among the highest yielding crosses were Pepitilla × Chalqueño, Pepitilla × Tuxpeño, Maíz Dulce × Comiteco, Comiteco × Celaya, and Pepitilla × Maíz Dulce.

The data reported by Wellhausen (1965) did not include many important agronomic traits, and, for this reason, it is not possible to assess from these data the practical usefulness of this obviously high yielding germplasm. (Chalqueño and Pepitilla have very weak roots, while Tuxpeño and Comiteco tend to have very late maturity even when grown under short day conditions). However, such work is fairly typical of what needs doing in many tropical regions: widescale testing of crosses among a diverse set of materials. For example, Darrah et al. (1972) found that crosses between a local Kenyan variety and a collection of the Ecuadorian race Montaña were suitable for production as one of Kenya's first hybrids. Similarly, in Brazil, Paterniani (1970, 1972) has reported that intervarietal and topcross hybrids involving Caribbean germplasm (mostly Cuban and Caribbean Tropical Flints) with Tuxpeño derivatives outyield the local H6999B double cross check by as much as 20% with improved agronomic traits as a bonus.

Among the Caribbean germplasm evaluated by Wellhausen (1965), a collection belonging to the race Tusón and designated Antigua 2D and a composite of collections called Antigua Group 2 have been shown to combine well with Tuxpeño and with Corn Belt Dents. This material is relatively early and short in stature as compared to most other tropical varieties.

The Cuban Flints are reported by Wellhausen (1965) to combine well with the Mexican dents, especially Tuxpeño. Timothy (1963) reported that the Cuban Flints have been widely used in Colombian corn breeding programs along with Tuxpeño, Costeño, Puya Grande, and the synthetics ETO and Venezuela I, discussed later.

Our experience in tropical corn breeding supports, in general, Wellhausen and Timothy's conclusions relative to the usefulness of the germplasm discussed above. [We might note that the evaluation of germplasm utility would be greatly facilitated if the International Maize Adaptation Nurseries (IMAN) program (CIMMYT 1972a, 1972b, 1974) were expanded and publicized. These trials included materials from 13 countries tested in 47 countries in 1971. Outstanding materials in the 1970 trials were from Australia, Jamaica, Kenya, Brazil, Mexico, and Peru.] The sections which follow include additional observations relative to the performance of the races mentioned earlier and refer also to other sources of germplasm which we believe to be of interest.

Mexican Dents

The most outstanding single source of Mexican Dents is the race Tuxpeño. This race, widely distributed on the east coast of Mexico, possesses excellent combining ability, good stalk quality, and good resistance to *Helminthosporium spp.* Its principal disadvantages are late maturity, tall plants with high ear placement, poor roots, and susceptibility to sugarcane mosaic.

There are several derivatives of Tuxpeño, both white and yellow. Some of these have given excellent performance in crosses with lines derived from Coastal Tropical Flint and Tusón. Some Tuxpeño lines have also exhibited good combining ability with material derived from Cuban Flint and Coastal Tropical Flint (especially the varieties Tiquisate, Mayorbela, and Venezuela I, described later).

Tuxpeño germplasm is now widespread throughout the tropical world and is an important constituent of many improved varieties and hybrids.

Tusón

Tusón is likely one of the best sources of tropical corn germplasm known today. Lines derived from this race combine well with lines from Tuxpeño, Cuban Flint, Chandelle, and southern USA dents. The race possesses excellent ear type, good grain quality, and a high degree of tolerance to sugarcane mosaic.

Coastal Tropical Flint

This race is widely spread throughout the lowland tropics and its influence is apparent whenever tropical corn is grown on a commercial scale. Among the many outstanding tropical varieties which have Coastal Tropical Flint in their background are ETO, Tiquisate Golden Yellow, Metro, Mayorbela, and Venezuela I. Tiquisate was developed in the 1940's by Dr. I.E. Melhus and his coworkers at the Iowa State University Tropical Research Station in Guatemala. It was derived from two Cuban varieties (probably Cuban Flint and Coastal Tropical Flint) to which were added some local varieties from coastal Guatemala. The plants and ears of Tiquisate resemble Cuban Flint. A selection of Tiquisate, developed at Bogor, Indonesia, and known as Metro, is used extensively as a commercial variety in that country. Mayorbela was developed in Puerto Rico in the 1930's. It traces back to the Mayor farm and the Isabela substation of the Mayaguez Experiment Station. In the late 1930's, this source of material was outcrossed to an inbred line (probably from the USA) followed by selection within the resulting population. Mayorbela is a reasonably good source of earliness, stalk strength, low ear placement, and grain quality. Venezuela I was developed by Langham (1942) in Venezuela primarily from Caribbean races and varieties.

Coastal Tropical Flint has been a productive source of elite tropical lines. In addition to combining ability, these lines contribute to excellent grain quality, good husk cover, stalk quality, good roots, and resistance to *Helminthosporium* spp.

Cuban Flint-Cateto

This racial complex, known as Cuban Flint in the Caribbean Islands, as Cateto in Brazil, and Argentine Flint in Argentina, is particularly useful in hybrid combinations with dents. The race and lines derived from it combine well with Tusón, Tuxpeño, and Coastal Tropical Flint. Cuban Flint is susceptible to virus diseases and must therefore be combined with virus-resistant lines, if it is to be used in areas where corn virus diseases are prevalent.

Chandelle

Among tropical germplasms, Chandelle is an excellent source of prolificacy, low ear placement, and virus resistance. It combines well with Coastal Tropical Flint and Haitian Yellow. The race and lines derived from it tend to have poor roots.

Haitian Yellow

Collections of this race from the vicinity of Jeremie, Haiti, have proven to be an excellent source of root and stalk strength, traits which are not easy to come by in tropical corn. Because of its outstanding stalk and root qualities, Haitian Yellow should play an increasingly important role in tropical corn improvement.

ETO

This synthetic variety developed in Colombia in the 1940's by Chavarriaga (1966) has contributed significantly to corn improvement in the tropics and subtropics. The variety has a broad genetic base, which includes the Colombian races Común and Chococeño and the synthetic Venezuela I. The latter consists primarily of Caribbean races and varieties. To this broad mixture, known as Colombia I, were later added numerous lines and varieties from Mexico, Puerto Rico, Cuba, Venezuela, Brazil, Argentina, and the USA. Selection over a period of years resulted in the new variety ETO. The abbreviation represents "Estacion Tulio Ospina," the station at Medellín where the selection work was done.

ETO is available in both white and yellow endosperm forms. It is high yielding and combines well with the Tuxpeños. The variety includes a wide range of maturities, the earliest of which are no later than some lines in use in the Central USA Corn Belt.

Despite the excellent performance of ETO in many tropical areas, it appears to have generally poor adaptation to conditions in the Caribbean (Sehgal, 1966). It is also quite susceptible to sugarcane mosaic.

ACKNOWLEDGMENTS

Paper No. 4444 of the Journal Series of the North Carolina Agric. Exp. Stn., Raleigh, NC 27607. This investigation was supported in part by National Institutes of Health Research Grant GM 11546 from the National Institute of General Medical Sciences.

LITERATURE CITED

Anderson, Edgar. 1943. Races of *Zea mays*. II. A general survey of the problem. Acta Americana 1:58-68.

----. 1944a. Homologies of the ear and tassel in *Zea mays*,Ann., Mo. Bot. Gard. 31:325-344.

----. 1944b. Maiz Reventador. Ann. Mo. Bot. Gard. 31:301-316.

----. 1945. Maize in the New World. p. 27-42. *In* C.M. Wilson (ed.), New crops for the New World. MacMillan, New York. 295 p.

----. 1946. Maize in Mexico — A preliminary survey. Ann. Mo. Bot. Gard. 33:147-247.

----. 1947. Field studies of Guatemalan maize. Ann. Mo. Bot. Gard. 34:433-467.

----. 1959. Zapalote Chico: An important chapter in the history of maize and man. Actas del Congr. Int. de Americanistas (San José) 33:230-237.

----. n.d. Corn before Columbus. Pioneer Hi-Bred Corn Company, Des Moines, Iowa. 24 p.

----, and W.L. Brown. 1952. Origin of Corn Belt maize and its genetic significance. p. 124-148 *In* J.W. Gowen (ed.) Heterosis. Iowa State Coll. Press, Ames.

----, and ----. 1953. The popcorns of Turkey. Ann. Mo. Bot. Gard. 40:33-48.

----, and H.C. Cutler. 1942. Races of *Zea mays*: I. Their recognition and classification. Ann. Mo. Bot. Gard. 29:69-89.

Atkinson, Alfred, and M.L. Wilson. 1914. Corn in Montana — history, characteristics, and adaptation. Montana Agric. Coll. Exp. Stn. Bull. 107.

Beverly, R. 1705. The history and present state of Virginia. London. (Republished 1947. Univ. of North Carolina Press, Chapel Hill. 366 p).

Blumenschein, Almiro. 1973. Chromosome knob patterns in Latin American maize. p. 271-277 *In* Adrian M. Srb (ed.), Genes, enzymes and populations. Plenum Publ. Corp., New York.

----, and R. Deuber. 1968. Milhos cultivados no Nordeste Brasileiro. O Solo 60 (2): 15-27.

Brandolini, A. 1969. European races of maize. Annu. Corn Sorghum Res. Conf. Proc. 24:36-49.

----. 1970a. Maize. p. 273-309 *In* O.H. Frankel and E. Bennett (eds.), Genetic resources in plants — their exploration and conservation. F.A. Davis Co., Philadelphia.

----. 1970b. Razze Europee di maiz. Maydica 15:5-27.

----. 1971. Preliminary report on South European and Mediterranean maize germ plasm. p. 108-116. *In* I. Kovacs (ed.) Proc. of the Fifth Meeting of the Maize and Sorghum Sect. of EUCARPIA. Akadémiai Kiadó, Budapest. 290 p.

----, and G. Avila. 1971. Effects of Bolivian maize germ plasm in South European maize breeding. p. 117-135 *In* I. Kovács (ed.). Proc. of the Fifth Meeting of the Maize and Sorghum Sect of EUCARPIA. Akademiai Kiadó, Budapest. 290 p.

----, and G. Mariani. 1968. Il germplasma italiano nela fase attuale del miglioramento genetico del mais. Genet. Agric. 22:189-206.

Brieger, F.G., J.T.A. Gurgel, E. Paterniani, A. Blumenschein, and M.R. Alleoni. 1958. Races of maize in Brazil and other eastern South American countries. Natl. Acad. Sci. — Natl. Res. Council Publ. 593. Washington, D.C. 283 p.

Brown, W.L. 1949. Numbers and distribution of chromosome knobs in United States maize. Genetics 34:524-536.

----. 1953. Maize of the West Indies. Trop. Agric. 30:141-170.

----. 1960. Races of maize in the West Indies. Natl. Acad. Sci. — Natl. Res. Council Publ. 792. Washington, D.C. 60 p.

----, and E. Anderson. 1947. The northern flint corns. Ann. Mo. Bot. Gard. 34:1-29.

----, ----. 1948. The southern dent corns. Ann. Mo. Bot. Gard. 35:255-268.

----, E.G. Anderson and Roy Tuchawena, Jr. 1952. Observations on three varieties of Hopi maize. Am. J. Bot. 39:597-609.

Carter, G.F. 1945. Plant geography and culture history in the American Southwest. Viking Fund Publ. Anthropol. No. 5. New York. 140 p.

----, and Edgar Anderson. 1945. A preliminary survey of maize in the southwestern United States. Ann. Mo. Bot. Gard. 32:297-322.

Chavarriaga, E. 1966. Maíz ETO, una variedad producida en Colombia. Inst. Colombiano Agropecuario. Separata de la Revista I.C.A. 1(1):5-30.

CIMMYT. 1972. International maize adaptation nurseries (IMAN). Annu. Rep. 1970-91:96-98. Mexico City. 115 p.

Committee on Genetic Vulnerability of Major Crops. 1972. Genetic vulnerability of major crops. Natl. Acad. Sci. Washington, D.C. 307 p.

CIMMYT, 1972a. International maize adaptation nurseries (IMAN). Annu. Rep. 1970-91:96-98. Mexico City. 115 p.

----. 1972b. Results of the first international maize adaptation nursery (IMAN) 1970-71. CIMMYT Information Bull. No. 7. Mexico City. 51 p.

CIMMYT. 1974. Results of the second and third international maize adaptation nursery (IMAN) (1971-72, 1972-73). CIMMYT Information Bull. No. 12. Mexico City. 118 p.

Committee on Genetic Vulnerability of Major Crops. 1972. Genetic vulnerability of major crops Natl. Acad. Sci. Washington, D.C. 307 p.

Committee on Preservation of Indigenous Strains of Maize. 1954. Collections of original strains of corn, I. Natl. Acad. Sci. — Natl. Res. Council. Washington, D.C. 300 p. (mimeo).

----. 1955. Collections of original strains of corn, II. Natl. Acad. Sci. — Natl. Res. Council. Washington, D.C. 298 p. (mimeo).

Costa-Rodrigues, L. 1969. Races of maize in Portugal. Agron. Lusitana 31:239-284.

Covor, Alexandru. 1972. Rasele De Porumb Din Romania. Acad. De Ştiünte Agricole Şi Şilvice. Bucuresti 186 p.

Cutler, H.C. 1946. Races of maize in South America. Bot. Mus. Leafl., Harvard Univ. 12:257-299.

----, and G.A. Agogino. 1960. Analysis of maize from the Four Bear Site and two other Arikara locations in South Dakota. Southwestern J. of Anthropol. 16:312-316.

----, and L.W. Blake. In press. North American Indian Corn. Handbook of North American Indians. Vol. 3. Smithsonian Inst. Washington, D.C.

Darrah, L.L., S.A. Eberhart, and L.H. Penny. 1972. A maize breeding methods study in Kenya. Crop Sci. 12: 605-608.

Eberhart, S.A. 1971. Regional maize diallels with U.S. and semi-exotic varieties. Crop Sci. 11:911-914.

Edwards, R.J., and E.R. Leng. 1965. Classification of some indigenous maize collections from southern and southeastern Europe. Euphytica 14:161-169.

Galinat, Walton C. 1970. The cupule and its role in the origin and evolution of maize. Massachusetts Agric. Exp. Stn. Bull. 585. Amherst. 24 p.

----. 1971. The evolution of sweet corn. Massachusetts Agric. Exp. Stn. Res. Bull. 591. Amherst. 20 p.

----, and J.H. Gunnerson. 1963. Spread of eight-rowed maize from the prehistoric Southwest. Bot. Mus. Leafl., Harvard Univ. 20:117-160.

Girola, C.D. 1919. Variedades de maiz cultivadas en Argentina: maices Argentinos y aclimatados. Talleres Graficos J. Weiss y Preusche, Buenos Aires. 169 p.

Goodman, M.M. 1967. The races of maize: I. The use of Mahalanobis' generalized distances to measure morphological similarity. Fitotec. Latinoamer. 4(1):1-22.

----. 1968. The races of maize: II. Use of multivariate analysis of variance to measure morphological similarity. Crop Sci. 8:693-698.

----. 1972. Distance analysis in biology. Syst. Zool. 21:174-186.

----, and R. McK. Bird. In press. The races of maize. IV. Economic Botany.

----, and E. Paterniani. 1969. The races of maize. III. Choices of appropriate characters for racial classification. Econ. Bot. 23:265-273.

Grant, U.J., W.H. Hatheway, D.H. Timothy, C. Cassalett D., and L.M. Roberts. 1963. Races of maize in Venezuela. Natl. Acad. Sci. — Natl. Res. Council Publ. 1136. Washington, D.C. 92 p.

Grobman, Alexander, Wilfredo Salhuana, and Ricardo Sevilla, with P.C. Mangelsdorf. 1961. Races of maize in Peru. Natl. Acad. Sci. — Natl. Res. Council Publ. 915. Washington, D.C. 374 p.

Hallauer, A.R. 1972. Third phase in the yield evaluation of synthetic varieties of maize. Crop Sci. 12:16-18.

----, and J.H. Sears. 1972. Integrating exotic germ plasm into Corn Belt maize breeding programs. Crop Sci. 12:203-206.

Hatheway, W.H. 1957. Races of maize in Cuba. Natl. Acad. Sci. — Natl. Res. Council Publ. 453. Washington, D.C. 75 p.

Hernandez X., E. 1949. Plant exploration in Cuba. Report to Dr. J.G. Harrar, Director of the Rockefeller Agricultural Program in Mexico. April 1, 1949. Mexico City. (mimeo).

----, and G. Alanis F. 1970. Estudio morfologico de cinco nuevas razas de maiz de la Sierra Madre Occidental de Mexico: Implicaciones filogeneticas y fitogeograficas. Agrociencia 5:3-30.

----, and G. Alanis F. 1970. Estudio morfologico de cinco nuevas razas de maiz de la Sierra Madre Occidental de Mexico: Implicaciones filogeneticas y fitogeograficas. Agrociencia 5:3-30.

Kato Y., T.A. 1975. Cytological studies of maize *(Zea mays* L.) and teosinte *(Zea mexicana* Schrader Kuntze) in relation to their origin and evolution. Mass. Agric. Exp. Stn. Bull. 635. Amherst, Mass.

----, and A. Blumenschein. 1967. Complejos de nudos cromosómicos en los maices de América. Fitotec. Latinoamer. 4(2):13-24.

Kramer, H.H., and A.J. Ullstrup. 1959. Preliminary evaluation of exotic maize germ plasm. Agron. J. 51:687-689.

Kuleshov, N.N. 1929. The geographical distribution of the varietal diversity of maize in the world. Trudy po Prikladnoi Botanike, Genetike, i Seleksii (Bull. Appl. Bot., Genet. and Plant Breeding, Lenin Acad. Agric. Sci., U.S.S.R.) 20:506-510.

----. 1930. The maize of Mexico, Guatemala, Cuba, Panama, and Colombia. p. 492-502 *In* S.M. Bukasov (ed.) The cultivated plants of Mexico, Guatemala, and Colombia. Trudy po Prikladnoi Botanike, Genetike, i Seleskii (Bull. Appl. Bot., Genet. and Plant Breeding, Lenin Acad. Agric. Sci., U.S.S.R.) Prilozhenie (Suppl.) 47.

Langham, D.C. 1942. Venezuela I, una seleccion de maiz recomendable. Ministerio de Agricultura y Cria. Cir. No. 2. Caracas, Venezuela.

Leng, E.R., A. Tavčar, and V. Trifunović. 1962. Maize of southeastern Europe and its potential value in breeding programs elsewhere. Euphytica 11:263-272.

Longley, A.E. 1938. Chromosomes of maize from North American Indians. J. Agric. Res. 56:177-195.

----. 1941. Chromosome morphology in maize and its relatives. Bot. Rev. 7:263-289.

----, and T.A. Kato Y. 1965. Chromosome morphology of certain races of maize in Latin America. Int. Center for the Improvement of Maize and Wheat Res. Bull. No. 1. Chapingo, Mexico. 112 p.

Mangelsdorf, P.C. 1954. New evidence on the origin and ancestry of maize. Am. Antiquity 19:409-410.

----. 1974. Corn, its origin, evolution, and improvement. Harvard Univ. Press. Cambridge, Mass. 262 p.

----, and J.W. Cameron. 1942. Western Guatemala — A secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl., Harvard Univ. 10:217-252.

----, and R.G. Reeves. 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Stn. Bull. 574. College Station, Texas. 315 p.

Marino, A.E. 1934. La agricultura en la Quebrada de Humahuaca (Jujuy). Lab. de Bot. de la Fac. de Agron. y Vet. Buenos Aires. 65 p. (mimeo).

McClintock, Barbara. 1959. Genetic and cytological studies of maize. Carnegie Inst. Washington Yearb. 58:452-456.

----. 1960. Chromosome constitutions of Mexican and Guatemalan races of maize. Carnegie Inst. Washington Yearb. 59:461-472.

Mochizuki, N. 1968. Classification of local strains of maize in Japan and selection of breeding materials by application of principal component analysis. p. 173-178 *In* Symposium on Maize Production in Southeast Asia. Agriculture, Forestry, and Fisheries Research Council, Ministry of Agriculture and Forestry, Kasumigaseki, Chiyoda-ku, Tokyo, Japan.

Nelson, Jr., O.E. 1952. Non-reciprocal cross sterility in maize. Genetics 37:101-124.

----. 1960. The fourth chromosome gametophyte factor in some Central and South American races. Maize Genet. Coop. News Letter 34:114-116.

Nickerson, N.H. 1953. Variation in cob morphology among certain archaeological and ethnological races in maize. Ann. Mo. Bot. Gard. 40:79-111.

----. 1954. Morphological analysis of the maize ear. Am. J. Bot. 41:87-92.

----. and A.P. Covich. 1966. A collection of maize from Darién, Panama. Econ. Bot. 20:434-440.

Parker, V., I., and O. Paratori B. 1965. Distribución geográfica, clasificación, y estudio del maiz *(Zea mays)* en Chile. Agric. Tecnica 25(2):70-86.

Parodi, L.R. 1932. Notas preliminares sobre plantas subamericanas cultivadas en la provincia de Jujùy.Gaea 4(1):19-28.

----. 1935. Relaciones de la agricultura prehispánica con la agricultura Argentina actual. Anales Acad. Nac. Agron. y Vet. de Buenos Aires 1:115-167.

Paterniani, E. 1970. Heterose em cruzamentos intervarietais de milho. Universidade de São Paulo, Escola Superior de Agricultura "Luiz de Queiroz," Departmento e Instituto de Genética Relatório Cientifico 1970:95-100. Piracicaba, S.P., Brazil. 158 p.

----. 1972. Capacidade de combinação de linhagens exóticas em cruzamento intervarietal. Universidade de São Paulo. Excola Superior de Agricultura "Luiz de Queirox." Departmento e Instituto de Genética Relatório Cientifico 1972:83-85. Piracicaba. S.P., Brazil. 128 p.

----. and M.M. Goodman. In press. Races of maize in Brazil and adjacent areas. Int. Center Improvement of Corn and Wheat Publ. Mexico City.

Patiño. V.M. 1956. El maiz Chococito. noticia sobre su cultivo en America ecuatorial. Am. Indigina 16:309-346.

Paviličić, J. 1971. Contribution to a preliminary classification of European open-pollinated maize varieties. p. 93-107 *In* I. Kovács (ed), Proc. Fifth Meeting of the Maize and Sorghum Sect. of EUCARPIA. Akadémiai Kiadó, Budapest. 290 p.

----. and V. Trifunovic. 1966. A study of some important ecologic corn types grown in Yugoslavia and their classification. J. Sci. Agric. Res. 19(66):45-63 [also in Arhiv za Poljoprivredne Nauke 19(66):44-62].

Ramirez E., Ricardo. D.H. Timothy, Efrain Diaz B., and U.J. Grant, with G.E. Nicholson Calle. Edgar Anderson, and W.L. Brown. 1960. Races of maize in Bolivia. Natl. Acad. Sci. — Natl. Res. Council Publ. 747. Washington. D.C. 159 p.

Roberts. L.M., U.J. Grant, Ricardo Ramirez E., W.H. Hatheway, and D.L. Smith, *with* P.C. Mangelsdorf. 1957. Races of maize in Colombia. Natl. Acad. Sci. — Nat. Res. Council Publ. 510. Washington, D.C. 153 p.

Rodriguez, A., M. Romero, J. Quiroga, and G. Avila, with A. Brandolini. 1968. Maices Bolivianos, F.A.O. Rome, Italy. 243 p.

Sanchez-Monge, E. 1962. Razas de maíz en España. Ministerio de Agricultura Monografias No. 13. Madrid. 179 p.

Sehgal, S.M. 1966. Inbred-hybrid method of maize improvement. Proc. Caribbean Foods Crops Soc. 4:45-51.

Sprague, G.F. 1971. Genetic vulnerability in corn and sorghum. Proc. Annu. Corn and Sorghum Res. Conf. 26:96-104.

Stevenson, J.C., and M.M. Goodman. 1972. Ecology of exotic races of maize. I. Leaf number and tillering of 16 races under four temperatures and two photoperiods. Crop Sci. 12:864-868.

Stonor, C.R., and E. Anderson. 1949. Maize among the hill peoples of Assam. Ann. Mo. Bot. Gard. 36:355-404.

Sturtevant, E.L. 1899. Varieties of corn. USDA Office of Exp. Stn. Bull. 57. Washington, D.C. 108 p.

Suto, Tihara, and Yoshio Yoshida. 1956. Characteristics of the Oriental maize. p. 375-530. *In* H. Kihara (ed.), Land and crops of Nepal Himalaya. Vol. II. Fauna and Flora Research Society, Kyoto University. Kyoto, Japan. 563 p.

Timothy, D.H. 1963. Genetic diversity, heterosis, and the use of exotic stocks in maize in Colombia. p. 581-593 *In* Statistical genetics and plant breeding. Natl. Acad. Sci. — Natl. Res. Council Publ. 982. Washington, D.C. 623 p.

----, W.H. Hatheway, U.J. Grant, Manuel Torregroza C., Daniel Sarria V., and Daniel Varela A. 1963. Races of maize in Ecuador. Natl. Acad. Sci. — Natl. Res. Council Publ. 975. Washington, D.C. 147 p.

----, Bertulfo Peña V., and Ricardo Ramirez E., with W.L. Brown and Edgar Anderson. 1961. Races of maize in Chile. Natl. Acad. Sci. — Natl. Res. Council Publ. 847. Washington, D.C. 84 p.

Troyer, A.F., and W.L. Brown. 1972. Selection for early flowering in corn. Crop Sci. 12:301-304.

Van der Walt, W.J., and R.A. Brink. 1969. Geographic distribution of paramutable and paramutagenic *R* alleles in maize. Genetics 61:677-695.

----, Alejandro Fuentes O., and Antonio Hernández Corzo, with P.C. Mangelsdorf. 1957. Races of maize in Central America. Natl. Acad. Sci. — Natl. Res. Council Publ. 511. Washington, D.C. 128 p.

---, L.M. Roberts, and E. Hernández X., with Paul C. Mangelsdorf. 1951. Razas de maíz en México. Su origen, características, y distribución. Folleto Técnico Secretaria de Agricultura y Ganaderia No. 5. Mexico, D.F. 237 p.

----, L.M. Roberts, and E. Hernández X., with Paul C. Mangelsdorf. 1952. Races of maize in Mexico. The Bussey Inst., Harvard Univ. Cambridge, Mass. 223 p.

Wallace, H.A., and W.L. Brown. 1956. Corn and its early fathers. Michigan State Univ. Press. East Lansing. 134 p.

Wellhausen, E.J. 1965. Exotic germ plasm for improvement of corn belt maize. Proc. Annu. Hybrid Corn Ind.-Res. Conf. 20:31-50.

Will, G.F. and G.E. Hyde. 1917. Corn among the Indians of the Upper Missouri. St. Louis. (Republished 1964, Univ. of Nebraska Press, Lincoln. 323 p.)

Wolf, M.J., H.C. Cutler, M.S. Zuber, and U. Khoo. 1972. Maize with multilayer aleurone of high protein content. Crop Sci. 12:440-442.