

Hybridization in Rare Plants: Insights from Case Studies in *Cercocarpus* and *Helianthus*

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It is now evident that hybridization can have both beneficial and harmful consequences for the conservation of biological diversity (Cade 1983). In some instances, hybridization may lead to greater genetic diversity, increased fitness, and adaptation to new environments (Stebbins 1942; Anderson 1949; Harlan 1983). Furthermore, in certain rare cases hybridization may be the only possible way to preserve the germplasm of a rare and endangered taxon. For example, hybridization was used to preserve the alleles of the now extinct dusky seaside sparrow, *Ammospiza maritima nigrescens* (Avisé and Nelson 1989).

Hybridization can also lead to the loss of genetic diversity through the genetic assimilation of a smaller population by a larger one (Cade 1983). Genetic assimilation is most likely to be a serious problem for small relict populations or island endemics when they come in contact with a numerically larger or reproductively more successful species. There are many animal species endangered because of this process, including the cutthroat trout (Allendorf and Leary 1988), Pecos pupfish (Echelle and Conner 1989), Mohave chub (Soltz and Naiman 1978), Tecopa pupfish (Soltz and Naiman 1978), yellow-crowned parakeet (Taylor 1975), Seychelles turtle dove (Cade 1983), Mexican duck (Heusmann 1974), and red wolf (Mech 1970). In contrast, there are few known examples of plant species endangered by hybridization despite the great potential for gene flow between close relatives (Anderson 1949; Heiser 1973) and the high frequency of hybridization in island floras (Gillett 1972).

A second possible harmful consequence of hybridization is outbreeding depression. That is, hybrids between genetically differentiated taxa often have reduced fitness (Templeton 1986). Reduction in fitness can occur in first-generation hybrids or may appear only in later generation hybrids or backcrosses. Outbreeding depression usually results from meiotic abnormalities or the disruption of coadapted gene complexes (Dobzhansky 1948, 1970; Sage et al. 1986). Outbreeding depression has been detected in both plants (Price and Waser 1979) and animals (Sage et al. 1986). It has been suggested that certain salmonid fishes may be endangered as a result of this process (Allendorf and Leary 1988), but the possibility of outbreeding depression has generally been ignored in studies of rare plants.

In addition to the general beneficial and harmful consequences of hybridization, hybridization has a direct impact on plant taxonomy and management decisions. Taxonomy and systematics, although sometimes considered among the least important and challenging of the biological disciplines, are critical to conservation biology because they provide the fundamental basis for management decisions (Avice and Nelson 1989). Unfortunately, classical taxonomic methodologies are often inadequate for the precise identification of, and differentiation between, first-generation hybrids, introgressive races, and bona fide hybrid species (Rieseberg et al. 1988). Furthermore, it is presently unclear how these categories should be protected under present laws, such as the U.S. Endangered Species Act (G. Nabhan pers. commun.).

In this chapter, I discuss the evolutionary consequences and management implications of hybridization in three rare plant species: *Cercocarpus traskiae* Eastwood (Rieseberg et al. 1989), *Helianthus paradoxus* Heiser (Rieseberg et al. 1990), and *Helianthus exilis* A. Gray (Rieseberg et al. 1988). It is hoped that these studies will serve as general models for the detection and documentation of hybridization and subsequent recovery strategies.

CERCOCARPUS TRASKIAE

Cercocarpus traskiae, California's rarest tree (Figure 11.1), is confined to a single canyon (Wild Boar Gully) on the southwest side of Santa Catalina Island in Los Angeles County. First collected by B. Trask in 1897 (Thorne 1967), the population has declined from more than 40 individuals to only seven adult plants today.

The decline of *C. traskiae* appears to be directly related to the introduction of large herbivores such as goats, sheep, and pigs to the island during the early nineteenth century (Thorne 1967). Although the Santa Catalina Island Conservancy has made modest efforts to reduce herbivore activity during the past two to three decades, the grazing and rooting activities of goats, pigs, and the recently introduced mule deer remain a serious threat to *C. traskiae*.

Active management of *C. traskiae* began with fencing of two individuals in the late 1970s by the Santa Catalina Island Conservancy (Martin 1984). In 1985, the Conservancy constructed a larger fence around the two adults and around good habitat area approximately 124 m on a side. Only a single seedling was found in 1984, but over 70 seedlings were observed in this area by the fall of 1988. Unfortunately, the establishment of young seedlings outside of the fenced areas appears unlikely, owing to the lack of leaf litter and to the inevitable browsing by herbivores. In addition to the emergence of seedlings, cuttings from the adult trees have been propagated at the Rancho Santa Ana Botanic Garden, and some of these specimens have been returned to test plots on the island.

In addition to herbivore threats, the long-term survival of the species is threatened by limited genetic diversity and by the occurrence of hybridization between *C. traskiae* and the more common *Cercocarpus* species on the island, *C. betuloides* Nutt ex T. and G. var. *blancheae* (C. K. Schneid) Little.

Analysis of 17 isozyme loci by Rieseberg et al. (1989) demonstrated that *C. traskiae* had extremely low levels of genetic variation. Mean values for the proportion of polymorphic loci (P), mean number of alleles per locus (A_p), and mean heterozygosity

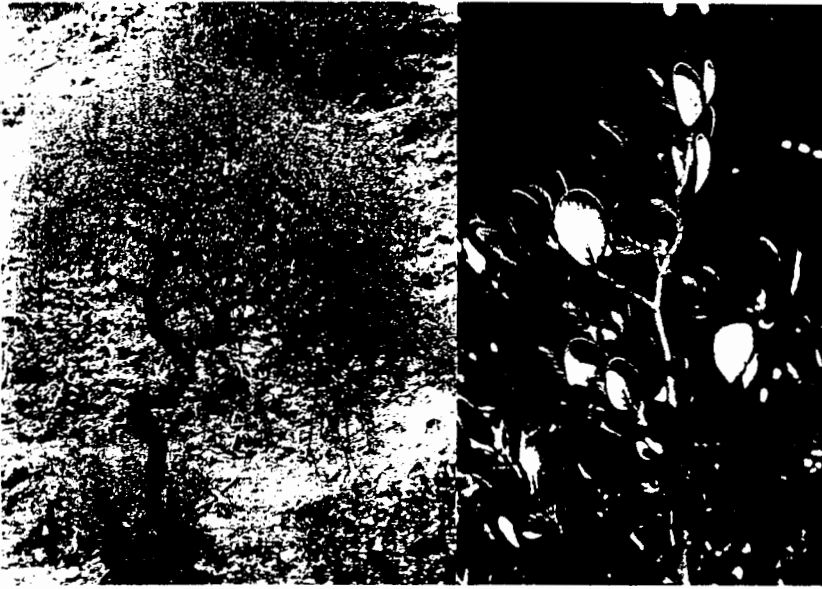


Figure 11.1. (left) California's rarest tree, *Cercocarpus traskiae*. (right) *Cercocarpus traskiae* leaves (From Rieseberg et al. 1989)

(H) of 0.12, 1.12, and 0.04, respectively, are much lower than the mean values of 0.50, 1.85, and 0.15, respectively, reported by Hamrick et al. (1979) for other out-crossing plant species. *Cercocarpus traskiae* is also genetically impoverished relative to most restricted species (Hamrick 1983; Karron 1987a). Nevertheless, levels of genetic variation in *C. traskiae* are only slightly lower than values reported for *C. betuloides* ssp. *blancheae* ($A_p = 1.24$, $P = 0.18$, and $H = 0.05$ [Rieseberg et al. 1989]).

Isozyme evidence was also used to examine the question of hybridization in *Cercocarpus* (Rieseberg et al. 1989). Isozymes are useful for detecting hybridization at the diploid level because the allozymes present in each of the parental species either are or are not found combined in the putative hybrid (Gallez and Gottlieb 1982). Comparison of *C. traskiae* with a nearby population of *C. betuloides* var. *blancheae* revealed the presence of five "pure" adult *C. traskiae* trees, two hybrid trees, and one "pure" *C. betuloides* var. *blancheae* tree in Wild Boar Gully. All seedlings examined were F_1 progeny of two of the "pure" *C. traskiae* trees.

Conservation Considerations

The threat of genetic assimilation, such as that observed in *C. traskiae*, has generally been ignored in most studies of rare plants. This is a serious oversight, given the high potential for gene flow in plants and the high frequency of hybridization in island floras (Gillett 1972). Island plants are extremely susceptible to hybridization and subsequent genetic assimilation because of geographical and edaphic limits to a species range and

population size, the general lack of chromosomal sterility barriers among closely related species, invasion and colonization by closely related exotics, and the increasing loss and disturbance of habitat due to human activities (hybridization tends to be much more frequent in recently disturbed areas [Anderson 1949]). For example, in Hawaii, hybrids involving endemic species have been reported for a large number of genera, including *Argyroxiphium* (Carr and Kyhos 1981), *Scaevola* (Gillett 1966), *Lipochaeta* (Sherf 1933a, 1933b), *Railliardia* (Sherf 1934), *Stachytarpheta* (Moldenke 1959), *Argemone* (Sherf 1944), *Antidesma* (Rock 1913), *Dodonaea* (Leveille 1911), *Dubautia* (Sherf 1933a, 1933b, 1934, 1952, 1956; Carr and Kyhos 1981), *Bidens*, (Sherf 1951, 1952), *Hibiscadelphus* (Baker and Allen 1976), *Nania* (Leveille 1911), and *Viola* (Scottsberg 1939). Hybridization is also common on the California islands (S. Junak pers. commun.), and Liston, Rieseberg, and Mistretta (unpublished) have recently shown that a *Lotus* taxon endemic to San Clemente Island may be threatened by hybridization and introgression. Nonetheless, many more detailed studies of the occurrence and consequences of hybridization in endemic island species are needed before the potential threat of genetic assimilation to the genetic integrity of island floras can be estimated.

In the case of *C. traskiae*, Rieseberg et al. (1989) made the following management suggestions:

1. The single *C. betuloides* var. *blancheae* individual in Wild Boar Gully should be eliminated. Although this individual apparently has not parented any of the *C. traskiae* seedlings observed to date, this is probably because the seedlings occur under trees some distance from the *C. betuloides* var. *blancheae* individual. If any of the three adjacent *C. traskiae* trees flower and produce seedlings, however, the *C. betuloides* var. *blancheae* individual will be a possible parent.
2. Established cuttings representing the five "pure" *C. traskiae* trees should be transplanted to other areas on Santa Catalina where the risk of hybridization is minimal. Thus two or three new populations of this species can be established. The necessary cuttings to initiate this transplant program are already growing at the Rancho Santa Ana Botanic Garden.
3. All nonnative herbivores should be removed from Wild Boar Gully, and a zero population level should be maintained.

The first two management suggestions given for *Cercocarpus traskiae* are generally applicable to most cases of genetic swamping and can be summarized as the following general strategy: eliminate the less desired species from the area of hybridization and/or transplant the rare population to a remote location where the other hybridizing taxon does not occur.

In some cases, it may also be necessary to eliminate all hybrid or introgressive individuals as well as the less desired species. For example, introgressed populations of cutthroat trout are being eliminated by poisoning in order to avoid altering the biological characteristics of this species (Allendorf and Leary 1988). In contrast, the destruction of hybrid *C. traskiae* trees was not recommended by Rieseberg et al. (1989) because limited genetic diversity was deemed to be as severe a threat as hybridization to the long-term preservation of this species. The decision whether or not to eliminate hybrid individuals should be based on the relative severity of the threats

of hybridization and limited genetic diversity. The case of *C. traskiae* may be somewhat unique because one-third of the total genetic diversity observed for *C. traskiae* would be lost by destroying the hybrid individuals. It is unlikely that this large a proportion of the total diversity of a species would be lost by eliminating hybrids in most hybridizing rare plant populations.

Although transplanting endangered populations to remote locations may seem to be an ideal solution to problems of hybridization and genetic swamping, this option has many potential difficulties. First, it may be difficult to duplicate the habitat of the original population. For example, *C. traskiae* occurs in soil derived from a rock type (igneous saussurite gabbro) found nowhere else on Santa Catalina Island (Martin 1984). Second, survival rates in introduced populations may be low. Thus the original population may be depleted by repeated attempts to establish new populations. Finally, we know very little about the interspecific interactions that may be necessary for the survival of many rare plant species. For example, an animal-pollinated plant species will not be able to reproduce successfully in the absence of its pollinator.

HELIANTHUS PARADOXUS

Helianthus paradoxus is a rare annual sunflower known only from two populations in Pecos County, Texas; one population in Reeves County, Texas; and a third, possibly extinct population in Dexter, New Mexico (Heiser 1958; Rogers et al. 1982; J. Poole pers. commun.). The species has recently been proposed for protection under the U.S. Endangered Species Act of 1973 (R. Perez pers. commun.). Although restricted to a fairly arid region, *H. paradoxus* occurs in brackish saline waters (12,000–14,000 ppm sodium chloride concentration). Turner (1981) suggested that *H. paradoxus* is simply a hybrid swarm between *H. annuus* L. and *H. petiolaris* Nutt., two closely related annual sunflowers, that was first established in the Fort Stockton area between 1945 and 1947 with irrigation that followed World War II. This hypothesis, Turner felt, could best explain the New Mexico–Texas disjunction. Additional evidence for this hypothesis is the morphological similarity of *H. paradoxus* to some individuals found in known hybrid swarms of *H. annuus* and *H. petiolaris* and the lack of collections of this species from Pecos County prior to 1947. Given these data, Turner suggested that “*Helianthus paradoxus* as a species should be viewed with some skepticism.”

Several other authors, in contrast, consider *H. paradoxus* to be a distinctive species (Heiser 1958; Rogers et al. 1982; Chandler et al. 1986). Heiser (1958) noted that although *H. paradoxus* is probably most closely related to *H. annuus* and *H. petiolaris*, the relationship does not appear to be a close one. *Helianthus paradoxus* can be consistently distinguished from both *H. annuus* and *H. petiolaris* by its glabrous pales, phyllaries, leaves, and stem; leaf and phyllary shape; late flowering time (Heiser 1958); and complete lack of sesquiterpene lactones (Spring and Schilling 1989). Heiser (1965) showed that *H. paradoxus*, although highly fertile inter se, is chromosomally distinct from both *H. annuus* and *H. petiolaris*. Finally, *H. paradoxus* is morphologically monomorphic, whereas known hybrid swarms of *H. annuus* and *H. petiolaris* are remarkable for their morphological diversity (Heiser 1947). These data indicate that *H. paradoxus* must be considered a legitimate species. A possible solution to the

two very different views of Heiser and Turner is that *H. paradoxus* is a stabilized hybrid derivative of *H. annuus* and *H. petiolaris* (Rieseberg et al. 1990). That is, *H. paradoxus* originated via hybridization some time ago, but is now a fertile vigorous species reproductively isolated from its parental species.

Helianthus annuus and *H. petiolaris* are widespread, polytypic species that are easily distinguished by a number of morphological and chromosomal features (Heiser et al. 1969; Schilling and Heiser 1981; Chandler et al. 1986). The species have similar ranges, occurring commonly in the western United States and less frequently eastward (Heiser et al. 1969). Although both species grow together in a variety of locations and hybrid swarms are common (Heiser 1947), the two taxa are found on different soil types. In general, *H. annuus* is restricted to heavy soils, and *H. petiolaris* to dry, sandy soils (Heiser 1947). Artificial hybridization experiments have revealed that the two species are very different chromosomally (Heiser 1947; Whelan 1978; Ferreira 1980; Chandler et al. 1986), and first-generation hybrids are nearly sterile. Fertility of second-generation plants is highly variable, however, suggesting that it may be possible to overcome the sterility barrier in the F₂ and later generations (Heiser 1947).

To test the hypothesized hybrid origin of *H. paradoxus*, Rieseberg et al. (1990) examined populations of *H. annuus*, *H. petiolaris*, and *H. paradoxus*, using isozyme, nuclear ribosomal DNA (rDNA), and chloroplast DNA (cpDNA) evidence. Ribosomal DNA variation can be used to detect hybridization directly because rDNA, like allozymes, is additively combined in hybrids (Doyle et al. 1985). Genetic additivity is not expected for cpDNA because cpDNA is generally maternally inherited and nonrecombinant (Sears 1983). However, cpDNA can be used to establish parentage in F₁ hybrids, differentiate between primary and secondary intergradation, and determine polarity in suspected cases of hybrid speciation (Rieseberg et al. 1990).

Their detailed genetic analysis revealed several diagnostic genetic markers differentiating *H. annuus* from *H. petiolaris*, including two isozyme loci, ten rDNA mutations, and three cpDNA mutations. Assuming a recent hybridization event, the expectation is for the hybrid taxon to possess an identical (or nearly identical), maternally inherited chloroplast genome of one parent, and an additive, biparentally inherited allozyme and rDNA pattern from both parents. If *H. paradoxus* was not derived by recent hybridization, allozyme and rDNA additivity would not be expected, and cpDNA analysis would place it with one of its two putative parents but exhibiting a number of autapomorphies, or perhaps even place it as a sister group to the other two species. *Helianthus paradoxus* combined the alleles and rDNA repeat types of its two proposed parents and had no unique alleles. Furthermore, all 30 *H. paradoxus* individuals had the chloroplast genome of *H. annuus*, a condition indicating that *H. paradoxus* cannot be ancestral to *H. petiolaris* and *H. annuus*. These data indicate, therefore, that *H. paradoxus* must have been derived through hybridization. However, because no seed was available from the New Mexico population of *H. paradoxus*, it was not possible to determine whether *H. paradoxus* was the product of more than one hybridization event.

The absence of unique alleles, the presence of a single cpDNA type, and the occurrence of only two small deletions in the rDNA of *H. paradoxus* suggest that *H. paradoxus* is not an ancient taxon. This view is concordant with its limited geographical distribution and lack of morphological variation. In contrast, both *H. annuus* and

H. petiolaris are geographically widespread, morphologically highly variable, and polytypic—characteristics which suggest that they may be more ancient.

It is also interesting to note that *H. paradoxus* is neither morphologically nor chemically intermediate between *H. annuus* and *H. petiolaris*. It lacks all the sesquiterpene lactones present in its relatives (Spring and Schilling 1990); flowers in late fall, in contrast to the summer flowering time of *H. annuus* and *H. petiolaris*; has glabrous leaves, phyllaries, and stems (varying degrees of pubescence are found on the leaves, phyllaries, and stems of its parents); and varies in the direction of neither parent in leaf and phyllary shape. Furthermore, *H. paradoxus* occurs in brackish or saline marshes, a habitat that cannot be considered intermediate between that of *H. annuus* (heavy soils that are wet in the spring but dry by midsummer) and *H. petiolaris* (dry, sandy soils). Thus data from morphology, secondary chemistry, and ecological distribution—three common approaches to the study of hybrid speciation—are misleading in the case of *H. paradoxus*. The discrepancy observed between the molecular data and other data sets is not surprising, since morphological features, chemical characters, and ecological distribution may be under strong selective pressures, whereas molecular markers tend to be neutral.

Although past events regarding the origin of *H. paradoxus* cannot be inferred with certainty, it appears likely that stable fertile types, probably tolerant to saline conditions, were selected from hybrid derivatives of *H. petiolaris* and *H. annuus*. These types differed morphologically and cytologically from the parental types, thus indicating the formation of a new species. Therefore, hybridization not only was responsible for the origin of *H. paradoxus*, but also may have served as a source of new variation (or at least new recombination) for the adaptation of *H. paradoxus* to its unique environment.

Conservation Considerations

The role of hybridization as a source of genetic and taxonomic diversity in a number of plant groups has been the subject of speculation for over half a century (Anderson and Hubricht 1938; Anderson 1949; Stebbins 1950; Lewontin and Birch 1966; Heiser 1973). More recently, a number of thorough electrophoretic studies have detected an increased frequency of rare alleles in hybrid zones (reviewed in Barton and Hewitt 1985). It has been hypothesized that their increase is due to higher mutation rates, intragenic recombination, or relaxed selection. Given the potential importance of natural hybridization as a source of new genetic diversity, natural hybrids and introgressants, where they play no obvious harmful role to an endangered species, should be considered a significant component of genetic diversity within a plant gene pool.

The questions of whether F_1 hybrids, hybrid swarms, introgressive races, or bona fide hybrid species qualify for protection under state or federal endangered species laws are more difficult. These are critical questions because stretching the Endangered Species Act to cover first-generation hybrids, for example, would damage the credibility of the endangered species program and would waste the limited resources of various plant management agencies. In this light, the criteria of Jolly (1989) for protection of hybrid taxa appear appropriate. He suggests protection for the hybrid taxon if (1) its evolution has proceeded beyond the point where crossing of the parental stock

could re-create the plant considered, (2) it is taxonomically distinct, and (3) it is sufficiently rare or imperiled. *Helianthus paradoxus* would be protected under these criteria, whereas F₁ hybrids would not.

The possible favorable aspects of hybridization for conserving rare taxa were first noted by Stebbins (1942), who argued that it should be possible to inject new variability and therefore new aggressiveness into rare species through hybridization with more widespread relatives. He further suggested that new hybrid derivatives might be easier to establish in new sites than the original rare species (see also Barrett and Kohn, Chapter 1). Both of these ideas seem problematic, however, given our present knowledge of outbreeding depression (Templeton 1986; Huenneke, Chapter 2). Furthermore, introgression of alien genes into a rare species may result in the homogenization of valuable locally adapted populations and eventual homogenization of the rare species with its more widespread relative. Nevertheless, hybridization may be useful in captive-breeding programs as a last-ditch effort to preserve the germplasm of a rare and endangered taxon. A well-known example is the dusky seaside sparrow, where hybridization was employed because of the lack of living females (Avisé and Nelson 1989).

Two factors may threaten the long-term existence of *H. paradoxus*. First, tractor-drawn mowers that scalp Texas highway right-of-ways undoubtedly inflict damage to one of the three known populations of *H. paradoxus*, which grows along Texas Highway 18. Second, both populations in Pecos County, Texas, are threatened by petroleum-production activities in the area that impede water flows.

Both threats listed above are due to human activities. Although it may be possible to convince the Texas Highway Department to refrain from mowing in this area during the summer and early fall of each year, it is unlikely that petroleum-production activities can be limited because they are on private land. This is unfortunate, since the brackish waters of Leon Creek also provide habitat for a rare endemic amphipod (*Gammarus pecos*) and two endangered fishes (*Cyprinodon bovinus* and *Pecos gambusia*) (Echelle et al. 1989). It may be best, therefore, to place large quantities of seed into long-term cryogenic storage and attempt to establish new populations of *H. paradoxus* at less-threatened sites. Both of these options may be possible because *H. paradoxus* is an annual plant, produces large quantities of viable seed, and is represented by several thousand plants in the wild. Furthermore, its natural habitat should be easily duplicated in both Texas and New Mexico.

HELIANTHUS EXILIS

One of the classic cases of hybridization and introgression in plants involves the three annual sunflowers of California: *H. annuus*, *H. bolanderi*, and *H. exilis* (Heiser 1949). *Helianthus annuus* is a common roadside weed in California, occurring frequently in the Central Valley and in southern California. *Helianthus annuus* was already in the state when the first botanical collections were made and was used by Native Americans for various purposes (Heiser 1949). Because it does not now occur in natural sites in California, it was likely introduced relatively recently by Native Americans (Heiser

1949; Stebbins and Daly 1961). *Helianthus bolanderi* and *H. exilis*, in contrast, are native to California. *Helianthus exilis* is an endangered species; its habitat is poor, moist serpentine soil in the Inner Coastal Range of mountains west of Sacramento. *Helianthus bolanderi* is widespread and weedy, and invades fields, ditches, and roadsides in the Central Valley of California (Heiser 1949). *Helianthus bolanderi* is sympatric with *H. annuus* in the Central Valley, and the two taxa form extensive hybrid swarms in areas of contact. Using morphological and cytological data, Heiser (1949) hypothesized that *H. bolanderi* developed in California through the introgression of genes from the recently introduced *H. annuus* into *H. exilis*. Although *H. annuus* and *H. bolanderi* do hybridize, and although *H. bolanderi* approaches *H. annuus* in a number of morphological characters, no evidence of gene exchange away from hybrid swarms was documented by Heiser (1949).

Nevertheless, because of the morphological evidence for introgression (Heiser 1949), most authors have considered *H. bolanderi* and *H. exilis* to be closely related introgressive races. Thus *H. exilis* is considered to be a synonym of *H. bolanderi* in recent taxonomic treatments of the annual sunflowers (Heiser 1949, 1978; Heiser et al. 1969; Schilling and Heiser 1981) and has therefore been ignored by the Office of Endangered Species of the U.S. Fish and Wildlife Service. This situation has not changed even in light of morphological studies by Jain and students (Oliveri and Jain 1977), which suggest that *H. exilis* is a unique and threatened species distinct from *H. bolanderi*.

To determine whether *H. bolanderi* actually originated by the introgression of genes from *H. annuus* into *H. exilis*, Rieseberg (1987) analyzed variation in morphology, flavonoids, and allozymes, as well as restriction-site variation of chloroplast DNA and ribosomal RNA genes (results from the allozyme, cpDNA, and rDNA studies are reported in Rieseberg et al. 1988). Morphological data were in complete agreement with those of Heiser (1949), confirming the morphological intermediacy of *H. bolanderi* relative to *H. exilis* and *H. annuus*. In contrast, flavonoid, allozyme, rDNA, and cpDNA evidence does not support the proposed introgressive origin of *H. bolanderi*. Although close to 50 taxon-specific markers were used in this study, no evidence of interspecific gene transfer was obtained. In addition, *H. bolanderi* possesses a unique cpDNA, which was outside the range of variation observed for each putative parental species (Figure 11.2). Mean sequence divergence observed between the cpDNAs of *H. bolanderi* and *H. exilis* was 0.30%. This estimate is comparable to sequence divergence values observed between closely related species of other plant groups (Rieseberg et al. 1988) and is higher than sequence divergence values observed among most other annual sunflower species (Rieseberg unpubl. data). In fact, this much cpDNA sequence divergence had never been observed within a plant species. This value is also extremely high given the proposed recent divergence of *H. exilis* and *H. bolanderi*. (Heiser [1949] suggests that *H. bolanderi* may have been derived as recently as during the past several hundred years.) In contrast, based on cpDNA divergence estimates, Rieseberg et al. (1988) suggest that the two species may have diverged as long as 3 million years ago. These data indicate, therefore, that *H. bolanderi* was not derived by introgression during the past several hundred years, as hypothesized, but is relatively ancient in origin. These data further show that *H. bolanderi* and *H. exilis* are ancient and distinctive species and should be considered as such.

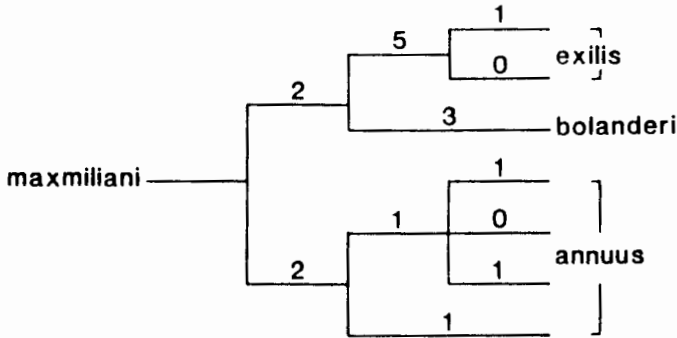


Figure 11.2. Phylogenetic tree of populations of *Helianthus annuus*, *H. bolanderi*, and *H. exilis* based on 17 restriction-site mutations. The tree is rooted relative to *H. maxmiliani* restriction sites. The number of mutations is given above each branch. (Redrawn from Rieseberg et al. 1988)

Conservation Considerations

This study, along with the previous study of *H. paradoxus*, demonstrates the limits of classical taxonomic methodologies for studying questions of hybridization and introgression in plants. Morphological intermediacy, the criterion used for testing hybridity in most studies, has been misleading in both *H. paradoxus* and *H. bolanderi*. This is not particularly surprising, since it has been known for some time that there are many other explanations for morphological intermediacy (reviewed in Heiser 1973). Nor is this the first time in which a faulty understanding of evolutionary relationships has resulted in misdirected management efforts (Avice and Nelson 1989). In short, when questions of hybridity are raised with respect to rare plants, detailed genetic studies may be necessary for their appropriate identification, classification, and management.

The primary threat to *H. exilis* is extensive mining and development in its native habitat in Napa, Lake, and Colusa counties of north central California. In particular, many of the *H. exilis* populations occur on Homestake Mining lands and are endangered by future mining developments. Members of the California Native Plant Society have shown that 13 of the 64 populations in the Knoxville area of Napa County have already been destroyed (G. Nabhan pers. commun.).

The following management strategies are recommended: (1) recognition of *H. exilis* as a unique and threatened species and subsequent establishment of status survey reporting for this taxon; (2) amelioration of development pressures near known sites; (3) collection of seed for long-term cryogenic storage; and (4) establishment of new populations of *H. exilis* at less-threatened sites. As in the case of *H. paradoxus*, *H. exilis* is an annual sunflower that produces large quantities of seed. Thus sufficient quantities of seed for both cryogenic storage and the establishment of new populations should be obtained easily. It may be much more difficult to find sites for the establishment of new populations, however, because *H. exilis* is a serpentine endemic, and its natural habitat is rapidly being lost because of development in northern California.

GENERAL DISCUSSION

The problem of hybridization and introgression in rare plants raises questions as to exactly what genetic resources we are trying to preserve and why. Native alleles characteristic of the rare species are not lost via hybridization and subsequent genetic assimilation; they are simply diluted by alleles from the widespread species. Nor are rare plant populations lost through hybridization. The populations remain, although they may come to resemble more closely their more widespread congener or some new compilospecies (Harlan and de Wet 1963). Thus we might take the position of Stebbins (1942) that introduction of new genetic variability in a rare species through hybridization with a more widespread species might actually be beneficial in terms of creating a more aggressive, adaptable species.

There are a number of reasons, however, for fearing the effects of widespread hybridization and introgression in rare plants. First, I can think of no justification for exchanging several distinct rare plant species, each with its own unique growth form and habitat requirements, for a single widespread compilospecies. The advantages of maintaining a number of distinct rare species is clear from an aesthetic viewpoint. From a genetic standpoint, it should be noted that dilution of alleles characteristic of rare plant species may lead to their eventual loss. A second danger of genetic assimilation is the loss of genetically discrete, ecologically specialized plant populations in both widespread and rare species. Finally, widespread hybridization and introgression may result in severe outbreeding depression. Whether outbreeding depression would be a temporary or a long-term problem in hybrid plant populations is unclear.

In summary, hybridization in rare plants may have a number of harmful consequences, including the genetic assimilation of a rare taxon by a numerically larger one, loss of locally adapted populations, and outbreeding depression. These negative consequences have generally been ignored in studies of rare plants, despite their high potential for interspecific gene flow. On the other hand, it is clear that hybridization may be beneficial in certain groups of plants, leading to greater genetic and taxonomic diversity. There are no criteria, however, for the protection of F_1 hybrids, hybrid swarms, introgressive races, or bona fide hybrid species under state or federal endangered-species laws. Both of these problems are exacerbated by the inadequacy of classical taxonomic methodologies for accurate identification of, and differentiation among, the various classes of hybrids listed above. A better understanding of the possible consequences of hybridization in rare plants and the accurate identification of plant hybrids should contribute to the conservation of plant diversity.

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