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*American Journal of Botany*, Vol. 66, No. 2 (Feb., 1979), 198-206.

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*American Journal of Botany* is currently published by Botanical Society of America.

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## THE ORIGIN AND EVOLUTIONARY RELATIONSHIPS OF 'HUAUZONTLE' (*CHENOPODIUM NUTTALLIAE* SAFFORD), DOMESTICATED CHENOPOD OF MEXICO<sup>1</sup>

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### A B S T R A C T

A New World assemblage of tetraploid *Chenopodium* species (section *Chenopodium*, subsection *Cellulata*) includes two domesticates, *C. quinoa* of Andean South America and *C. nuttalliae* of Mexico. Both have been combined into a single species and the Mexican form has been considered as a possible derivative of *C. quinoa*. The domesticates and related, sympatric weed forms, *C. berlandieri* of North America and *C. hircinum* of the Andes, were examined for variation in morphological and biochemical characteristics and also were included in a program of artificial hybridization. Results indicate that the domesticated forms are more closely related to their sympatric weeds than to each other. The Mexican cultigen is placed as a subspecies of *C. berlandieri*, the taxon from which it most likely evolved under human selection in North America. Possible origins for the Andean weed-crop complex are considered. Southward migration of a North American tetraploid appears to be more likely than independent allotetraploidy in South America. Of the North American tetraploids examined, *C. berlandieri* var. *zschackei* of the western U.S. shows closest affinities to the Andean complex.

CITIZENS of the Aztec nation in pre-Columbian Mexico were required to pay an annual tribute to their central government. Payment was often in the form of agricultural products and, from records of tribute paid after Spanish conquest (Cooper-Clark, 1938), we can ascertain relative importance of various crop plants in native Mexican agriculture. These records indicate that one of the most significant tribute items, with an annual payment of about 160,000 bushels, was a dicotyledonous, grain-producing "pseudocereal" known as 'huauthli' or 'guautli.' Aside from its value as a food resource, this crop also played a significant role in Mexican religious activity, including ceremonial human sacrifice (Safford, 1916). Use of the crop was evidently suppressed by the Spanish and it was largely replaced as an agricultural commodity in post-conquest Mexico by domesticated grasses. Today we know very little about 'huauthli' and its uses. There is, in fact, some doubt concerning the identification of the crop. It is believed to have been made up of grain from domesticated species of *Amaranthus*

and *Chenopodium*. Opinions differ, however, with regard to the relative importance of these taxa (cf. Reed, 1944; Sauer, 1950; and Hunziker, 1952).

Whatever its significance in pre-Columbian Mexican agriculture, there can be little doubt that a domesticated chenopod was utilized by the Aztec (Safford, 1917; Hunziker, 1952). The plant is often described as being in relict, declining cultivation at the present time (Sauer, 1950; Simmonds, 1965; 1976), and this may be the case if current production is compared to that of pre-Columbian times. However, strains of the most common cultivar, 'huauzontle,' have been selected recently for commercial production as a broccoli-like vegetable (Laborde, 1962), and it can be found under cultivation as an irrigated row crop in several agricultural centers of central Mexico. The other two cultivars, cv. 'chia,' a grain crop, and cv. 'quelite,' a spinach-like vegetable, appear to be produced and utilized on a local basis.

Uncertainty concerning pre-Columbian significance and current production of the Mexican domesticated chenopod also extends to its origin and evolutionary relationships. The Andean grain chenopod, *Chenopodium quinoa* Willd., was described in 1797. This was thought to be a unique element of New World agriculture until 1917 when Safford described a second domesticated species from Mexico, *C. nuttalliae*. Aellen (1929) later concluded that the Mexican domes-

<sup>1</sup> Received for publication 3 August 1978; revision accepted 24 October 1978.

This study was funded by grants from The National Science Foundation (GB-41000), The Society of Sigma Xi, and the Indiana University Foundation. We wish to thank Dr. Ronald L. McGregor for providing numerous plant collections, Ing. Efraim Hernandez X. for assistance with collecting activities in Mexico and the directors of US and F for loans of *Chenopodium* material.

ticate was not specifically distinct from *C. quinoa*, a position followed by floristic workers (Standley, 1931; MacBride, 1936). Later work has shown that both domesticates are tetraploid ( $2n = 4x = 36$ ) with the alveolate pericarp typical of section *Chenopodium*, subsection *Cellulata*. They have been hybridized artificially with the production of backcross progeny (Heiser and Nelson, 1974).

Recently Simmonds (1976) indicated that, "the similarity of quinoa and huauzontle in grain characters, and the strong probability that they are conspecific, suggests that the Mexican crop represents an early migrant quinoa population . . . ." Possible conspecificity between the two domesticates has led other specialists to suggest a South-to-North pre-Columbian diffusion. Dresler (1953) lists *C. nuttalliae* as a possible Andean introduction to Mexican agriculture and Standley and Steyermark (1949) indicate that, "the plant was introduced into central Mexico . . . ."

Aellen originally placed both domesticates into the same species because of their great morphological similarity. Both show a fairly conspicuous syndrome of adaptations resulting from domestication in the form of morphological and physiological changes under human selection that provide an interesting example of convergent evolution similar to that of the domesticated grasses (Harlan, deWet, and Price, 1973). Diffuse inflorescences of the wild types have become highly compacted and terminalized, and anthesis is synchronous within these head-like inflorescences. Wild type mechanisms for fruit dispersal and germination dormancy have been lost, fruit size has increased dramatically in grain cultivars and fruit of most cultivars is light colored because of an extreme reduction of the testa.

If *C. nuttalliae* is an early introduction into Mexico, then this "pseudocereal" adaptive syndrome must have evolved in South America. Aellen (1929) suggested that the wild progenitor could have been similar to *C. hircinum* Schrad., an alveolate-fruited, tetraploid weed of the Andes known as 'aspha quinua.' Hunziker (1952) has indicated that the cultivated *C. quinoa* var. *melanospermum* Hunziker could represent an intermediate form between the more specialized light-fruited cultivars and *C. hircinum*. Aellen later (Aellen and Just, 1943) placed Ecuadorian elements of *C. hircinum* within *C. quinoa* as *C. quinoa* spp. *milleannum* (Aellen) Aellen, pointing out morphological similarities between these Andean weeds and *C. berlandieri* Moq., a tetraploid weed of subsection *Cellulata* from western North America (see Aellen, 1929). León (1964) saw a center of diversity for *C. quinoa* on

the altiplano of Peru and Bolivia, but indicated that weed forms from that area are derivatives of the domesticate. Gandarillas (1968) has suggested that allotetraploidy could have occurred in the Andes with the semi-domesticated diploid *C. pallidicaule* Aellen (section *Chenopodium*, subsection *Leiosperma*) contributing a genome.

If the conspecific hypothesis is not correct, and both domesticates are distinct species, then both could have evolved the "pseudocereal" adaptive syndrome independently, a phenomenon not without precedent in New World agriculture (Heiser, 1965; Pickersgill, 1977). This position is supported by Hunziker (1952) who sees *C. nuttalliae* as a native Mexican domesticate. Nelson (1968) judged both domesticates to be distinct species on the basis of a bimodal pattern of leaf shape variation. He also found genetic complementation for the light-fruited condition (Heiser and Nelson, 1974), a characteristic unique to the domesticates. It is therefore possible that they evolved this critical characteristic independently.

If *C. nuttalliae* is not the result of diffusion from the South, then its origins must be sought elsewhere. A likely candidate is *C. berlandieri*, the only tetraploid member of subsection *Cellulata* that is sympatric with the Mexican domesticate.

Data presented here were generated to test these two hypotheses concerning the origin of *C. nuttalliae*, i.e., derivation from *C. quinoa* vs. independent domestication. This work began with field collections in Mexico where all three cultivars of *C. nuttalliae* were acquired from markets and cultivated fields. Populations of *C. berlandieri* were found to be relatively common in Mexico, many in association with cultivated stands of *C. nuttalliae* and one which contained what appeared to be morphological intermediates between weed and domesticate. Accessions of *Chenopodium berlandieri* from the western United States were also secured. Identifications of material representing *C. berlandieri* used in this study were verified by the late Dr. H. A. Wahl. Mexican accessions were assigned by him to var. *sinuatum* (Murr) Wahl, western U.S. accessions to var. *zschackei* (Murr) Murr. As indicated above, the Andean weed form of subsection *Cellulata* has received diverse taxonomic treatments. For convenience, we will refer to it simply as *C. hircinum*.

A small sample of two other chenopod species was included in this study in order to compare their phenetic relationships to the four taxa under consideration. *Chenopodium bushianum* Aellen is an alveolate-fruited tetraploid of northeastern North America. The archaeological record has shown that an unusually large-fruited

chenopod was heavily utilized by prehistoric inhabitants of the eastern deciduous forests. Ethnobotanical specialists have suggested that this material represents either a large-fruited wild form (*C. gigantospermum* Aellen), an indigenous domesticate, or an introduction of *C. nuttalliae* from Mexico (see Struever and Vickery, 1973). Recent SEM examination (Wilson, 1976a) has shown that many of these archaeological samples can be readily assigned to subsection *Cellulata* on the basis of pericarp or testa morphology, thus eliminating the first possibility (see also Asch and Asch, 1977). Size comparisons indicate that several archaeological samples exceed the range of fruit size variation in modern *C. bushianum*, the only alveolate-fruited species that currently occurs in the eastern woodland area (Wilson, Heiser, and Schilling, unpubl.). Four samples of *C. bushianum* are included in the taximetric analysis described below in order to obtain a preliminary picture of phenetic relationships between it and related North American tetraploids.

Both *C. berlandieri* and *C. bushianum* have been combined with *C. album* L. in various floristic treatments (Hitchcock and Cronquist, 1973; Gleason and Cronquist, 1963; Radford, Ahles, and Bell, 1968). Two accessions of this smooth-fruited (section *Chenopodium*, subsection *Leiosperma*) hexaploid were also included to test phenetic affinities.

**MATERIALS AND METHODS**—The following plant material was utilized in the procedures described below: *C. quinoa*—35 accessions from Ecuador, Peru, Bolivia and Chile; *C. hircinum*—31 accessions from Ecuador, Peru, Bolivia; *C. nuttalliae*—38 accessions from eight Mexican states; *C. berlandieri*—16 accessions from ten Mexican states (var. *sinuatum*) and 40 accessions from 12 states of the United States Southwest and Plains (var. *zschackei*); *C. bushianum*—4 accessions from the eastern United States and Canada; *C. album*—2 accessions from Bolivia. Details as to the source of these accessions are given in Wilson (1976b). Herbarium specimens are deposited at Indiana University and Texas A&M University.

**Experimental hybridization**—Artificial hybridization with *Chenopodium* material is complicated by self-compatibility and small flowers in compacted inflorescences. Previous crossing work with the domesticated chenopods has been limited to the use of cytoplasmic male sterility (Simmonds, 1971; Heiser and Nelson, 1974), which does not allow evaluation of  $F_1$  pollen fertility. This problem was overcome in this study through the use of photoperiodically induced

protogyny. Restrictions imposed by this procedure did not allow a full series of reciprocal crosses in that only a limited number of accessions could be used as egg parent. These included several accessions each of *C. quinoa*, *C. nuttalliae*, and only one accession of *C. hircinum*. Accessions of *C. berlandieri* either did not show induced protogyny, or were not homozygous for those recessive characteristics that are needed to identify hybrid plants.

The selected egg parent accessions mentioned above show strong protogyny when inflorescence development is initiated by transfer from 16-hour to 8-hour photoperiodic conditions. Pollen transfer is accomplished during the period of protogyny. This is not 100% effective and subsequent anthesis produces a mixed progeny resulting from artificial hybridization and self-pollination of the egg parent. Hybrid plants are identified by the presence of dominant genetic characteristics present in the pollen parent and absent in the selected egg parent strains. These include characters of pigmentation (see Simmonds, 1971), pubescence and co-dominantly expressed isozyme markers.

Hybrid fertility is evaluated by staining pollen in lactophenolaniline blue. Results represent average stainability of three to six  $F_1$  plants per cross. Hybrids of known pollen stainability have been tested for fruit set capability upon both self-pollination and cross-pollination from fully fertile parental accessions. Results show a general correlation between pollen stainability and fruit-set. Pollen stainability is therefore assumed to be a reasonably accurate indication of fertility. Parental accessions produced from 80 to 100% stainable pollen.

**Morphological comparison**—Phenotypic plasticity, a characteristic that is typical of colonizing species, has generated some taxonomic confusion in *Chenopodium* (Wahl, 1952–53; Cole, 1960). Accessions used for comparative morphological analysis were therefore sown simultaneously and grown under relatively uniform environmental conditions. Material representing 129 accessions, four plants per accession, was grown in the greenhouse from September to December. The two largest cauline leaves were taken from each plant after 55 days of growth. These were pressed, dried and measured to the nearest mm for blade length, width at  $\frac{1}{2}$  length, width at widest point, width at top  $\frac{1}{4}$  length, and distance from widest point to base. The plants were scored during growth for presence or absence of stem pigmentation, leaf pigmentation and pubescence. Plants were harvested at maturity, pressed, dried and measured to the nearest cm for total height, inflorescence length, width, and

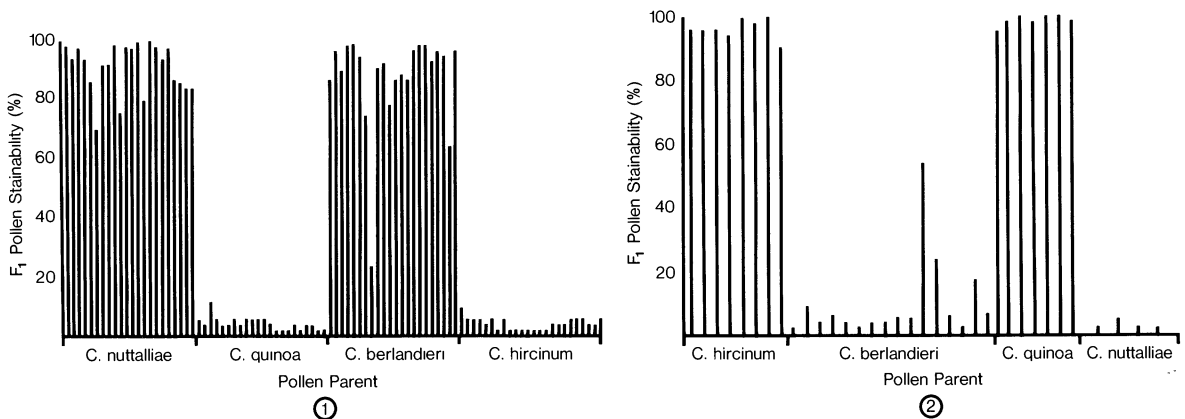


Fig. 1, 2. 1. Results of artificial hybridization with *C. nuttalliae* as egg parent. 2. Results of artificial hybridization with *C. hircinum* as egg parent.

distance from longest inflorescence branch to apex. Mature plants were also scored for fruit retention, pericarp coloration, seed coloration, fruit diameter and weight, and germination dormancy.

Variation among accessions was examined through the use of scatter diagrams and combined with isozyme and crossability results for taximetric comparison. A total of 30 characters was machine-analyzed using Gower's coefficient of similarity and the WPGMA clustering algorithm. The program was provided by Dr. Edward Schilling.

*Isozyme analysis*—Variation at two polymorphic leucine aminopeptidase gene loci was examined via horizontal starch gel electrophoresis. Methods and segregation data are discussed elsewhere (Wilson, 1976a).

**RESULTS—Experimental hybridization**—Data resulting from artificial hybridization are inserted parenthetically in the following account. These include (from left to right): 1) number of hybridizations between taxa under discussion involving at least one novel parental accession, 2) range of F<sub>1</sub> pollen stainability (%) and 3) average stainability (%). Crossing results are summarized in Fig. 1 and 2. Space limitations prevent inclusion of complete data from several crossing combinations. Data presented were randomly selected from a full listing of crossing results which can be found in Wilson (1976b).

An accession of *C. hircinum* from Ecuador produced fertile F<sub>1</sub> hybrids when other weed accessions from Ecuador, Peru and Bolivia were used as pollen parent (8, 89–99, 97). Hybridization between this accession and domesticated accessions from Ecuador, Peru, Bolivia and Chile also resulted in full F<sub>1</sub> fertility (7, 96–99,

97). Those progeny of weed × weed and weed × domesticated F<sub>1</sub> plants examined to date show equally high fertility.

As indicated above, *C. nuttalliae* includes three relatively distinct cultivated varieties that also differ in method of utilization. Intercultivar hybridization has shown that these domesticated types are essentially interfertile (26, 36–99, 91). There appear to be no internal barriers to gene flow between *C. nuttalliae* and *C. berlandieri* var. *sinuatum* (22, 70–99, 93). Most hybrids resulting from crosses between *C. nuttalliae* and *C. berlandieri* var. *zschackei* of the United States are also highly fertile (48, 5–99, 77), although one Californian accession consistently produced nearly sterile hybrids with *C. nuttalliae*, and several others from scattered locations in the Great Plains produced hybrids of intermediate fertility. Several F<sub>1</sub> progeny of *C. nuttalliae* × *C. berlandieri* crosses have retained high fertility and show normal Mendelian segregation for alleles at pigmentation and isozyme loci.

Crosses between accessions of *C. quinoa* and *C. nuttalliae* result in hybrids of uniformly low fertility (29, 0–11, 4). Hybridization between *C. hircinum* and *C. nuttalliae* produce similar results (30, 0–9, 3). Hybrids between *C. nuttalliae* and the Andean complex rarely set fruit upon self-pollination, although back-crossing from either parent produces fruit set that is roughly equivalent to F<sub>1</sub> pollen stainability. Twenty-one back-cross progeny resulting from *C. nuttalliae* pollination of *C. nuttalliae* × *C. quinoa* F<sub>1</sub> plants of different parentage show an elevated pollen stainability (23–72, 41) and some fruit set upon self-pollination. These progeny show expected segregation for alleles at LAP-B.

Hybrids between *C. berlandieri* and the Andean complex show a general low fertility (20, 0–

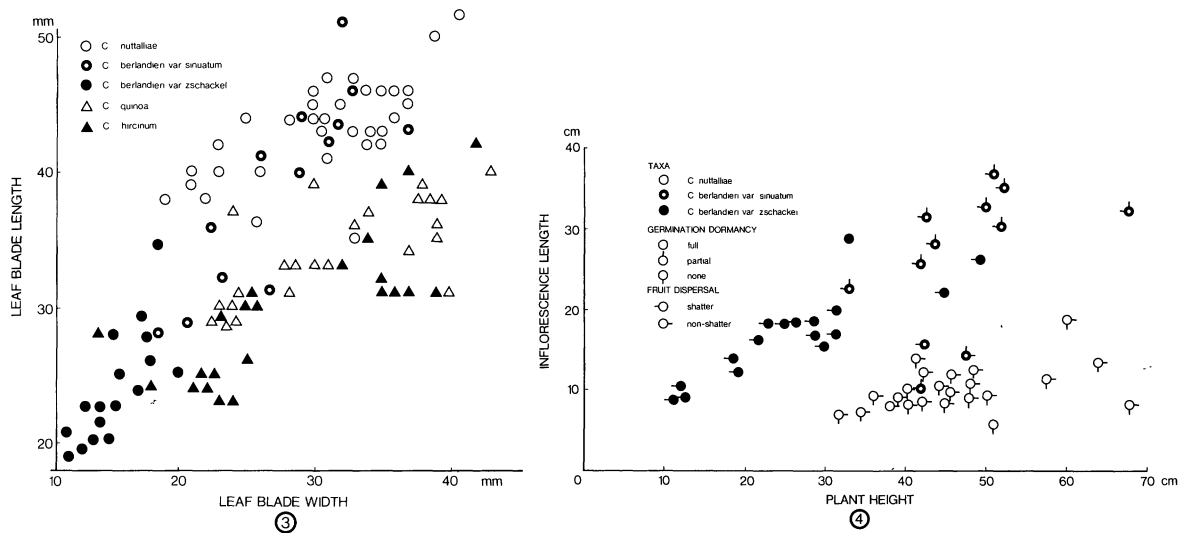


Fig. 3, 4. 3. Variation in leaf blade dimensions among accessions of the taxa under consideration. 4. Variation in plant height, inflorescence length, germination dormancy and fruit dispersal among accessions of *C. berlandieri* and *C. nuttalliae*.

54, 11), although several accessions of *C. berlandieri* var. *zschackei* produce partially self-fertile  $F_1$  hybrids when crossed with spontaneous and domesticated Andean material (5, 10–54, 28).

These results show that accessions assignable to *C. quinoa* and *C. hircinum* share a high level of genomic similarity which appears to occur throughout the range of distribution. Human selective pressure has apparently developed and maintained the adaptations of the Andean domesticate without bringing about a high level chromosomal differentiation between it and the associated weed. Morphological distinctiveness of weed and crop is probably attributable to disruptive selection, a phenomenon often associated with crop plant evolution (Doggett and Majisu, 1968). The two types occupy similar habitats and are primarily wind pollinated. These factors probably work together to hinder the development of complete reproductive isolation. It therefore appears that *C. quinoa*, like many other domesticated plants (Harlan, 1965), includes a “companion weed” that has maintained some genetic contact with the domesticate. This, at least, would explain the absence of genomic differentiation in the Andean weed-crop complex, and also account for the presence of reported intergrading populations.

A similar situation appears to exist in the Mexican area of chenopod cultivation, with populations assignable to *C. berlandieri* var. *sinuatum* representing the companion weed form of *C. nuttalliae*. Again, crossing results demonstrate the potential for gene flow between weed and

crop. Habitat preference, reproductive biology, intergrading populations and lack of extensive genomic differentiation indicate that this potential has been realized to some extent. Crossing data also suggest that, with isolated exceptions, a high level of chromosome homology exists between the Mexican domesticate and populations of *C. berlandieri* var. *zschackei* distributed well beyond the range of cultivation to the North.

The high level of fertility between the domesticated chenopods and their sympatric weeds is in contrast to the consistent sterility of  $F_1$  plants resulting from hybridization between the North and South American weed-crop complexes. The cause of this sterility is not known, although the relatively uniform, partial elevation of fertility in back-cross progeny indicates that the sterility factor is either multi-genic or chromosomal. Whatever its cause, the barrier does suggest a level of genetic-chromosomal differentiation between North and South American “primary gene pools” (sensu Harlan and deWet, 1971) that has not occurred within them. *Chenopodium berlandieri* var. *zschackei* is the only taxon of the North American complex that will produce partially fertile hybrids in crosses with South American tetraploids. These results support Aellen’s (1929) notion, based on morphological comparisons, that this taxon is a possible link between the North and South American tetraploids.

*Morphological comparisons*—Results of the uniform environmental growth study are presented in Fig. 3–5. Comparison of leaf blade length vs. width (Fig. 3) demonstrates a basic

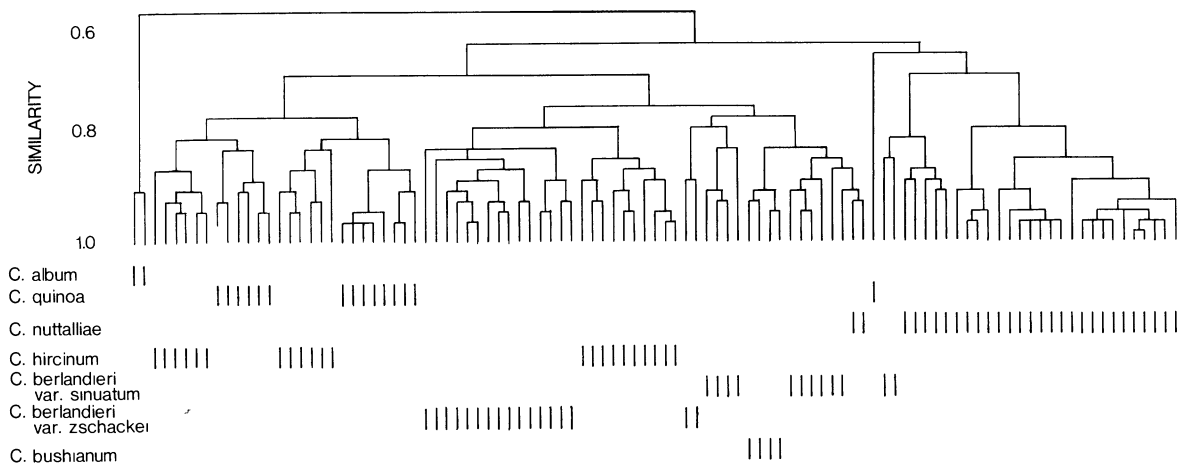


Fig. 5. Phenogram resulting from numerical analysis of 30 characters.

phenetic similarity between the Mexican domesticate and *C. berlandieri* var. *sinuatum*. Leaves of this Mexican complex are generally larger than *C. berlandieri* var. *zschackei* and longer than the Andean accessions. With few exceptions, accessions of the two domesticated forms are distinct from each other with regard to leaf shape. It is significant that this basic dissimilarity occurs in a characteristic that is evidently not under direct human selective pressure. As indicated above, the domesticated taxa are similar in characters that are part of the adaptive syndrome of domestication, such as fruit coloration, fruit size and inflorescence shape. Dissimilarity in leaf characters that are not associated with this syndrome suggests that gross morphological similarities may be the result of evolutionary convergence under human selection.

The similarity in leaf shape between *C. nuttalliae* and its sympatric weed is in contrast to the general dissimilarity between Mexican weed and cultigen with regard to inflorescence length vs. plant height (Fig. 4). The domesticated forms have evolved a highly terminalized and compacted head-like inflorescence under human selection. Weedy accessions show a dispersion of the inflorescence branches that is roughly proportional to plant height. Three accessions of *C. berlandieri* var. *sinuatum* deviate from the weed-type inflorescence pattern and show similarities to the domesticated condition. One of these also retains fruit at maturity, a characteristic that is otherwise limited to the domesticate. Many accessions of *C. berlandieri* var. *sinuatum* show a partial lack of germination dormancy, another characteristic of the domesticated adaptive syndrome, although this could be part of the "weedy" adaptive strategy in southern populations of *C. berlandieri*.

The occurrence of domesticated characteristics in spontaneous weed populations is not surprising in view of the complete interfertility and sympatry of the Mexican domesticate and its weed form. Similar circumstances occur within the South American area of chenopod cultivation and similar genetic interaction probably also occurs there (Heiser and Nelson, 1974). Under uniform environmental conditions some accessions of *C. hircinum* show unusually large fruit, condensed inflorescence branches and other characters of the domesticated syndrome (Wilson, 1976b). General phenetic similarity between some *C. hircinum* and *C. quinoa* accessions is indicated by Fig. 3, 5.

With one exception, accessions of *C. nuttalliae* and *C. quinoa* show a high level of phenetic dissimilarity when numerous characters are evaluated (Fig. 5). Accessions of *C. nuttalliae* occupy a single cluster of the phenogram, with the exception of two accessions which occur in the cluster that is otherwise occupied by accessions of *C. berlandieri* var. *sinuatum* and *C. bushianum*. Two accessions of *C. berlandieri* var. *sinuatum* occur in the *C. nuttalliae* cluster. Again, a close relationship between *C. berlandieri* var. *sinuatum* and *C. nuttalliae* is indicated. Accessions of *C. quinoa* occur in a major cluster that also contains accessions of *C. hircinum*. Other *C. hircinum* accessions show phenetic similarity to *C. berlandieri* var. *zschackei*. Morphological similarity between *C. hircinum* and *C. berlandieri* var. *zschackei* was noted by Aellen (1929) on the basis of comparisons of herbarium material. Taximetrics indicate that accessions of *C. berlandieri* var. *zschackei* are phenetically closer to *C. hircinum* than to *C. berlandieri* var. *sinuatum*. This pattern of relationships suggests that *C. berlandieri* var. *zschackei* may represent the

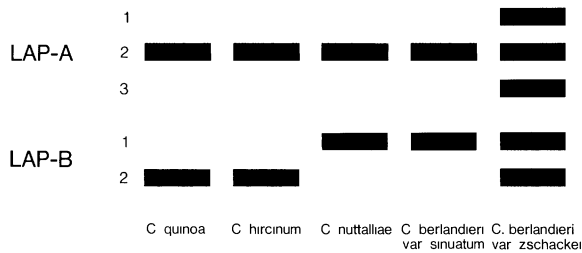


Fig. 6. Electrophoretically detectable alleles of the leucine aminopeptidase enzyme system in accessions of the taxa under consideration.

basal element from which the domesticates and their companion weeds were derived. Crossing data support this hypothesis. Of the North American complex, only accessions of *C. berlandieri* var. *zschackei* produced at least partially self-fertile  $F_1$  hybrids when crossed with accessions of the South American complex. All other hybrids between the North and South American complexes are essentially incapable of fruit set upon self pollination. Elucidation of this possible link between the North and South American tetraploids will require a more detailed examination of variation within the entire *Cellulata* group.

All taxa involved in this study have been assigned to *C. album* L. at one time or another. As indicated in Fig. 5, phenetic relationship between alveolate-fruited accessions and two accessions of *C. album* is relatively remote. Surprisingly, accessions of *C. bushianum* cluster with *C. berlandieri* var. *sinuatum* rather than var. *zschackei*. This alignment does not conform to geographic relationships between taxa, i.e., the ranges of *C. bushianum* and *C. berlandieri* var. *zschackei* overlap along the Mississippi valley.

**Isozyme analysis**—Genetic analysis has indicated that two unlinked gene loci code for leucine aminopeptidase (LAP) in these tetraploid chenopods (Wilson, 1976c). Both loci are polymorphic. Distribution of alleles among the taxa under consideration is depicted in Fig. 6.

All material from the Andes, both domesticated accessions (33) and spontaneous accessions (23), were monomorphic at LAP-A2 and LAP-B2. No electrophoretically detectable variation in active alleles occurred at either locus, although two Peruvian accessions of *C. hircinum* segregated for lack of activity at LAP-B. This apparent genetic identity between Andean domesticated forms and their companion weeds correlates well with the data presented above and supports the inclusion of both types within a single species.

Accessions of the Mexican domesticate (34) and *C. berlandieri* var. *sinuatum* (15) are also

electrophoretically identical for the LAP isozyme system. These Mexican plants produce LAP-A2, which is also fixed in the Andean complex, and LAP-B1, an allele that is either absent or extremely rare in the South American plants. This identity between weed and domesticate, along with the results of experimental hybridization and morphological comparison, is not consistent with their current alignment as distinct species.

Complete homozygosity for active LAP isozymes in accessions from areas of chenopod cultivation is remarkable in comparison to the extreme variation in accessions of *C. berlandieri* var. *zschackei* from the western United States. The fixed allele at LAP-A in the southern populations, LAP-A2, occurs in 29 of the 38 populations of *C. berlandieri* var. *zschackei* sampled to date. LAP-A1 is present in 18 of these populations and LAP-A3 has been observed in 21. Only one to five plants have been examined per population, yet 22 populations contained at least two LAP-A alleles and eight produced all three. Despite a small sample size per population, two-banded heterozygotes have been detected in several populations. Allozyme diversity at LAP-A appears to be most intense in populations from Kansas, Nebraska and South Dakota.

The fixed allele at LAP-B in Andean accessions, LAP-B2, occurs in all *C. berlandieri* var. *zschackei* accessions sampled to date, with exception of two. These plants, from Nebraska and South Dakota, produce what appears to be LAP-B1, the fixed allele of the Mexican weed-crop complex.

Isozyme diversity in *C. berlandieri* var. *zschackei* corresponds to the extreme morphological variation of this taxon which, as defined by Wahl (1952–53), includes four sub-species and numerous varieties of Aellen (1929). The relatively high level of biochemical and morphological variation within *C. berlandieri* var. *zschackei* supports the notion that this taxon is a basal element from which the North American tetraploids were derived (Wahl, 1952–53). In addition, it is the only tetraploid that is sympatric with the two American alveolate-fruited diploids, *C. neomexicanum* Standley and *C. watsonii* A. Nelson, one of which is most likely ancestral to the tetraploid complex. Isozyme variation also correlates with other data suggesting a link between *C. berlandieri* var. *zschackei* and the South American complex. LAP-B2 is fixed in the Andean populations, nearly fixed in *C. berlandieri* var. *zschackei* and absent in those Mexican accessions sampled to date.

**DISCUSSION**—Crossing studies involving accessions of domesticated chenopods from



Mexico and South America and related weed forms indicate that the Mexican and Andean weed-cultigen complexes comprise two biological species. Internal barriers to hybridization are not present between weed-domesticate pairs in either South America or Mexico, and there appear to be no external barriers to gene exchange between the domesticates and their sympatric weed forms. Weed populations occur in close physical association with domesticated populations under cultivation. As accessions of both types from a given latitude and altitude show similar photoperiodic requirements and as the plants are basically anemophilous, the occurrence of what appear to be intergrading populations in both areas of chenopod cultivation is predictable. This, plus morphological and electrophoretic similarities between weed and domesticates of each area, indicates that both domesticated chenopods are accompanied by a companion weed throughout their ranges of distribution. It logically follows that if the classification of these plants is to reflect biological relationship, then both the North and South American weed-crop complexes should each be treated as distinct species. Nomenclatural change for the Mexican domesticate is as follows:

***Chenopodium berlandieri* ssp. *nuttalliae*** (Safford) Wilson & Heiser comb. n. *Chenopodium nuttalliae* Safford, J. Wash. Acad. Sci. 8: 521. 1918. TYPE: MEXICO. Purchased at the Xochimilco market by Zelia Nuttall, 25 November 1917 (US!).

*Chenopodium pueblense* H. S. Reed, Madroño 10: 139. 1950. TYPE: MEXICO. Cultivated in Berkeley, California from seed collected at Calpan, Puebla, 2460 m, H. S. Reed 2038, 6 May 1948 (UC).

A “provisional and conservative” treatment of ssp. *berlandieri* has been provided by Wahl (1952–53). Of the four taxa listed, var. *sinuatum* is most closely aligned to the domesticated subspecies. The more complex problem of nomenclatural changes for the Andean complex will be taken up elsewhere.

Patterns of relationship delineated by this study do not support the hypothesis that the Mexican domesticate is the result of pre-Columbian diffusion of *C. quinoa* from Andean South America. It appears that the three Mexican cultivars evolved from an ancestral *C. berlandieri* type under human selection in Mexico, although point of origin cannot be determined with a high degree of certainty until variation within the entire North American tetraploid complex is better understood.

Several possibilities remain with regard to the

origin of *C. quinoa*. It could have evolved independently in South America with no influence from the North. Possible progenitors include typical *C. hircinum* of lowlands to the East, or an extinct Andean wild form that could have been displaced or assimilated by the companion weed. The *C. quinoa* complex could have resulted from an independent allotetraploid event in South America as suggested by Gandarillas (1968), although this does not appear to be likely. Current distribution of alveolate-fruited diploids is limited to North America, and there are tenuous but discernable links between some Andean accessions and *C. berlandieri* var. *zschackei*. Aellen (1929) pointed out morphological similarities between these taxa which are reflected here in Fig. 5. In addition, of the members of the North American complex, only accessions of *C. berlandieri* var. *zschackei* produce self-fertile hybrids in crosses with South American accessions. They also share the LAP-B2 allele which is absent in accessions of the Mexican domesticate and its companion weed.

These data suggest that the Andean complex may have had its origin in the North. Initial dispersal of the *zschackei*-like ancestor into South America could have occurred prior to human occupation of the area. If so, subsequent evolution of the domesticated forms would be truly independent, but based on similar ancestral genomes. It is also possible that the *zschackei*-like progenitor of *C. quinoa* could have developed adaptations to human disturbance in North America with subsequent unintentional dispersal by man into South America. In this instance, both domesticated forms would have shared those initial modifications from wild type to “attractive weed” that Sauer (1965) saw as preadaptations for annual seed crop domestication. Later evolution of the “pseudocereal” adaptive syndrome could have occurred independently in Mexico and South America. Another possibility is that a single domestication could have originally occurred in Mexico with later human dispersal of the domesticate into the Andes. In this case, the Andean companion weed would be a derivative of the ancestral domesticate, and both Andean and Mexican domesticates would share a single phylogenetic lineage with no convergence with regard to the “pseudocereal” syndrome. A part of this syndrome, the highly reduced testa of white-fruited cultivars, appears to be controlled at different gene loci in the North and South American domesticates (Heiser and Nelson, 1974). It is therefore reasonable to assume that this condition, which is not found in wild or weedy chenopods, evolved independently in North and South American areas of cultivation. However, each domesticated type in-

cludes black-fruited strains that manifest the full "pseudocereals" adaptative syndrome, with the exception of the reduced testa. Such a strain, assignable to cv. 'chia' of the Mexican domesticate, could have been ancestral to the Andean complex if there was a single original domestication in Mexico.

The origin of *C. quinoa* is an intriguing and complex problem, especially if more than one of the possibilities mentioned above has been involved. Efforts are now underway to examine *C. hircinum* (sensu Schrader, not Aellen) of lowland Argentina and Brazil to determine its relationship to the Andean complex. Additional data are being accumulated with regard to *C. berlandieri* var. *zschackei* and its possible ties to the South American, alveolate-fruited chenopods. Results of these studies should bring the origin and relationships of *C. quinoa* into better focus.

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