PATTERNS OF VARIATION IN EXOTIC RACES OF MAIZE (ZEA MAYS, GRAMINEAE) IN A NEW GEOGRAPHIC AREA

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ABSTRACT.-Over the past 3000 years exotic races of maize (Zea mays L.) were introduced, evaluated, sometimes discarded but often modified, and incorporated into North American agriculture. Present-day northern Mexico has served as a source area for many races. Whether maize was able to produce (i.e., yield acceptable products and viable propagules) in the new area or not after the first growing season was critical. A key factor in the success may have been the method of dispersal, for example gradual diffusion or long-distance jump-dispersal. This study examined the biological patterns of variability for the long distance jump-dispersal by using five contemporary Tarahumara races of maize from northern Mexico and a Papago race from southern Arizona as exotics and one contemporary Puebloan race, Hopi Blue maize, from southwestern United States as a native standard. Comparisons among morphological characters, developmental patterns, and productivity were made to develop the baseline for evaluating the biological and ecological factors for successful introduction and change of a component in the subsistence agricultural system. The maize was grown under a uniform environment in the experimental gardens of the Dolores Archaeological Program in southwestern Colorado.

INTRODUCTION

The movement of cultivated plants is as important as the origin of agriculture and the spread of agricultural techniques. The dispersal of cultivated plants provides information on the history of the plants as well as evidence of human contacts and trade (Carter 1945, 1979; Heiser 1965; Pickersgill 1972; Sauer 1969). Usually the evidence for dispersal of cultivated plants is derived from both modern and archaeological specimens which represent plants that were successfully introduced and established. These plants may have a particular geographic pattern and may be retained today or may be associated with past periods. The extant plants could also reflect long-term presence with modifications or could represent recent introductions. Plants may have been introduced in the past and their occurrence at different time periods would be recorded archaeologically (Ford 1979; Harlan and de Wet 1973). These patterns as well as variations in them tell us of the *products* of introduction of new plants but they reveal limited information about the *process* of introduction or exotics.

Recent reevaluation of archaeological plant remains in North America suggests that complexes of various crops moved along certain pathways at various time periods from present-day Mexico into present-day United States (Ford 1980). The developing picture suggests the movement of different plants at different times. One possible interpretation of this pattern is that only some plants were successful at any particular place at a given time period while other plants were not successful. What happened in the process of introduction? We only have the remnants of the final products left today.

Maize (Zea mays L.) has received considerable attention in the last forty years with respect to its origin and diffusion. Maize agriculture appears to have been introduced into

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the American Southwest by about 2000-1000 BC and slowly spread northward into Colorado and Utah by about 200 BC (Ford 1980; Woodbury and Zubrow 1979). The routes of the Upper and Lower Sonoran Complexes for the introduction of maize, beans and cucurbits followed the Mexican Sierra Madre Occidental and its western coastal plain (Ford 1980; Kelley 1966; Spence 1978). Subsequent introductions of maize succeeded and appeared to have had an impact upon the cultures in the area. Between AD 900-1100 in present-day northwestern Mexico, a rapid evolutionary spurt in maize occurred which transformed the maize being grown. This rapid change has been attributed to genetic recombination, heterosis and mutagenic effects of teosinte introgression (Mangelsdorf 1974) which suggests the introduction, acceptance, incorporation and selection of exotic races and their products. Similar patterns occurred in the present-day southwestern United States during the Pueblo II period (AD 900-1100). This introduction and modification of maize is thought to have been more productive and to have led to the expansion of agriculture in the arid Southwest. In fact, it is this increased biological diversity and subsequent productivity of the maize rather than a favorable climate which may have led to the expansion of agriculture and human populations in the region (Galinat and Gunnerson 1963; Mangelsdorf 1974). The establishment of exotic races as well as their hybridization with native races would provide the genetic basis for increased diversity which would amplify the patterns of variations of plant responses to the environment. These variations would be evaluated and selected upon by humans for desirable products and the favored races would be continued. The rise of the Fremont maize races in the American Southwest as well as the Cristilino de Chihuahua in northwestern Mexico and its counterparts in the Puebloan races suggests the importance of the dispersal of exotics into the Southwest and their effects on the local cultures. The specific evidence and patterns of movement and incorporation of exotic races into the Four Corners area based upon archaeological materials will not be presented in this paper because there is no uniform analysis of the maize materials at this time. However, establishing a framework for identifying the biological parameters of such movement and incorporation could contribute to a more meaningful interpretation of available archaeological specimens.

It is difficult to understand the process of dispersal¹ when we are presented with only static fragments of the past. In order to go beyond the descriptive phase and enter the explanatory phase of plant-human interactions, we must look at the patterns of responses of the plants in order to explain the results we observe. In examining the process we must look at the patterns of variation in the plants as responses to various environmental factors. Then this information can be combined with perceptions and values of the cultivated plants by certain cultures and with the characters which are influenced by human selection (for examples of maize, see Benz and Bye, in prep.; Clawson and Joy 1979; Johannessen 1982; Winkelmann 1976).

Maize may have been introduced as a package of various races associated with other cultivated plants and weeds. This complex may have moved slowly with a series of short steps (i.e., diffusion). Each step would have involved cultivation and subsequent selection and movement. On the other hand, a large distance between source area and the new home area may have been accomplished in a short period of time (i.e., jump-dispersal).

The environmental factors of the source area and the new home area may vary and consequently influence the expression of genetically fixed plant responses. Light, temperature and moisture are usually considered the dominant abiotic environmental factors which affect plant growth (Eastin et al. 1969; Milthorpe and Moorby 1974). Light is important as the source of energy which is fixed by the plant as well as the stimulus for developmental and growth patterns. Temperature affects rate of growth, length of growing season, and evapotranspiration rate. Uptake of moisture from the soil and moisture loss through evapotranspiration are critical to the metabolic pathways and nutrient transport. These factors often work together. The photoperiod (ratio of light to darkness) and the length of the growing season influence the initiation of flowering and subsequent fruiting. Temperature, in terms of absolute extremes as well as cumulative degree-days. affects the rates of growth and maturation. Moisture uptake and evapotranspiration rate strongly influence the growth and reproductive patterns of different races.

The responses of the plants of different races to the different environmental factors can be compared with one another. Those plants with desirable characteristics can be maintained by obtaining reproductive seeds for subsequent planting. Also hybridization of open pollinated plants, such as maize, can increase the genetic diversity within populations; the selection of progeny over generations could produce distinct local varieties. Plants with less desirable characteristics would not be as highly valued and consequently may not be continued. The differential reproductive potential, which is limited by biological and cultural factors, determines the success and duration of the maize races over time and the products that could be observed in the archaeological, historical and contemporary records. The critical points include: 1) increase of intraspecific genetic diversity and phenotypic variation, 2) preferential selection and subsequent planting of seeds from plant populations, and 3) comparison of several forms or races so as to select certain ones and discard others based upon the divergence of the characters in response to the new ambient environment.

THE SETTING

For the purpose of this study, the new home area was located in southwestern Colorado, ca. 10 km northwest of Dolores, Montezuma County. The source areas for the exotic maize package were the Sierra Madre Occidental of southwestern Chihuahua and the Basin and Range Physiographic Province of southern Arizona. A brief description of the environment at the Coloradoan home area and the Chihuahuan source area is presented below so as to compare the similarities and differences of the two extreme environments.

The new home area is located in the ecotone between the Ponderosa Pine Forest (with oak) and the Pinon-Juniper Woodland (with oak) at an elevation of ca. 2200 msm. The general area is situated at about latitude 37° 21'N where there are ca. 14³/₄ hours of light on the longest day during the growing season (Fig. 1).

The relationship between temperature and precipitation is critical. This can be expressed graphically in an ecological climate diagram (Walter 1979) using the relationship that 10° C equals 20 mm of precipitation based upon monthly means. This relationship between the temperature line and the precipitation line represents the intensity of moisture stress in the environment. Where the precipitation line is below the temperature line, aridity is assumed; the height of the difference represents the intensity of the drought and the width is related to the duration. Where the precipitation line is above the temperature line, humidity is assumed. This relationship when based upon several years of data should reflect the overall macroclimatic patterns although variation from year to year as well as over long periods of time is expected.

In the Dolores home area, the data for the general ecological climate diagram (Fig. 2a) is derived from the Cortez weather station. It is located ca. 23 km south of the study area is situated at ca. 1900 msm. It is the closest long-term weather recording station. Even though the specific data may be different from the Dolores home area, the general pattern should be similar. It should be noted, however, that the 1979 and 1980 weather patterns of the Cortez station were different from the normal pattern and that the limited data from the upper and lower garden sites of the Dolores home area were different from the Cortez records (Fig. 3a and b). The aridity usually occurs during the growing season which is calculated as the time between the dates of the 50% probability of the last spring freeze ($0^{\circ}C$) and the first fall freeze. Soil moisture is regenerated by the winter precipitation. The normal growing season is about 131 days. During the 1979 season in Cortez, the aridity was more pronounced during the longer than normal growing season of 157 days but the precipitation during the non-growing season was greater (Fig. 3a). In the Dolores home area there was even less precipitation and an unusually short growing

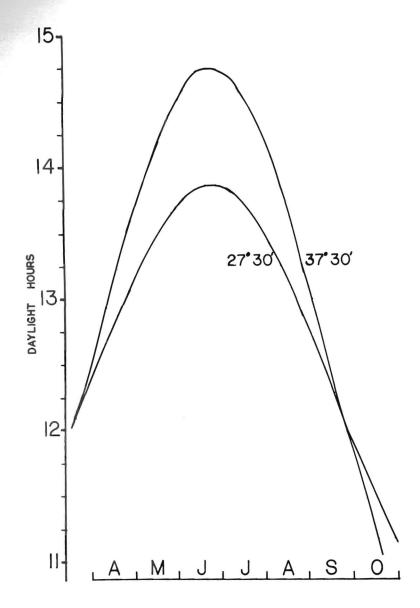


FIG. 1-Comparison of day length (as measured by daylight hours) for 27° 30'N in Chihuahua, Mexico, and for 37° 30'N in southwestern Colorado, United States, for April through October (based upon data extrapolated from Smithsonian Institution 1963).

season (87 days). During the 1980 season in Cortez, the aridity was even more pronounced than normal and worse than 1979 season (Fig. 3b). Even though the precipitation peaked during the winter months, the overall precipitation for 1980 was less than normal. In addition drought was extreme at the beginning of the growing season. The growing season at Cortez was a little longer than normal (137 days). In the Dolores home area, the precipitation was a little greater than at Cortez but the overall aridity was more pronounced than normal. The growing season was much shorter in both the lower garden (67 days) and the upper garden (98 days). In summary, the general growing season in the new home area can be characterized by a short arid growing season and by a non-growing season precipitation pattern.

The exotic package source area is located in the Pine-Oak Forest (with ponderosa

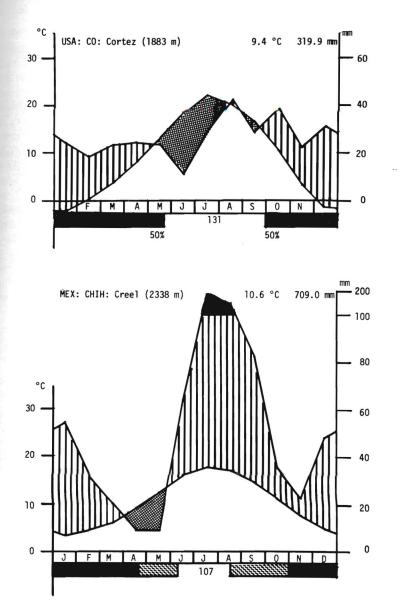


FIG. 2-Ecological Climate Diagrams (following procedures outlines by Walter 1979). 2a: Cortez, Montezuma County, Colorado, (based on weather data from 1951-1973) and 2b: Creel, Municipio de Bocoyna, Chihuahua, (based on weather data from 1953-1970).

pine) at an elevation of ca. 2200 msm. The general area is situated about latitude 27° 45'N where there are ca. 13³/₄ hours of light on the longest day during the growing season (Fig. 1). The relationship between temperature and precipitation is based upon the long term recording station located in Creel, municipio de Bocoyna (Fig. 2b). A short period of aridity occurs prior to the growing season in April and May. The heaviest precipitation falls during the growing season. The growing season is about 107 days.

The Coloradoan home area and the Chihuahuan home area are situated at similar altitudes and have comparable vegetation. Aridity is part of the climatic pattern of both areas but is more intense and of longer duration in Colorado. Also, the aridity period in Colorado occurs during the growing season while in Chihuahua it comes prior to the growing season. Chihuahua is wetter (709 mm per year) than in Colorado (320 mm per

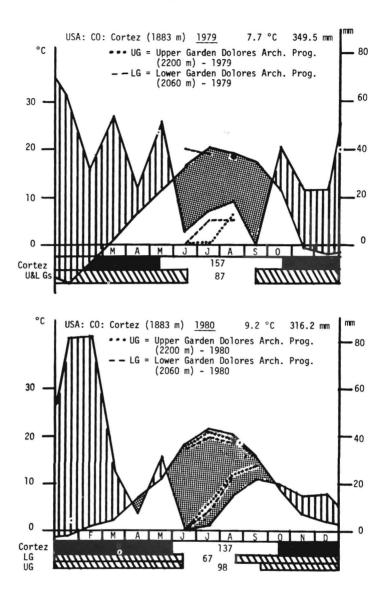


FIG. 3-Ecological Climate Diagrams for Cortez and for upper and lower gardens of Dolores Archaeological Program based on weather data from 1979 (3a) and 1980 (3b).

year) and the majority of the precipitation occurs as rain during the growing season in Chihuahua while the majority of the precipitation falls as snow during the winter or nongrowing season in Colorado. The mean annual temperatures in the source area and in the new home area are similar $(10.6^{\circ}C \text{ and } 9.4^{\circ} \text{ C}, \text{ respectively})$ but the growing season is longer in the general Coloradoan new home area (131 days) than in the general Chihuahuan source area (107 days). However, the growing season of the specific new home area in Dolores is shorter than the growing season of the general home area in Cortez and appears to be more similar to the Chihuahuan source area.

Overall the vegetation, elevation, and mean annual temperature are similar but the daylength, aridity, mean annual precipitation, and seasonal fluctuation of monthly mean temperatures are different. The length of average growing season seems to be different on a general scale but may be similar on the specific site. Although not discussed here, the

soils are different in that the Coloradoan home area is dominated by Aridisols and Entisols derived from sedimentary bed rock while the Chihuahuan source area is dominated by Mollisols derived from volcanic bed rock.

Even though the Chihuahuan maize races, which are grown today by the Tarahumara subsistence agriculturists, would seem to require a more moist regime than that found in southwestern Colorado, a study was conducted to look at the responses of these exotic Mexican grown in the Four Corners region. These plants were grown in the new home area of southwestern Colorado as a consequence jump-dispersal. As discussed above, the Sierra Madre Occidental has served as a migration route, if not a source area, for the introduction of such cultivated plants as maize into the American Southwest. Although it is impossible to recreate the actual events of movement of maize from the Sierra Madre into the Four Corners area, it is possible to investigate some parts of the process associated with dispersal and to produce results which may be compared with archaeological and contemporary materials. The comparison of divergent responses of members from an exotic package (i.e., various races of maize representing intraspecific crop variation) with a native standard from the Colorado-New Mexican home area will allow some insights into the process of dispersal of maize into the Southwest from northwestern Mexico. Also, these insights will provide an analog and allow for a better understanding of the products which are left in the archaeological record.

MATERIALS AND METHODS

The races used in this study are those maize for which we could readily obtain kernels for planting. Each collection³ represents (with one possible exception) one landrace⁴ for each taxonomic race. For simplicity, we will refer to each collection as a distinct race. Hopi Blue flour maize, a variety of the Puebloan race (Brown et al. 1952; Carter and Anderson 1945), came from the 1979 crop grown in the Dolores garden. The original seed source from northern New Mexico was provided by Bob Gallegos. Because this race was adapted to the Four Corners region and had performed successfully in our first season, it was used as the native standard with which other races could be compared. Papago white flour maize, a variety of the Pima-Papago race (Carter and Anderson 1945), was obtained from Gary Nabhan in Tucson, Arizona. This race is considered similar to prehistoric Basketmaker maize (Anderson and Cutler 1942) and is noted for its rapid maturation and drought hardiness (Castetter and Bell 1942). Ears of Apachito⁵, Azul⁵, Cristalino de Chihuahua⁵, Blando de Sonora⁶, and Blanco^{5,7} races (Hernández and Alanis 1970; Wellhausen et al. 1952) were collected from the Tarahumara Indians in the vicinity of Creel, Chihuahua. This group of one flour variety, Blando, and four flint varieties was considered in exotic package. From our discussions with Tarahumara farmers in October 1979, and October 1980, and our observations of maize plants in the fields at harvest time, these races appeared to be a unified package because of their similarities in growth responses, rate of maturation, morphology, and yield potential.

To compare the performance of the five Tarahumara varieties and the Papago maize with the standard Hopi Blue, kernels of all races were planted and raised under uniform conditions in the gardens of the Dolores Archaeological Program near Dolores, Colorado. Twenty hills of each race were planted on June 8, 1980. Hills were spaced at 1 m by 1 m with an additional 1 m boundary surrounding each plot. Three or four plants developed in each hill, and overall crop density averaged 1.75 plants per m². Seeds were inbibed before planting and 5 liters of water were applied to each hill at the time of planting and once again after seedlings had emerged. No further irrigation was supplied. Total rainfall between planting and harvest was 6.1 cm. Records were kept during the growing season on rate of growth and maturation of plants from each race. At maturity of the plants in mid-September, a series of morphological variables was measured on 20 plants from each race. Ears were harvested September 28-30, 1980, approximately 112 days after planting.

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RESULTS AND DISCUSSIONS

Crop productivity of different races was determined by growth and development patterns, morphological characters of mature plants, and yield of ears. Patterns of divergence or similarity between the exotic races and the native standard indicate factors that affect the ability of introduced races to mature in a new geographic region, demonstrate ecological and morphological differences between plants of different races, provide comparison of yield potential between introduced and native races, and show divergence among races within the exotic package when it is introduced into a new region. The data are derived from the populations in the upper garden rather than the lower garden which experienced a short growing season.

Growth rates and development.-Differences in the growth rates and development as measured at time of maturation of the maize races grown at Dolores appear to be responses to temperature and photoperiodic sensitivity. For all races, increase in plant height and number of leaves prior to tasselling was directly related to accumulated heat units. The duration of vegetative growth between planting and flowering is dependent on temperature, and one effect of cool nights is to prolong this period of growth (Brouwer et al. 1973; Shaw 1976). Mean daily temperatures of 15-18° C, as recorded in Dolores from June to September (Fig. 4), can retard maize maturation (Jenkins 1941). This should not have affected the Tara humara races since the temperatures during the growing season in Chihuahua are similar to those recorded for Dolores. However, the effect was strongly pronounced in the Papago maize. This type of maize is reported to produce ears in 60-65 days near Tucson (Gary Nabhan in Meals for Millions 1981), but required 100 days in Dolores. Monthly mean temperatures for a similar period in Tucson range from 26-30° C. Because maize growth is so temperature dependent, the number of days between planting and maturation varies greatly with site location and climate and is not a constant for any race (Wallace and Bressman 1949).

Photoperiod also affects the time of flowering in sensitive races of maize (Francis 1973; Mangelsdorf 1974). Plants of maize often grow taller and have more leaves when grown at higher latitudes because of delayed floral initiation; vegetative growth goes on longer through the growing season before the tassel and silks develop. Mature plants of the four Tarahumara flint races (Apachito, Azul, Blanco, and Cristalino) had from 14 to 18 leaves per stalk at maturity and ranged from 130 to 225 cm tall in the Dolores garden. In the Tarahumara region, plants matured on approximately the same schedule as those in Dolores, and also had 14 to 18 leaves at maturity and ranged from 125 to 250 ml tall. In this case, the differences in vegetative growth and rate of maturation due to a latitudinal shift of 10° did not exceed the range of phenotypic variation shown by plants in both settings. Plants of the flour race, Blando, however, did show a response to a latitudinal shift. In Chihuahua, Blando plants were similar in height and rate of maturation to those of the other four races, but in Dolores the Blando plants were taller than those of the other four races and ears had only developed to the milk stage by early October.

Hernández and Alanis (1970) report that Azul maize flowers in 65 days after planting and Apachito maize flowers in 55 days; both tasselled at 60 days in Dolores and produced silks in 72 days. The delay between tasselling and silking in Dolores was a symptom of drought stress on the plants (Aldrich and Leng 1965). This delayed silking is the basis for reports that corn matures more slowly under drought conditions (Hack 1942). Sensitivity to drought was most extreme in the Tarahumara race Azul, which wilted severely at midday, and least noticeable in the Papago flour maize, which kept normal leaf color and position. This sensitivity may be related to the number of tillers per plant in either race. The total leaf surface area of Azul was greatly increased by the 3-4 tillers per stalk which developed. Very few plants of Papago maize produced tillers. The standard Hopi Blue maize was intermediate in both number of tillers and tolerance of

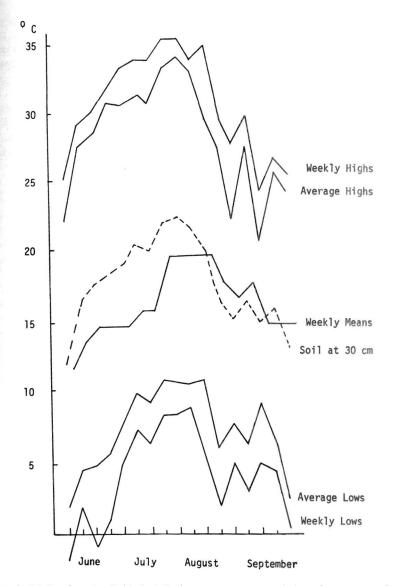


FIG. 4—Air (solid lines) and soil (dashed line) temperatures recorded at the upper garden of the Dolorres Archaeological Program and reported as weekly means, weekly extreme means (average highs and lows), and absolute extremes (weekly highs and lows) for the 1980 season.

drought. Because the average summer rainfall in Chihuahua is so much greater than that in Dolores (Fig. 2), it was expected that all plants of Tarahumara maize would be affected by drought stress more than plants of either Hopi Blue or Papago maize. This hypothesis was supported by observations of leaf response on hot afternoons in late July and August. However, the Tarahumara plants produced normal mature ears and showed neither poor kernel set nor incomplete filling at the tips of the ears, characteristic manifestations of drought stress.

Morphological characters of mature maize plants.-Races of maize are traditionally distinguished on the basis of ear and kernel characteristics (Anderson and Cutler 1942; Brown and Goodman 1977). Since vegetative characters are more plastic than reproductive characters, they are less useful in discriminating between races (Goodman and Pater-

niani 1969). However, as races evolve in restricted geographic areas, they are selected for adaptation to local climatic conditions (Bird 1970) in addition to biotic and cultural factors. This process has resulted in a divergence of developmental and vegetative characters as well as ear and kernel characters. When introduced into a new area, differences in these characters will influence the potential productivity and successful reproduction of the exotic race.

One aspect of the architecture of mature maize plants is the location of the main ear on the stalk. Ears were borne as low as the ninth and tenth nodes in Hopi Blue and Papago maize, as high as the fourteenth in Blando, and in between at the eleventh and twelfth nodes in the four Tarahumara flint races. In addition to this variation in ear location relative to the nodes, the average ear height ranged from only 50 cm in Hopi Blue to 102 cm in Blando. Ear placement may be related to yield potential. Mangelsdorf (1965) reports that leaves above the ears supply photosynthates to the developing kernels, and that leaves below the ear supply the root systems. He predicted that if plants from races which bear ears low on the stalk have more leaves above the ear, they should show increased yield but decreased root system development compared with plants from other races with higher ears. These predictions were not substantiated by the plants at Dolores. Hopi Blue and Papago maize plants had both the lowest ears and the most leaves above the ear but did not have identical increased yields. Both showed good drought resistence compared to the Tarahumara races.

Morphological characters, which were measured on a sample of 20 plants from each race, were chosen to represent the dimensions, proportions, vegetative vigor, and potential yield of ears. Some characters were based on previous studies of maize (Goodman and Paterniani 1969; Wellhausen et al. 1952), and others were added for this study (Table 1). Although one-way analysis of variance showed that significant differences among the seven races from each other. Some characters showed much more variation than others. For example, plant height to the tassel base ranged from 134 ± 4 cm in Papago to 194 ± 4 cm in Blando, but both had tassels 38-40 cm tall.

TABLE 1.-Morphological measurements of maize plants, based on previous studies of characters important in racial determination (Goodman and Paterniani 1969; Welhausen et al. 1952) with some characters added or modified for the purposes of this study.

- 1. Height of plants to tops of leaves.
- 2. Height of plants to node of the base of the tassel.
- 3. Length of tassel along primary axis from base to top.
- 4. Height of stalk from ground to node at which top ear develops.
- 5. Number of leaves, including the first four which develop from the embryonic plumule.
- 6. Number of leaves above the top ear and below the tassel.
- 7. Length along the midrib of the leaf subtending the top ear.
- 8. Width of that leaf, measured midway down its length.
- 9. Number of tillers produced by the main stalk.
- 10. Number of primary branches on the tassel.
- 11. Number of mature ears per plant.
- 12. Number of secondary ears per plant that arise on the tillers or on the main stalk below the primary ear, and do not develop to maturity but can be consumed as "green" corn.
- 13. Number of axillary ears arising between the husks of the primary ear on a stalk. These are tiny but can be consumed entire.

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To test the strength of the relationship between different characters and test hypothesis of correlation, the Pearson's r coefficient was determined for several pairwise combinations of variables. The results support the hypotheses that (1) height to leaftops, height to tassel base, and height to top ear are strongly related, (2) total number of leaves, number of leaves above the top ear, and measures of height are strongly related, (3) leaf length and leaf width are strongly related, and (4) number of tillers is independent of the other variables.

A multivariate approach was needed to utilize the information on morphological characters while recognizing the correlation between them. The purpose of the analysis was to emphasize the significance of the morphological differences between races, which imply differences in potential productivity and successful introduction of races. Discriminant function analysis was performed on the data set to create linear combination of variables which maximize the differences between the races. Using the functions created in this analysis, 120 of 143 cases (84%) could be properly assigned to one of the seven races. Thus, this analysis confirms that racial differences can be distinguished on the basis of vegetative plant morphology as well as ear and kernel morphology. A plot (Fig. 5) of the results from this analysis clearly separates the Tarahumara races from the Southwestern races, and further separates the races within the two main groups, so that Hopi Blue and Papago are distinct and the Tarahumara races also spaced out slightly. Because of the great morphological plasticity of maize plants, the functions used in this classification would not necessarily apply to plants grown in other gardens. Approaches to racial classification based on more conservative characters are more universally applicable. However, for the purpose of indicating differences among plants of various races that could affect the successful growth, maturation, reproduction, and acceptance of exotic maize in a new region, this type of analysis in helpful.

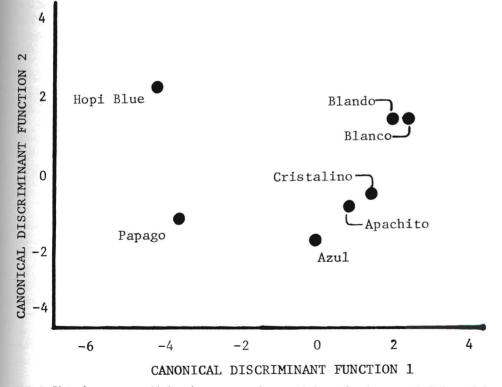


FIG. 5-Plot of group centroids based upon vegetative morphology of maize grown in Dolores, Colorado. Group centroids for each of the seven races of maize are presented for the first two discriminant functions.

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Yield of ears in different races of maize. - Ears of Papago maize and the four Tarahumara flint races reached the milk stage by September 12-15, one week in advance of Hopi Blue and 2-3 weeks in advance of Blando. Maize ears may be harvested and consumed at this stage, but usually kernels are not fully mature until 3-4 weeks later and ears increase greatly in weight and carbohydrate content during this period. Differences in degree of maturity of the ears at the time of harvest at the end of the growing season have important consequences. The fate of races introduced into the Southwest from regions further to the south depends on the ability of the plants to produce seeds in the new setting. After harvest in late September and subsequent drying, ears were sorted into categories of immature and nature for measuring the weighing. Immature cars were those that had been picked with kernels in the milk stage. Their kernels shrank during drying and were small, wrinkled, and light colored. Fully mature ears had large, well-filled, bright-colored kernels. Intermediate ears were common. Since later germination tests showed that the seeds from intermediate ears were viable even though they were not fully filled kernels, these intermediate ears had reached reproductive maturity and were grouped with the fully mature ears. Fully mature ears are culturally important as a major food staple, but reproductively mature ears are also important as a possible means of renewing the plant population and establishing a race in a new region.

The four Tarahumara flint races (Apachito, Azul, Blanco, and Cristalino) produced mature ears that were very similar in length and weight (Table 2). Average ear weight in Blando was much less because these ears were not fully mature but only reproductively mature. Ears of Papago flour were slightly shorter and lighter than in the four Tarahumara flint races. Ears of Hopi Blue were significantly longer and heavier at maturity than ears of the other races.

In Blanco, Cristalino, Hopi Blue, and Papago maize the immature ears were those produced at lower nodes of the main stalk or on the tillers. They were shorter than the top ears and of course weighed much less. This trend was even more pronounced in Apachito and Azul which produced very short immature ears. In Blando, however, many of the top ears on the stalks were immature. These were as long as or longer than the mature ears produced on other stalks of that race.

Immature ears can be consumed fresh but are less desirable as a food source after drying. The pericarp and glumes are more fully developed than the endosperm in these immature ears and constitute a larger proportion of the dried kernels. In mature ears, 75% of the weight is in the kernels and most of this is in the endosperm.

Total yield of immature and mature ears from twenty hills of each race is presented in Table 3. Again it appears that the four Tarahumara flint races (Apachito, Azul, Blanco and Cristalino) produce similar numbers and weights of both immature and mature ears. Blando produced as many total ears, but fewer reached maturity so the total weight produced was very low. Hopi Blue produced numbers and weights of mature and immature ears intermediate between the four flint races and Blando. Papago flour maize produced the most mature ears and the greatest weight of both mature and total ears. This variation among races is summarized in Figure 6, which shows number and dry weight of mature ears produced per plot of each race.

Among subsistence agriculturalists, maize ears are carefully selected at harvest time as seed sources for the coming year (Beaglehole 1937; Whiting 1939). Some traditional farmers are very conservative about maintaining their own seed stock. Others take interest in unusual or exotic races and grow trial plots to compare with their traditional forms (Johnson 1972). The introduction of maize from Mexico into the Southwest depended on many factors including the importation of seeds, the growth and maturation of the plants, and the cultural acceptance of the new crop. As Sauer (1967:139) summarized:

The diffusion of corn...undoubtedly required a long time. The older forms of maize may be considered as having required a long, warm, moist season, more rapidly maturing forms developing by slow selection on the successive boreal fringes of its cultivation and in part also on the drier margins. Slow ecologic selection was demanded of all crops that diffused through a wide latitudinal and altitudinal range, the diffusive energy of such a crop being probably a complex expression of its desirability and of inherent ecologic plasticity.

TABLE 2.-Length and weight of mature and immature cars of seven races of maize. n = 140.

Race	– Mature Ears –			
	No. of ears	Length (cm)	Weight (gm)	
Apachito	26	17.1 ± 0.68	58.3 ± 5.06	
Azul	23	16.2 ± 0.55	58.5 ± 4.40	
Blanco	21	17.9 ± 0.52	55.8 ± 5.01	
Cristalino	28	17.4 ± 0.93	63.0 ± 5.97	
Blando	4	18.4 ± 2.14	28.0 ± 2.09	
Papago Flour	27	17.4 ± 0.39	52.0 ± 2.42	
Hopi Blue	8	19.6 ± 1.22	71.7 ± 11.50	

	– Immature Ears –				
	No. of ears	Length (cm)	Weight (gm)		
Apachito	10	10.3 ± 0.77	8.3 ± 2.00		
Azul	15	8.4 ± 0.57	6.9 ± 0.78		
Blanco	14	11.9 ± 0.88	14.0 ± 2.86		
Cristalino	18	11.8 ± 0.86	13.8 ± 2.73		
Blando	27	21.5 ± 2.12	14.7 ± 2.83		
Papago Flour	11	13.4 ± 1.05	17.3 ± 3.40		
Hopi Blue	42	13.4 ± 0.64	20.7 ± 3.19		

RACE	Mature	–Mature Ears –		– Immature Ears –		—Total Ears —	
	Total No.	Wt. (gm)	Total No.	Wt. (gm)	Total No.	Wt. (gm)	
Apachito	67	3630	47	540	114	4170	
Azul	60	3240	60	640	120	3880	
Blanco	62	3400	48	670	110	4070	
Cristalino	53	3250	35	550	88	3800	
Blando	14	600	95	1400	109	2000	
Papago Flour	89	4550	44	740	133	5290	
Hopi Blue	40	1700	67	1400	107	3100	

TABLE 3.—Total yield of mature and immature ears of seven races of maize. Ears were harvested September 26, 1980 from twenty hills of each race, grown at $1m \times 1m$ spacing in $3m \times 4m$ plots in Dolores, Colorado.

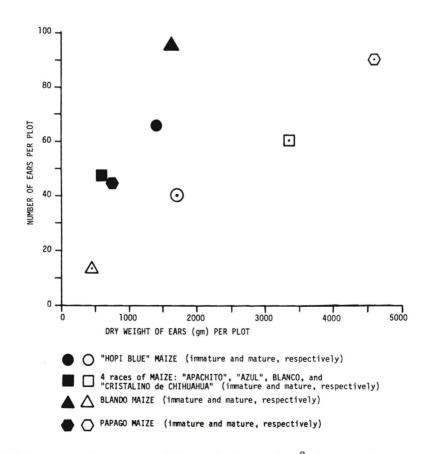


FIG. 6-Immature and mature ear yields per plot (area = 25 m^2 ; density = $1.75 \text{ plants per m}^2$) at upper garden of Dolores Archaeological Program during 1980 season. Note: the square approximates the yield of one of four Tarahumara flint races; these four races had similar yields.

SUMMARY

1. Maize can be introduced into a new region by means of jump-dispersal where the kernels from a source area are carried a great distance in a short time and established in a new region. In this study, five Tarahumara races of maize from southwestern Chihuahua, Mexico, and one Pima-Papago race from southern Arizona were grown in gardens in southwestern Colorado and compared with a native standard Hopi Blue of the Puebloan race. This jump represents a shift of ca. 10° latitude or ca. 1260 km for the Tarahumara races and a shift of ca. 5° latitude or ca. 630 km for the Papago race. The source areas and new home area differ in photoperiod, temperature and precipitation patterns. Plants of all races produced mature ears in the first year.

2. Blando was the only Tarahumara race of maize that showed prolonged delay in floral initiation in the new home area. This can be attributed to photoperiodic effect. Papago maize required 50% more days to mature in southwestern Colorado than in southern Arizona possibly because of retarded growth at lower temperatures. Extreme aridity during the growing season produced symptoms of drought stress of the foliage in the Tarahumara races, but ear production and quality did not seem to be strongly affected. The Papago and Hopi maize plants did not show drought stress symptoms. In all races, ears reached at least the state of reproductive maturity.

3. Although the five Chihuahuan races were considered similar in terms of growth responses, rate of maturation, morphology, and yield potential in their native setting, a divergence was observed among these races when they were grown in southwestern Colorado. The four flint races, Apachito, Azul, Blanco, and Cristilino de Chihuahua, matured earlier and produced more mature ears than the native standard, Hopi Blue flour variety. The flour race, Blando de Sonora, did not reach full maturity but yielded some ears which were reproductively mature. Plants of these five exotic races also showed divergence in vegetative morphology. Papago flour maize matured earlier and produced more mature ears than any other race in the Dolores garden, including the native standard, Hopi Blue flour maize.

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NOTES

- 1. Dispersal is a general term which is broadly applied to the concept movement of organisms from one area to another. It has been used in many ways and is the source of some confusion. Also, certain plants are considered to be adapted for short distance dispersal with gradual expansion of their ranges, others for long range distance dispersal, and others for both strategies. A useful framework for understanding dispersal is presented by Pielou (1979:242-243). Three modes of the spread of a species are: 1) *jump-dispersal* which describes the movement of individual organisms across great distances in a short period of time with successful establishment of the population and its descendants, 2) *diffusion* which is the gradual movement of populations across hospitable environments over a longer period of time, and 3) *secular migration* where diffusion is greatly reduced such that the species undergoes appreciable evolutionary change. Baker (1971) has provided a series of criteria for testing the dispersal of a plant with or without human aid with reference to gradual range expansion (diffusion) and long-distance dispersal (jump-dispersal). The biological as well as the cultural characteristics of dispersal as a process are still in need of critical investigation.
- 2. In the case of maize, the seed or kernel is a one-seeded fruit which is technically known as caryopsis.
- 3. Specimens of the maize have been made for deposition in the Anasazi Cultural Heritage Center. Related collections are deposited in the Laboratory of Ethnobotany and Plant Systematics, Department of EPO Biology, University of Colorado, Boulder.
- 4. Landrace can be defined as a subset of a race which is highly variable in appearance and genetic diversity but which retains particular properties and characteristics (Harlan 1975).
- 5. These four races were obtained in October 1977 from a Tarahumara ranchito in Cusárare, ejido de Cusárare, municipio de Guachochic, at an elevation of ca. 2100 msm.
- 6. This race was obtained in October 1977 from a Tarahumara ranchito in the ejido de San Ignacio Arareco, municipio de Bocoyna, at an elevation of ca. 2200 msm.
- 7. This undescribed race is a white flint with morphological similarities to Apachito.

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POSTSCRIPT

Subsequent studies in the experimental garden as well as in the laboratory were planned to examine more carefully the biological and ecological factors affecting maize along with other cultivated plants and associated weeds as well as to integrate those results with cultural information and archaeological materials from the Dolores area and other regional archaeological sites.

Unfortunately, the objectives of the Dolores Archaeological Program changed resulting in the elimination of support for the Environmental Studies Group. Consequently, our experimental, field, laboratory, and literature studies were discontinued. None the less, two Master of Arts theses (R. Shuster, 1981. Factors affecting productivity in subsistence agriculture. Dept. of EPO Biology, University of Colorado. and B. Benz, 1981. Five modern races of maize from northwestern Mexico: archaeological implications. Dept. of Anthropology, University of Colorado.) and an introduction to a model integrating contemporary and archaeological data (R. Bye and R. Shuster, in press. Developing an integrated model for contemporary and archaeological agricultural subsistence systems. In P. and S. Fish (eds.). Prehistoric Agriculture Strategies in the Southwest. Arizona State University Anthropological Research Paper.) were completed. With the writing of these items and the resignation of R. Bye, the Environmental Studies Program came to an end before the relationship between the general theme of this paper and the archaeological and ethnobotanical evidence could be properly integrated.