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Crop/weed gene flow: *Chenopodium quinoa* Willd. and *C. berlandieri* Moq.

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Abstract. Introduction of the Andean grain chenopod (*Chenopodium quinoa*) into North America placed this crop within the distributional range of a related wild species, *C. berlandieri*. This wild species, native to the North American flora, is cross-compatible with *C. quinoa*. Isozyme analysis of progeny from *C. berlandieri* plants growing within and at the periphery of the *C. quinoa* fields, combined with fertility assessment and phenetic comparison among putative hybrids and parental types, indicates that over 30% of progeny from wild plants growing as weeds with *C. quinoa* in 1987 were crop/weed hybrids. This high incidence of interspecific gene flow from crop to weed appears to be the result of asymmetric pollen flow to free-living plants from high-density cultivated populations. The observed level of crop/weed hybridization, combined with heterosis and partial fertility of F_1 crop/weed hybrids, suggests that repeated annual cycles of *C. quinoa* cultivation within the North American range of *C. berlandieri* could produce introgressive change among sympatric wild populations. In terms of risk assessment for biotechnology, these results suggest that the breeding system may not provide an accurate indication of the potential for genetic interaction among predominately self-pollinating grain crops and their free-living relatives.

Key words: Hybridization – Gene flow – *Chenopodium* – Crop evolution – Quinoa

Introduction

Wild relatives of domesticated crop species provide a unique and economically important reserve of genetic diversity. This resource could be affected by genetic interaction between cultivated stands of transgenic crops and related wild types in the natural flora. Progress toward assessment of this potential risk requires information regarding the nature and extent of crop/weed gene exchange under natural conditions.

Chenopodium quinoa Willd. (sect. *Leprophyllum* Dumort., subsect. *Cellulata* Aellen and Iljin) includes both domesticated grain cultivars (subsp. *quinoa*) and free-living, weedy types [subsp. *milleanum* (Aellen) Aellen]. Domesticated populations include *'quinua'* landraces of the Andean uplands and *'quingua'* types that occupy lower elevations in central Chile. Phenetic studies of this polymorphic species (Wilson 1988a–c) reflect an unusual pattern of relationship. Both weed and crop populations share a low level of allozyme variation that shows no differentiation between sympatric domesticated and free-living populations of the Andes. Patterns of allozyme and leaf-shape variation indicate that Andean cultivars are more closely allied to Andean weeds than to *quingua* cultivars of the Chilean lowlands. Clinal trends of leaf-shape variation tend to show congruence among domesticated and free-living Andean populations. Free-living Andean populations also share with domesticated landraces a wide range of variation in fruit size and shape.

Hypothetical constructs regarding the origin and differentiation of *C. quinoa* (Wilson 1990a) include placement of the Andean crop/weed complex as a monophyletic, possibly co-evolving, unit. This putative crop/weed system, the possible product of human-mediated dispersal and genetic manipulation, shows patterns of variation that could reflect a history of cyclic hybridization and differentiation equivalent to that evoked to explain similar patterns of relationship in other domesticated plants (Harlan 1975). If crop/weed genetic interaction has been

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a central element in the origin of *quinua* cultivars, then it is reasonable to assume that the process is operative in extant populations. While putative crop/weed hybrids swarms are not difficult to find in Andean areas of chenopod cultivation, the lack of molecular differentiation between local populations of both types inhibits direct documentation of gene flow via progeny analysis. Research presented in this paper examines the potential for gene flow from crop to weed populations in the Andes by tracking actual gene flow in an unusual population system that was established by long distance dispersal of *C. quinoa* from its native range of distribution into North America.

A barley grower from central Washington State, U.S.A., Mr. John Marcille, tested several hundred landraces of *C. quinoa* in row-planted test plots that covered approximately 28 hectares of cultivated ground near Wauconda, Washington, in 1987. Test strains included typical Andean landraces from Ecuador, Peru, and Bolivia, as well as the low-elevation *'quingua'* types from coastal Chile. Establishment of this diverse population, in an effort to examine comparative yield, placed *C. quinoa* in local sympatry with *C. berlandieri*, a closely related, free-living species native to North America. Both species are tetraploids of subsection *Cellulata*. Synthetic interspecific hybridization is possible, although F_1 hybrids show low fertility (Wilson 1980). A visit to the Wauconda field in June of 1987 revealed that *C. berlandieri* occurred as a sporadic weed among the plantings of *C. quinoa*, essentially paralleling the niche of *C. quinoa* subsp. *milleanum* in Andean fields. While Andean strains of *C. quinoa* showed no indication of floral development, populations representing the *quingua* type of *C. quinoa* and *C. berlandieri* were initiating inflorescence primordia, and it appeared that both species would be in flower during July and August. This set of circumstances, combined with an assumed presence of allozyme markers for the two species, provided an opportunity to examine gene flow from crop to weed under conditions that were not established as an experimental test.

Materials and methods

A comparative foundation for the analysis of variation among *C. berlandieri* populations at the Marcille Farm was established in October 1987 by a series of fruit collections from populations occurring along the path of travel from Spokane to Wauconda. These included progeny from individual plants from a vacant lot in western Spokane (Fig. 1 – 'site A'), the margin of a wheat field west of Davenport (Fig. 1 – 'site B'), a clear-cut in a forest of the Coville Indian Reservation (Fig. 1 – 'site C'), and a vacant lot at Republic (Fig. 1 – 'site D'). Collections from the Marcille farm near Wauconda included one *C. berlandieri* population from a roadside approximately 0.5 km from the *C. quinoa* field (Fig. 1 – 'site E'), and *C. berlandieri* growing along the margin and within the *C. quinoa* plantings (Fig. 1 – 'site F').

Sample Sites - *Chenopodium berlandieri*

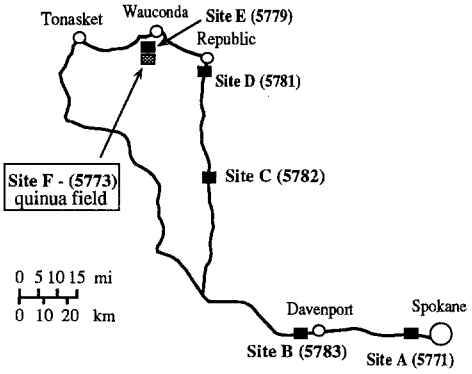


Fig. 1. Sample collection sites in northeastern Washington State identified by alphabetical sequence from Spokane to Wauconda and voucher collection number (HDW)

Variation represented by landraces of *C. quinoa* under cultivation at Wauconda was comparable, in terms of cultivar diversity and sample origin, to the sample used for prior analysis of intraspecific variation (Wilson 1988b). A random sample of 552 plants from 57 of Mr. Marcille's test strains produced a pattern of allozyme variation that is fully consistent with prior work and typical of the species. Comparative data representing *C. quinoa* and allied free-living taxa from South America were therefore derived from prior analyses of the group.

Electrophoretic examination of allelic variation in the isozyme systems leucine aminopeptidase (LAP), and phosphoglucoisomerase (PGI) followed procedures described by Wilson (1981a). Genetic interpretations of phenotypic variation (see Fig. 2) were based on prior work with these systems in *Chenopodium* (Walters 1987; Wilson 1988a). Pollen stainability was determined as the percentage of fully-stained (lactophenol cotton blue) grains among over 200 scored. Fruit and cauline leaf blade measurements were taken by automated image analysis and analyzed, using principal component analysis (PCA), as described by Wilson (1988a).

Leaf measurements consist of proportional sinus and leaf areas for lower, middle, and terminal areas of the leaf blade, total sinus area as a percentage of total leaf image area, angular measurements of the leaf tip and base, and length/width ratio. Analysis of leaf variation (see Fig. 3) was based on mean values from greenhouse-grown plants. Data for free-living populations from South America, extracted from those used by Wilson (1988a), were averages from 20 populations of *C. hircinum*, ten populations of *C. quinoa* subsp. *milleanum* from Bolivia (Cochabamba samples excluded), and 25 populations of the companion weed from Ecuador. Leaf variation among South American domesticated populations, a subset from Wilson (1988b), was represented by averages from 25 Bolivian populations (Cochabamba samples excluded), 15 samples from Ecuador, and ten samples of the Chilean *'quingua'* type. Samples from North American populations were represented by average values from six plants at site B, ten plants at site C, and five plants at site D. Leaf variation at site F was represented by average values of measurements taken from nine heterozygous (*Lap-1sm*) progeny from different parent plants and eight homozygous (*Lap-1ss*) progeny from different parent plants. Seven samples representing each genetic category are progeny from the same parent plant.

Fruit measurements include nine interval areas taken from fruits placed on edge. Each North American population (A

through E) was represented by an average of three fruit measurements. Fruit variation at site F was represented by average measurements taken from five fruits produced by a single, heterozygous (*Lap-1sm*) plant that was back-crossed to *C. quinoa*. Data for South America taxa were taken from the data sets generated for studies of free-living (Wilson 1988a) and domesticated (Wilson 1988b) populations. Each plotted point (see Fig. 4) for South American material represents an average of samples originating in the same state or province of Colombia, Ecuador, Peru, Bolivia, Chile, and Argentina.

Results

Isozyme phenotypes produced by 712 progeny seedlings from 52 *C. berlandieri* plants sampled at sites A through F are depicted in Fig. 2. Phenotypes for both LAP and PGI reflect the expression of two gene loci. Allelic identifications for variants at each locus are indicated in Fig. 2, directly below each phenotype, in terms of relative migration: slow (*s*), medium (*m*), fast (*f*), and null (no expression = n). Phenotypic identification from prior work with these systems in *C. berlandieri* (Walters 1987) place *Lap-1mm/Lap-2ss* and *Lap-1ff/Lap-2ss* as phenotypes LAP-2 and LAP-15 respectively. Phenotypes for PGI represent the slower two loci of a 3-locus system. Walters (1987) has identified *Pgi-2ss/Pgi-3ff* and PGI-2 and *Pgi-1ff/Pgi-3ff* as PGI-33.

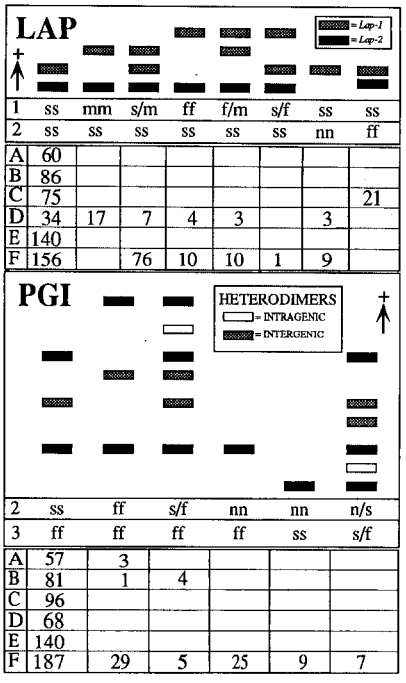
Isozyme phenotypes observed in progeny from plants at the sample sites (see Fig. 1) are indicated below each phenotype depicted in Fig. 2 by the number of plants showing the phenotype for each sample site, A through F.

Progeny from 24 plants at sample sites A, B, and C carried only the slow allele (s) at *Lap-1* and, with the exception of 21 progeny from three plants at site C, only the slow allele at *Lap-2*. The slower allozyme at *Pgi-2* was dominant at these three sites, although *Pgi-2f* was present at sites A and B. The 242 progeny examined from the three sites were monomorphic for *Pgi-3f*.

While progeny from nine plants at Site D showed no variation at PGI loci, variants for LAP included all three allozymes at *Lap-1* and a single-banded phenotype that appears to reflect a null allele at *Lap-2*. This population is unique among those sampled in that *Lap-1m* is present in the homozygous condition. This allele, the most common among *C. berlandieri* populations sampled by Walters (1987), produces an electromorph that is identical to the only active allele (*M!A*) found at *Lap-1* in *C. quinoa* (Wilson 1988b).

Progeny from seven plants occurring along the road leading to the Marcille farm, approximately 500 m from the planting of *C. quinoa* (site E), were uniform for the most common allozymes of populations A through D.

Progeny from 13 plants growing as weeds in Mr. Marcille's test plots of *C. quinoa* (site F) showed an unusually high level of heterozygosity. All but one of the



	1	2	3
	LAP	PGI	PGI
A	60	57	3
B	86	81	1 4
C	75 21	96	
D	34 17 7 4 3 3	68	
E	140	140	
F	156 76 10 10 1 9	187	29 5 25 9 7
	ss ss mm s/m ff f/m s/f ss ss	ss ff s/f nn nn n/s	ff ff ff ff ss s/f
	ss ss ss ss ss ss nn ff		

Fig. 2. Isozyme phenotypes observed in *C. berlandieri* from Washington State. Assumed genotypes at each of two loci for both isozyme systems are indicated directly below each phenotype (s = slow, m = medium, f = fast, n = null) Number of progeny from sampled plants showing each phenotype is indicated, by sample site (see Fig. 1), directly below each phenotype together with its genotypic interpretation

heterozygous seedlings carried *Lap-1m*, an allele that is fixed in *C. quinoa* and absent in the homozygous condition in 304 progeny examined from 20 plants at sites E and F. This asymmetry suggested gene flow from *C. quinoa*. Outcrossing was also indicated by congruent heterozygosity in progeny from plants that carried unusual alleles. Progeny arrays from two plants clearly indicated that the parents were homozygous for *Pgi-2f*. Of 32 progeny from these plants that were examined, only two from each plant carried the slow allele at *Pgi-2* (*s/f*). The same two individuals from each plant were also heterozygous at *Lap-1* (*s/m*), with all other progeny from the two plants showing *Lap-1ss*. Another instance involved 16 progeny of a single plant at site F. Nine of these showed a single-baded LAP phenotype (*Lap-1ss/Lap-2nn*), no evidence of activity at *Pgi-2*, and a unique, slow allele at *Pgi-3* (*Pgi-2nn/Pgi-3ss*). The remaining seven progeny were phenotypically heterozygous for both LAP (*Lap-1sm/Lap-2sn*) and PGI (*Pgi-2ns/Pgi-3sf*).

Outcrossing at site F was also indicated by morphological variation. All progeny from sampled plants at sites A through E were developmentally uniform with inflorescence primordia evident within 2 weeks of germination. Plant structure, in terms of leaf morphology and habit, was also relatively uniform among samples from

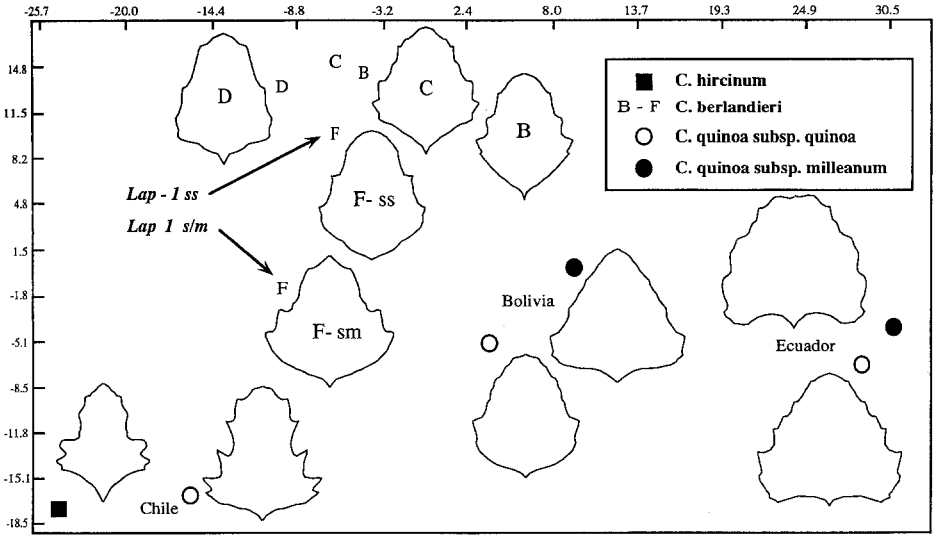


Fig. 3. Principal component plot resulting from the analysis of ten leaf blade measurements among South American taxa and *C. berlandieri*. Plotted points represent mean values from South American taxa, North American sites (B, C and D) or plants showing different LAP phenotypes from site F. Representative leaf images are taken from a single sample per group. Components 1 (x-axis) and 2 account for 61.8% and 29.50% of the variance respectively

these sites and among progeny from single plants. This was not the case for progeny from plants at site F. All plants with *Lap-1m* showed delayed floral development relative to homozygous sibs and, with regard to leaf morphology and habit, structural intermediacy between typical *C. berlandieri* from other Washington sites and *C. quinoa* growing at Wauconda. Most of the atypical progeny expressed terminal pigmentation, a character unique to domesticated *Chenopodium* and present in many strains under cultivation by Mr. Marcille.

An overview of phenetic relationships with regard to leaf morphology is presented in Fig. 3. Plotted points are identified by symbols. Leaf images associated with each symbol are taken from selected population samples of each group. Ordination of samples along the horizontal axis of this PCA plot, as indicated by percent variance contributed by variables for component 1, is mainly a function of base and tip angles, sinus areas at the middle and tip of the leaf blade, total sinus area, leaf blade area at the middle of the leaf, and length/width ratio. Narrow, lobed, acute leaves typical of *C. hircinum* represent one extreme whereas the broader, obtuse, unlobed leaves of Ecuadorian *C. quinoa* are placed at the other. Sample dispersion across the vertical axis is determined primarily by blade areas at the leaf base and tip, and sinus areas at the terminal and middle portions of the leaf image. This component acts to separate North and South American samples (B, C, and D). Leaf images representing site F were taken from progeny of a single-parent plant. Placement of the heterozygotes (*Lap-1sm*) from site F reflects phenetic separation from typical *C. berlandieri* of Washington State and linkage with Chilean *C. quinoa*.

Pollen counts from 33 progeny of parent plants at sites A, B, and C averaged 96.6% stainable. Eleven progeny from site D, representing all isozyme phenotypes depicted in Fig. 2, showed an average of 98.8% stainable pollen. Counts from 12 plants collected as fruit from site E produced an average of 99.0% stainable pollen. Average pollen stainability among 57 *Lap-1ss* progeny from the group of 13 parent plants at site F was 98.5%, whereas 36 *Lap-1sm* progeny from the same group of sampled plants averaged 1.4% pollen stainability with an individual high of 5.2%.

Fruit set in greenhouse-grown plants from site F was concordant with fertility estimates derived from pollen stainability. Heterozygous plants carrying *Lap-1m* did not set fruit upon self pollination, whereas all other progeny from the site set abundant fruit. The *Lap-1sm* progeny from site F did, however, produce some fruit when dusted with pollen from *C. quinoa*. The most distinctive structural difference between domesticated and free-living *Chenopodium* is fruit size, shape, and structure (Wilson 1981b). In terms of both size and shape, unique attributes of the domesticate should be evident from phenetic analysis (Fig. 4) of a putative hybrid and parental types. The plotting parameters for Fig. 4 are similar to those produced by a prior analysis of fruit variation (Wilson 1988a) in that ordination of samples along the horizontal axis is based on size, with measurements from interval areas at the central portion of the fruit highly weighted. Dispersion of samples along the vertical axis reflects variation in fruit shape in that marginal (tip and base of fruit image outlines) interval areas are highly weighted.

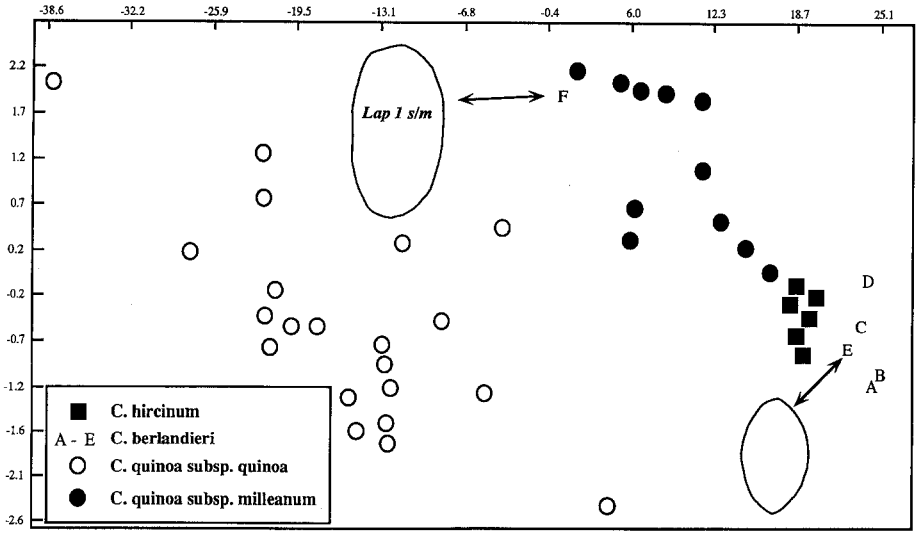


Fig. 4. Principal component plot resulting from analysis of nine fruit interval area measurements among South American taxa and *C. berlandieri*. Plotted points represent mean values from South American taxa, North American populations of *C. berlandieri* (see Fig. 1) and plants showing the *m* allele at *Lap-1* from site F. Representative fruit images are taken from a single measured sample from sites E and F. Components 1 (x-axis) and 2 account for 99.3% and 0.5% of variance respectively

Populations of *C. berlandieri* from Washington State are phenetically similar to *C. hircinum* of Argentina in that the fruits are small, bilaterally symmetrical with regard to the relatively acute margins, and uniform in terms of intraspecific variation. Domesticated populations of *C. quinoa* are characteristically variable with regard to both size and shape. This feature is shared by free-living populations of the species, although the pattern of variation extends from relatively large, truncate to obtuse-margined fruit toward the typical, wild-type condition.

Image outlines in Fig. 4 are taken from individuals fruits measured from a typical population of Washington State *C. berlandieri* (site E) and fruit produced by a single *Lap-1sm* plant from site F that was backcrossed to *C. quinoa*. The fruit outlines reflect structural differentiation that accounts for placement of the site F sample within the broader context of variation, as defined by PCA. In terms of both size and shape, fruits produced by the *Lap-1sm* from site F are clearly distinct from the parental type and aligned with samples representing *C. quinoa* subsp. *milleanum*. The overall increase in size, with disproportionate increases in marginal image areas, is fully consistent with a fruit structure that would be expected from a *quinoa/berlandieri* hybrid. Conversely, these large, truncate-margined fruit would not be produced by a typical wild-type from Washington State.

Discussion

Analysis of 262 progeny from 13 *C. berlandieri* plants that were locally sympatric with *C. quinoa* indicates that 86 carried the *Lap-1m* allozyme of *C. quinoa*. The heterozygotes, in sharp contrast to their homozygous sibs, show obvious structural differences that suggest intermediacy between *C. quinoa* and *C. berlandieri* and a marked reduction in fertility. Reduced fertility of these *Lap-1sm* plants provides a clear indication of hybridity and identification of the pollen parent. Pollen flow from diploid and hexaploid elements of the *C. album* group (subsection *Leiosperma*), also present as weeds in the Wauconda fields, are not cross compatible with tetraploids of subsection *Cellulata* (Wilson 1980). Intrasubsectional hybridization among North American elements of subsection *Cellulata*, such as *C. bushianum* of the northeastern U.S. (Wilson 1980) and *C. berlandieri* subsp. *nuttaliae* of Mexico (Wilson and Heiser 1979), results in pollen stainabilities that range from 24% to over 90%. Thus, F_1 hybrids showing less than 5% stainable pollen would not be expected from either 'wide' crosses or pollen flow from other North American elements of the subsection. However, artificial hybrids involving North and South American *Cellulata* species show an average pollen stainability of approximately 4% (Wilson and Heiser 1979). These data, fully congruent with quantitative phenetic analyses (Figs. 3 and 4), indicate quite clearly that 33% of the progeny from *C. berlandieri* sampled from site F are the result of interspecific gene flow involving *C. quinoa* as the pollen parent.

This is an unanticipated result in that both taxa represent differentially-adapted and geographically-isolated lineages in a self-compatible group of plants that is generally associated with autogamy (Walters 1987). While prior studies of genetic variation within populations of

the subsection have suggested facultative outcrossing (Walters 1987; Wilson 1981a), the level of gene flow from crop to weed observed at site F is remarkably high. This could be a result of the population structure at site F, which maximizes pollen production of the domesticate. Resources associated with the creation of the population were directed toward the establishement of a large, pure stand that shows synchronous anthesis and fruit set. In this case, most of the domesticated strains grown by Mr. Marcille represented populations of the *C. quinoa* lineage that are most likely to flower and set fruit under relatively low elevation, temperate conditions, i.e., the *'quingua'* types from central Chile (Wilson 1985). Consequently, in terms of pollen load, the Wauconda field was dominated by Chilean pollen which, given the many *quingua* strains involved, was probably maintained sequentially throughout the flowering period of *C. berlandieri*. Hybrid progeny from the few *C. berlandieri* plants growing in the *C. quinoa* planting at site F are the likely product of this disproportionate pollen load, combined with a breeding system in *C. berlandieri* that allows facultative outcrossing, probably through protogyny.

If synchronous anthesis and disproportionate pollen load account for the high level of crop/weed gene flow observed at Wauconda, then it is reasonable to assume that a similar dynamic is operative in Andean population systems which usually show the same general structure, i.e., sporadic weeds growing within a pure stand of domesticates. The Wauconda sample is, however, unique in that all observed instances of crop/weed hybridization represent primary genetic contact. As a result, all progeny from free-living plants fall cleanly into two classes; F_1 crop/weed hybrids vs typical wild-types. This is in contrast to Andean crop/weed populations which include a diversity of black-fruited, free-living types that range in structural phenotype from crop mimics to those showing a typical 'wild-type' morphology (Wilson 1988c, 1990a). Differences in phenotypic complexity between North and South American crop/weed systems would appear to be a function of time and introgression.

The 1987 harvest from Mr. Marcille's test plots included seed stock from a subset representing the most productive *C. quinoa* strains. These were sown for production in 1988. Results reported here indicate that weeds in and around the 1988 planting included a new type of weed, F_1 hybrids between *C. quinoa* and *C. berlandieri*. The interspecific hybrids, when grown under greenhouse conditions with typical *C. berlandieri*, are clearly heterotic, i.e., larger, more robust, and generally more vigorous than maternal plants. The hybrids also flower later than typical *C. berlandieri*. Thus, if hybrids were growing with *C. quinoa* at Wauconda in 1988, they were potentially able to compete with native weeds during the vegetative growth phase, and were also more likely to show congruent anthesis with the dominant pollen source, *C. quinoa*, during the reproductive phase. Given the same gene flow dynamics as the 1987 crop/weed population demonstrated in this study, and the capability of F_1 plants to set fruit when synthetically backcrossed to *C. quinoa*, it is reasonable to predict that, if interspecific hybrids were growing with the 1988 crop, they produced a backcross generation. While backcross progeny survive under greenhouse conditions, the plants show variable rates of vegetative growth and less vigor than the F_1. However, pollen stainability from six backcross progeny ranged from 0.9% to 73.4%, with an average of 17.9%, and several backcross plants set fruit upon self-pollination under greenhouse conditions. It is therefore quite possible that third generation *C. quinoa* populations grown under cultivation at Wauconda in 1989 would be sympatric with three free-living types; typical *C. berlandieri*, F_1 interspecific hybrids from the 1988 cohort, and backcross progeny produced by the 1987 group of hybrids. This type of population structure, combined with the gene flow dynamics evident in the 1987 population, would provide a foundation for the type introgressive crop/weed interaction that has been proposed to explain patterns of variation observed in Andean *Chenopodium* populations (Wilson 1990a) as well as numerous other crop/weed systems (Harland 1975; Small 1984; Ellstrand et al. 1989; Langevin et al. 1990; Wilson 1990b; Doebley 1992). Given the need to better understand crop/weed introgressive phenomena (U.S. National Research Council 1989) from both theoretical and practical (Ellstrand and Hoffman 1990; Till-Bottraud et al. 1992) points of view, a test of the hypothetical scenario described above would be particularly useful.

Large populations of *C. quinoa* have been established at several sites in the uplands of western North America at different times over the past 15 years (Wood 1988). All areas of introduction and subsequent chenopod grain production are within the range of *C. berlandieri*. If crop/weed genetic interaction extends beyond the primary formation of F_1 hybrids documented in this study, then free-living introgressants should be present among extant North American populations of *C. quinoa* and, as indicated by this study, clearly evident. Analysis of these temporally-sequenced contact points between crop and weed in North America should therefore provide a test of the hypothetical extrapolations generated by this study.

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