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Some reproductive and life history characteristics of rare plants and implications of management

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SOME REPRODUCTIVE AND LIFE HISTORY CHARACTERISTICS OF RARE PLANTS AND IMPLICATIONS OF MANAGEMENT

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Abstract.— Analysis of the vascular floras of Utah, Colorado, and California suggest that a syndrome of life form and reproductive characteristics separates rare and common species. Woody plants are heavily underrepresented, and herbs are overrepresented on the official lists of endangered and/or threatened plants of the floras considered. Few of the rare species are descended from wind-pollinated ancestors, but instead are derived from insect-pollinated stock. Theory suggests that many of the rare taxa will ultimately be shown to be self-pollinated. The date show a tendency for rare species to be better represented among taxa having bilaterrally symmetrical as opposed to radially symmetrical flowers. In aggregate, the results suggest that most rare taxa are equipped for rapid exploitation of small, unusual habitats. Because many rare taxa appear to be dependent on insects for reproduction, their survival depends not only on appropriate physical habitat but also on healthy pollinator populations. Reproduction of outcrossed taxa will be handicapped by road dust and other sources of atmospheric particulate which might foul stigmatic surfaces. Self-pollinated taxa may have little generic variability and thus be especially sensitive to environmental modifications. Because most rare taxa are dicotyledonous herbs, herbicides such as 2, 4-D which have been widely used in vegetation management for control of broadleafed plants can be expected to have highly deleterious effects on populations of rare species in the target area.

The goal of management in any discipline is control of the components of the system under consideration. The components of any system can be controlled only if their characteristics are understood. Once the critical characteristics and their dynamics through time are known, control strategies can be formulated and tested.

Currently we know a great deal about which plant species are so uncommon that their existence could be endangered by even moderate natural or manmade changes in the environment. We know less about the size and distribution of the populations of most rare species. Even less is known about the habitat requirements of the individual rare species. But perhaps our greatest ignorance concerning rare taxa relates to the specifics of their life history and reproductive biology. Before such taxa can be successfully managed, managers must understand the life cycle, longevity, and reproductive habits of each.

In this paper, I will examine various life form, longevity, and reproductive characters of endangered and/or threatened plant species of three states of the western United States: California, Utah, and Colorado. The incidence of a given characteristic among species listed as endangered or threatened in a particular state (U.S. Department of Interior 1975) will be compared to the incidence of that character in the entire seed plant flora of that state. By the use of appropriate statistical tests, characteristics that are over- or underrepresented among rare taxa can be identified, provided the incidence of each character is known among both rare taxa and the full flora of the state.

Methods

The basic data for this paper have been drawn from Munz and Keck's (1973) flora of California, a Soil Conversation Service Checklist of Utah plants (no date given), Harrington's (1964) flora of Colorado, and the U.S. Department of Interior's (1975) initial listing of endangered and threatened plant species. Characteristics of the individual taxa have been drawn from species descriptions in the floras, examination of herbarium material, and personal experience. Some taxa in all states could not be characterized adequately and were thus omitted from consid-

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eration (this deficiency was particularly serious for the California flora).

Suffrutescent (woody rooted herbs) taxa are treated as perennial herbs. Annual and biennial taxa were combined for the purposes of this paper. Mode of pollination (wind, water, or animal) was inferred for each taxon from floral structure, degree of exertion of stamens and stigmas, and published reports. The accessibility of the pollen and/or nectar to the average animal visiting the flower was deduced from floral structure. Flowers were considered to have restricted access to animals if they possessed any of the following characteristics: (1) petals, sepals, or calyx tube fused into a long (over 3 mm) tube of small diameter (as in some *Gilias*, *Oenotheras*, or *Cirsiums*), (2) nectaries positioned in tubes that extend away from the reproduction organs (as in *Delphinium* or *Aguilegia*), and (3) separate sepals and petals that are so positioned as to stand rigidly erect forming a narrow, false tube around the reproductive organs (as in *Erysimum*, *Streptanthus*, or *Vicia*). Not all sympetalous taxa were considered to have restricted access flowers. For instance, some *Campanula*, *Valeriana*, and *Kalmia* species were classified as being open and freely accessible to pollinators. Although composite flowers that include both ray and disk flowers could be considered to include both radially and bilaterally symmetrical components, I have classified such flowers as radially symmetrical. Composite flowers consisting of ray flowers alone have also been categorized as radially symmetrical in this study.

For the purposes of this paper, I have assumed that characteristics that are overrepresented among rare taxa (in comparison to the flora from which they have emerged) impart some survival advantage to the rare entity. Conversely, I assume that characteristics that are underrepresented put rare taxa at a survival disadvantage. It will be recognized that the foregoing assumptions are based upon yet another assumption, namely that most taxa that are designated as endangered or threatened are relatively recent in origin. This latter assumption implies that the rare taxon is commonly possessed of a suite of characteristics that permit it to be successful in spite of small populations and restricted habitat. I also recognize that the foregoing assumptions reveal still another assumption inherent in the analyses presented here: if characters that are overrepresented among rare taxa are viewed as enhancing their chances of survival, it must be assumed that ancient taxa that are not well suited to modern conditions and are thus in a state of population decline are uncommon entities on the lists of endangered and threatened species. This point will be considered further in the Discussion section.

In the analyses which follow, the chi-square statistic is used to determine whether a characteristic is over- or underrepresented among the taxa listed as endangered or threatened: the incidence of that character in the regional flora is used as the basis for comparison. In such analyses, the individual species become the statistical observations or replications in the compartments of the 2×2 contingency tables. Relationships were declared statistically significant only when the probability value for the relationship was .05 or less.

RESULTS

Characteristics of Regional Floras

Five regional floras have been analyzed in connection with this study (Table 1). Each flora has been analyzed to give the incidence of some or all of the following characteristics: percentage of the taxa that are woody (shrubs or trees), percentage that are wind pollinated, percentage that are short-lived (annual or biennial), percentage that have flowers that do not restrict animal access to pollen and/or nectar, and percentage that are radially symmetrical. The five floras are surprisingly similar in respect to the foregoing characteristics. The most different flora in respect to the characteristics considered is that designated as Wasatch Prevalent Species. As the name implies, that list ignores species that were sampled infrequently (Ostler and Harper 1978). An emphasis on the more common species of a region seems to unduly emphasize woody and wind-pollinated species: annuals appear to be underrepresented on the Wasatch Prevalent Species list. Whether the underrepresentation of annuals is attributable to the fact that the Wasatch Prevalent list ignores desert habitats or to some other cause is unknown.

The date (Table 1) demonstrate that woody species constitute between 10 and 15 percent of the state floras considered. In areas that are primarily desert (such as the Kaiparowits region of Utah), woody taxa may contribute almost 25 percent of the species in the flora. Wind-pollinated species contribute from 19 to 26 percent of the species in the regional floras studied. Short-lived species (annuals or biennials) furnish from 22 to 31 percent of all species in the regional floras under consideration. Animal-polluted flowers dominate all of the floras considered. In the Colorado flora and the two subsamples of the Utah flora, only from 32 to 41 percent of the zoophilous taxa have flowers that are fully opened (nectar and/or pollen readily reached by most animal visitors). Most of the zoophilous taxa in the Colorado and Utah floras are radially symmetrical (79 to 85 percent of the species).

The characteristics of the regional floras will serve as the basis against which characteristics of the endangered and threatened species of those floras will be compared. In the case of the Wasatch Prevalent Species list, no endangered or threatened species are included. Consequently, characteristics of species from the bottom third of the commonness gradient formed by arranging the prevalent species in order of decreasing average frequency will be compared with characteristics of those species which appear on the top third of the commonness gradient. Hopefully, such an analysis will reveal something about characteristics that enhance the survival of less common species.

Size and Longevity of Rare Taxa

In four of the five floras examined, woody plants are underrepresented among the endangered and threatened taxa (Table 2). The nonconforming flora is that of California: there woody plants are more common among endangered taxa than one would expect considering the number of woody taxa in the state flora, but the departure from random expectations is not statistically significant. Although most of the endangered woody species in California belong to three rapidly evolving genera (*Arctostaphylos*, *Ceanothus* and *Eriogonum*), a number of the taxa appear to be old entities that are survivors of ancient groups that are well adapted to only a few of the modern environments of the state. Species representative of apparently old, declining lineages include the following: *Cupressus goveniana* var. *abramsiana*, *Juglans hindsii*, *Lavatera assurgentiflora*, *Lyonothamnus floribundus*, *Fremontodendron decumbens*

TABLE 1. Number of species studied and characteristics of the floras considered. Floristic data sources appear at the bottom of the table. Blanks occur in the table where specific analyses have not been made.

	Flora				
Characteristic	California[1]	Utah[2]	Colorado[3]	Kaiparowits[4] (Utah)	Wasatch Prevalent[5] Species (Utah)
Size of flora	5,489	3,507	2,735	848	244
Percent woody species	14.0	10.1	11.0	22.1	21.3
Percent wind pollinated species	18.9	18.5	25.9	24.0	33.2
Percent annual or biennial species	30.7	21.9	22.7	25.1	12.3
Percent unrestricted access flowers (Zoophilous only)	–	–	40.4	32.0	39.9
Percent radially symmetrical flowers (Zoophilous only)	–	–	80.2	79.0	84.7

[1]Munz and Keck (1973)
[2]Soil Conservation Service (no date given)
[3]Harrington (1964)
[4]Welsh et al. (1978)
[5]Ostler and Harper (1978)

and *F. mexicanum*. The floras of Utah and Colorado appear not to have a significant representation of such ancient, woody taxa.

The weight of the evidences seems in favor of the hypothesis that larger (woody) species are underrepresented among rare species. Three reasons may be suggested for the underrepresentation of woody plants among rare taxa: (1) large size limits the number of individuals that can occupy any given area, (2) slower maturation rates are accompanied by lower rates of population growth, all other things being equal, and (3) long life and low reproduction rates impede the rate at which genotypes can be attuned to peculiar environments. The affect of organismal size on individuals per unit area is self-evident. The profound influence of age at first reproduction on intrinsic rate of increase of a population was demonstrated over a quarter of a century ago by Lamont C. Cole (1954 and Fig. 1). Unquestionably, the average age at onset of reproduction is older for woody plants than for herbs. Thus organismal size and age at first reproduction can be expected to combine to depress the population size of woody taxa in the early history of their existence. Theory strongly supports the concept that extinction rate is inversely correlated with population size and intrinsic rate of reproduction (Pielou 1969:17). Theorists conclude that most extinctions occur during the initial phase of population growth (Ricklefs 1979:649). Unfortulately, that is the period when slow-maturing organisms such as woody plants are at a particular disadvantage in terms of reproduction rate and population size. The chances of extinction for woody species is further enhanced by a slow rate of genetic fine-tuning to unique environments. Small, faster-reproducing (because of earlier maturation), and short-lived herbaceous taxa are almost certain to genetically adapt to new environments faster than woody taxa.

Given the advantages of small size and early reproduction, one might have expected

TABLE 2. The observed and expected occurrences of woody taxa among rare species of five floras. Expected values are based on the occurrence of woody taxa in the regional floras. A sample 2 × 2 contingency table appears at the bottom of this table. Expected values in the contingency table appear in parentheses.

	Flora				
Characteristic	California	Utah	Colorado	Kaiparowits (Utah)	Wasatch Prevalent Species (Utah)
No. of endangered and threatened species considered	234[1]	157	49	44	85[2]
No. of woody species observed	40	5	1	5	14
No. of woody species expected	33.0	15.1	5.3	9.5	22.9
Chi-square summation for the relationship	1.8	7.8	4.0	2.9	9.7
Significance of relationship	NS	**	*	NS	**

	Life form		
Species group	Herbs	Woody	Total Taxa
California endangered	194 (201)	40 (33)	234
California flora	4,721 (4,714)	768 (775)	5,489
	4,915	808	5,723

[1]Endangered species only considered
[2]No. endangered or threatened species included; species from the bottom third of the commonness gradient used instead
NS—not statistically significant
*—statistically significant at the .05 but not the .01 level
**—statistically significant at the .01 level

annual and biennial plants to be significantly overrepresented among the rare taxa. In only the California flora, however, were the short-lived taxa overrepresented, and even there the relationship fell far short of statistical significance (Table 3). In both Utah and Colorado, annuals and biennials were significantly underrepresented. Two possible reasons are offered for the results observed: (1) short life requires that a genotype by highly preadapted to the environment to be occupied, and (2) the relationship may be a taxonomic artifact because annual and biennial groups appear not to have received the close taxonomic scrutiny that numerous perennial herbaceous and wood plant groups have been exposed to. In respect to reason 1, many unique perennial herbs undoubtedly persist in potentially exploitable environments for many years before genetic recombinations are generated that permit the taxon to successfully colonize the site. Such extended periods of genetic "experimentation" would not be possible for annual or biennial taxa: in their case, the novel genotype must reach an open niche and be sufficiently well adapted to that environment to reproduce successfully in the first reproductive event. The probability that the novel genotype will be sufficiently preadapted to reproduce successfully in the potential niche during the first reproductive event is apparently small.

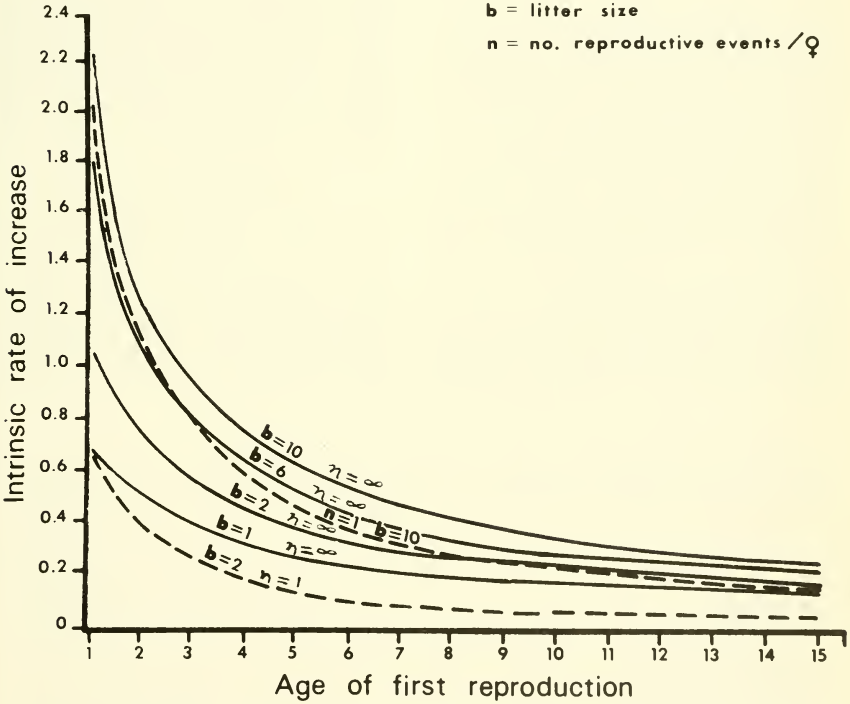

Fig. 1. The influence of age at first reproduction on rate of natural increase in population size. Note that delaying reproduction for even one reproductive period (from period 1 to period 2) for taxa that produce many offspring per reproductive event has a major effect on the intrinsic rate of poulation increase (about a 45 percent decline when b = 10 and the females reproduce repeatedly). Many perennial herbs reproduce in the first year of life, but many woody taxa delay reproduction for more than a decade. (Figure modified from Cole [1954]).

TABLE 3. Observed and expected occurrences of short-lived (annual and biennial) taxa among rare species of five floras. Expected values are based on the occurrence of short-lived taxa in the regional floras. Number of endangered and threatened species remains as in Table 2.

	Flora				
Characteristic	California	Utah	Colorado	Kaiparowits (Utah)	Wasatch Prevalent Species (Utah)
No. of short-lived taxa observed	80	15	4	9	9
No. of short-lived taxa expected	72.2	33.5	11.0	11.0	10.2
Chi-square summation for the relationship	1.3	13.6	5.8	0.5	0.3
Significance of relationship	NS	**	*	NS	NS

NS—Not statistically significant
*—Statistically significant at the .05 but not the .01 level
**—Statistically significant at the .01 level

Pollination of Rare Species

In all floras considered here, wind-pollinated taxa are underrepresented among the rare species. The relationship is significant at the .01 level in four of the five floras considered (Table 4). As Ostler and Harper (1978) have argued, wind pollination would be expected to be ineffective where species are represented by few, widely scattered individuals and where the species are small and overtopped by larger plants. Because small populations are a characteristic of all taxa listed as threatened or endangered, wind pollination would be expected to be a poor reproductive strategy for them. In addition, the threatened and endangered lists considered consist primarily of herbaceous (and thus small) organisms. Both Ostler and Harper (1978) and Freeman et al. (1979) show that wind pollination is heavily underrepresented among herbs, apparently because they are usually overtopped by woody vegetation that restricts wind flow and hinders movement of pollen to receptive stigmas.

Flower Symmetry

The data show a universal overrepresentation of bilaterally symmetrical flowers among the rare taxa of all floras (Table 5). It must be noted, however, that the values reported for California and Utah are conservative estimates only; the actual incidence of radially symmetrical flowers in those areas has not been tabulated directly

TABLE 4. Observed and expected occurrences of wind-pollinated taxa among rare species of five floras. Expected values are based on the occurrence of anemophilous taxa in the regional floras. Number of endangered and threatened species remains as in Table 2.

	Flora				
Characteristic	California	Utah	Colorado	Kaiparowits (Utah)	Wasatch Prevalent Species (Utah)
No. of wind-pollinated taxa observed	21	1	4	6	19
No. of wind-pollinated taxa expected	43.3	27.9	15.5	10.4	30.0
Chi-square summation for the relationship	14.7	33.0	12.7	2.6	12.7
Significance of relationship	**	**	**	NS	**

NS—Not statistically significant
*—Statistically significant at the .05 but not the .01 level
**—Statistically significant at the .01 level

(see Table 5 legend for assumptions for California and Utah). If the assumptions are valid for Utah, bilaterally symmetrical flowers are significantly overrepresented among rare plants there.

The overrepresentation of zygomorphic flowered species in the Kaiparowits flora narrowly misses significance at the .05 level. In aggregate, the data suggest that floral zygomorphy conveys a reproductive advantage to rare plants. That advantage perhaps lies in the fact that zygomorphy forces pollinators to approach flowers in a stereotyped way. Under such conditions (i.e., predictable positioning of the pollinator in the flower), selectin can operate to position stamens and stigmas within the flower so as to enhance the efficiency with which pollen is transferred from stamen to pollinator and from pollinator to stigma. Zygomorphy may also enhance the distinctiveness of flowers of different species and provide another cue to compliment color, size, and odor as characters that permit pollinators to distinguish flowers of one taxon from those of another. One would expect the degree of flower uniqueness to enhance fidelity between the flower and animal pollinators and thus improve reproductive success.

Restricted Access to Flowers

Taxa with flowers in which access to nectar and/or pollen rewards is restricted are overrepresented among the rare species in the three floras for which floral structure is known, but the relationship is statistically significant for the Wasatch Prevalent flora only (Table 6). Using a conservative estimate of the incidence of restricted access flowers in the California and Utah flora (i.e., the rate for Colorado from Table 1), contradictory results are obtained for California and Utah, although the results are not statistically significant for either flora. It seems reasonable to assume that mechanical barriers that restrict access of many insect taxa to nectar and pollen of a given plant species would encourage fidelity between that plant and adapted pollinators, because adapted pollinators would have greater assurance of a food reward at each visit (i.e., many potential competitors would be unable to harvest the floral rewards). The data lend only slight support to the foregoing assumption, however, and it is clear that mechanical hedges about floral rewards are much less useful adaptations to rare plants than small size, early onset of reproduction, animal pollination, or bilateral symmetry of the flower.

TABLE 5. Observed and expected occurrences of bilaterally symmetrical flowers among the animal-pollinated rare species of five floras. Expected values are based on the occurrence of bilaterally symmetrical zoophilous flowers in the regional floras except for California and Utah. Because the actual incidence of bilaterally symmetrical flowers is unknown in the latter two floras, expected values are based on the conservative assumption that bilateral flowers occur with a frequency in those floras equal to the frequency in the Kaiparowits flora (see Table 1).

	Flora				
Characteristic	California	Utah	Colorado	Kaiparowits (Utah)	Wasatch Prevalent Species (Utah)
No. of threatened and endangered species considered	214[1]	156	45	38	66[2]
No. of bilaterally symmetrical flowered species observed	52	48	12	13	12
No. of bilaterally symmetrical flowered species expected	45.3	33.5	9	8.2	9.8
Chi-square summation for the relationship	1.3	8.4	1.3	3.8	1.5
Significance of relationship	NS	**	NS	.10[3]	NS

[1]Endangered species only considered
[2]No. endangered or threatened species included: species from the bottom third of the commoness gradient used instead
[3]Statistically significant at the .10 but not at the .05 level
NS—Not statistically significant
*—Statistically significant at the .05 but not the .01 level
**—Statistically significant at the .01 level

Discussion

Results show that the California flora behaves differently from that of Utah and Colorado in respect to the frequency of both woody and short-lived taxa. The overrepresentation of rare woody taxa in California may be explained by the relatively high incidence of apparently ancient woody taxa there. Some of the ancient woody taxa of California have been enumerated in the Results section of this paper. If there is a significantly larger component of evolutionary old taxa in California than in Utah or Colorado, the divergent results reported in Table 2 for California and the two interior states would be expected. That is, in California ancient woody species that are rare may be viewed as taxa that were once more common but have steadily lost habitat to more modern species that are better adapted to current environments. If such is the case, the basic assumption underlying this paper (i.e., characteristics that are overrepresented among rare taxa must enhance their chances of survival) would not hold. Instead, characteristics considered to be selected against among recently evolved taxa that have successfully eluded extinction may be overrepresented in older floras that are now marginally adapted to and declining in modern landscapes.

The slight overrepresentation of short-lived taxa among endangered plants of California (Table 3) is unique for the floras examined. It should also be noted that the California flora supports significantly more annual plant species than any of the other floras considered (Table 1, Harper et al. 1978). It seems likely that annual plants have been more intensively studied in California than in the interior states, but differences in taxonomic treatment among the floras considered seem inadequate to explain the differences noted in Table 1 and in Harper et al. (1978, Table 3). A suitable explanation for the apparent greater success of annuals in California as opposed to Utah and Colorado is needed, but I am unable to supply such an argument.

The fact that most of the rare taxa in the floras considered are zoophilous or, at least, derived from zoophilous stock (Table 4) suggests the need for managers to use great care when insect control programs are implemented near populations of rare plants. Unless the taxa are self-pollinated or agamospermous (producing seed without fertilization), decimation of pollinator population would adversely affect reproductive success of the plant species in at least the year of treatment.

Unfortunately, the incidence of self-pollination and agomospermy among threatened and endangered species is almost totally unknown. Consequently, all rare taxa should be

Table 6. Observed and expected occurrences of restricted access flowers among the animal-pollinated rare species of five floras. The number of endangered and threatened taxa remains as in Table 5. Expected values are based on the incidence of flowers in which access to nectar and/or pollen is restricted in the regional floras, except for California and Utah. Because the actual incidence of zoophilous species having restricted access to floral rewards is unknown in the latter two floras, expected value is based on the conservative estimate that restricted access flowers occur with a frequency in those floras that is equal to the frequency in the Colorado flora (see Table 1).

	Flora				
Characteristic	California	Utah	Colorado	Kaiparowits (Utah)	Wasatch Prevalent Species (Utah)
No. of threatened or endangered taxa observed with restricted flowers	119	99	29	26	45
No. of taxa expected to have restricted flowers	127.1	93.3	26.9	25.5	39.1
Chi-square summation for the relationship	1.3	.9	.4	.04	5.6
Significance of relationship	NS	NS	NS	NS	*

NS—Not statistically significant
*—Statistically significant at the .05 but not the .01 level

treated as obligate outcrossers until proven otherwise. This point suggests that any management act that has the potential of diminishing pollen flow between separate individuals of any rare taxon should be carefully evaluated in terms of possible reproductive impairment of that plant. Thus, construction work or traffic over unpaved roads near populations of either wind- or animal-pollinated species should be carefully controlled or curtailed completely, because dust can foul stigmatic surfaces and essentially eliminate pollination of obligate outcrossers.

A knowledge of the breeding system of all rare taxa would markedly improve our ability to make wise management decisions concerning them. As noted above, outcrossing taxa will necessitate more management restrictions than self-pollinated or agomospermous taxa. On the other hand, self-pollinated and agamospermous taxa may be far less genetically diverse and hence more easily disturbed by environmental alterations than outbreeders. Furthermore, a knowledge of the breeding systems of rare plants would help phylogeneticists to better define the probable origins of the taxa and geneticists to estimate the likely amount of unique germ plasm in given taxa (Baker 1961).

Circumstantial evidence suggest that many of the threatened and endangered plant species will be shown to be self-pollinated or agamospermous. Such reproductive habits would be expected to be selected for in rare taxa for two reasons: (1) both habits would tend to preserve unique gene combinations that adapt rare plants to their habitat, and (2) both reproductive habitats would permit solitary individuals to successfully reproduce (Grant 1971).

Finally, it is worthy of note for managers that most of the rare taxa in all of the floras considered here are dicotyledons. Thus, the broad spectrum herbicides belonging to the 2, 4-D group (dichlorophenoxyacetic acid and near relatives) that have proven so effective against broadleaved plants can be expected to be dangerous to most rare plants. Herbicides of this group have been widely used in land management programs in the past for control of undesirable species. In the future, threat to endangered species must be added to the list of constraints that must be considered when use of such herbicides is considered.

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