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BOTANICAL BRIEFING

Stabilizing Selection and the Structural Variability of Flowers within Species

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Zoophilous flowers often appear to be precisely formed for pollen transfer and exhibit relatively little variability in structure within species. Functional optimization by the seemingly exacting requirements of pollen transfer may account for these observations. I used the results of a literature survey to examine the levels of intraspecific variation in flowers across a wide range of taxa. The least variable attributes were those potentially affecting the mechanical fit between flower and pollinator, which are potentially constrained by selection for pollination performance. I discuss six mechanisms by which plant-pollinator interactions could generate stabilizing selection on flowers. In addition, I consider the stabilizing roles of limiting resources and also two functionally-neutral mechanisms. Further work is required to identify the actual mechanisms by which selection stabilizes the evolution of flowers.

Key words: Stabilizing selection, flowers, pollination, variation.

INTRODUCTION

Zoophilous flowers often appear to be formed so as to place pollen on the body of a pollinator in a position where it will contact the stigma of a subsequently visited flower (Proctor, Yeo and Lack, 1996). As a general principle, natural selection is said to shape the evolution of flowers by matching flowers to their pollinators (Stebbins, 1970; Feinsinger, 1983). Thus, pollination biologists have viewed the structure of zoophilous flowers as precisely suited to meeting the seemingly exacting requirements of pollen transfer (Darwin, 1862; Straw, 1956; Galen, Zimmer and Newport, 1987; Armbruster, 1988). If flowers have been functionally optimized, then this may account for the relative invariability of flowers within species.

My first objective is to use a literature survey to examine the levels of intraspecific variation in various attributes of flowers across a wide range of taxa. My second objective is to explore the variety of mechanisms by which flower structure is said to influence pollen transfer and to evaluate the evidence that these mechanisms can stabilize the evolution of flowers.

I discuss only attributes of zoophilous flowers that exhibit either continuous variation (e.g. dimensions, masses of various floral organs, rates of nectar production) or at least quasi-continuous variation (numbers of pollen grains) and that have frequency distributions that are distinctly unimodal, so that it makes sense to refer to 'normal' and 'abnormal' individuals. The evolution of polymorphisms (e.g. heteromorphy, heterostyly, etc.) will not be directly addressed.

LITERATURE SURVEY

I collected CVs (coefficients of variation, SD/$\bar{x}$) relating to floral metrics from 52 published studies (Appendix 1). If more than one population of a species was studied, then a single representative was chosen. Similarly, where a polymorphism was studied, data from only one morph was utilized. Compound metrics (i.e. where one metric was subtracted from another), such as stigmatic exsertion, were eliminated because these could have means close to zero, which could inflate the CV. Additionally, the magnitudes of CVs were compared among functionally related categories (Table 1). No statistical comparisons were performed because the data are influenced by many confounding factors, including phylogeny, which negate the crucial assumptions of randomness and independence.

Overall, 365 CVs were obtained from 151 plant species distributed among 48 families (Appendix 1). Excluding the metrics of nectar production, the median CV was 0·14 (mean = 0·20, maximum = 1·53, $n = 307$) and the 95th percentile was 0·51 (Fig. 1). The least variable categories were the volumes of individual pollen grains, the dimensions of flowers' sexual parts and the dimensions potentially affecting the mechanical fit between flower and pollinator (Table 2). The most variable categories were related to biomass, gender and nectar production (Table 2). Indeed, the distribution of CVs relating to nectar production (Fig. 2) differed markedly from the distribution of CVs of other morphological dimensions.

Several conclusions have emerged. First, flowers are not invariable and some of their attributes are more variable than others. Second, the differences in variability among functional categories supports the assertion that natural selection mediated by pollination performance has set fairly precise constraints on certain attributes of flowers. For

TABLE 1. *Scheme used in the literature survey for grouping floral metrics taken from published studies into nine functionally-related categories*

Advertising (a)	Biomass (b)	Gender (g)
Corolla diameter	Androecium mass	Fraction viable pollen
Corolla size	Anther mass	Gender score
Corolla width	Gynoecium mass	Male fertility
Flower width	Perianth mass	Ovules per flower
Petal area	Petal mass	Pollen:ovule ratio
Petal length/width		Pollen per anther
Petal lobe length/width		Pollen per flower
Sepal length		

Meristic (m)	Nectar (n)	Pollen grain volume (p)
Carpels per flower	Nectar concentration	Pollen grain volume
Nectaries per flower	Nectar volume	
Petals per flower	NPR (mg hr^{-1})	
Stamens per flower	NPR (μl hr^{-1})	

Sexual dimensions (s)	Stigmatic area (t)	Vector matching (v)
Anther length	Stigmatic area	Corolla length
Gynoecium length		Floral tube length
Hypanthium length		Flower diameter
Nectary—mid anther		Flower length
Nectary—stigma		Nectar spur length
Ovary length		
Pistil length		
Stigma height		
Style length		

The parenthetic abbreviations are used in Appendix 1 to indicate the kind of data that were derived from studies that were included in the literature survey. 'NPR' refers to nectar production rate per flower.

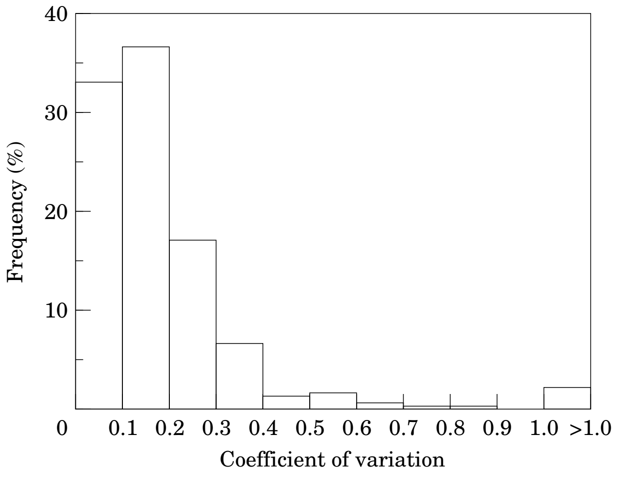

FIG. 1. Frequency distribution (%) of 307 coefficients of variation of floral attributes (excluding those relating to nectar production).

example, the relative invariability in the volume of individual pollen grains is consistent with a link with performance (Lau and Stephenson, 1993). Finally, the high variation in nectar production suggests a strong influence of the plants' age and environment (e.g. Southwick and Southwick, 1983).

TABLE 2. *Summary statistics of coefficients of variation* (*CV*) *in floral metrics grouped into nine categories of functionally-related floral attributes.*

Category	Median CV	Mean CV	*n*
Pollen grain volume	0·10	0·26	9
Sexual dimensions	0·11	0·18	54
Vector matching	0·13	0·14	106
Advertising	0·16	0·22	54
Meristic	0·17	0·16	13
Stigmatic area	0·20	0·23	6
Biomass	0·24	0·27	13
Gender	0·26	0·29	52
Nectar	0·57	0·54	58

Some caveats are necessary. Certain aspects of the data may not represent plants in general. Some unusually large CVs are probably included because the plants were chosen for study because of their variability (e.g. studies of meristic characters). Additionally, the comparison of CVs among functional categories may be affected by differences among categories in the representation of variable species or in the magnitudes of measurement errors.

To illustrate the implications of the survey, consider a floral dimension with a CV of approximately 0·15, which is

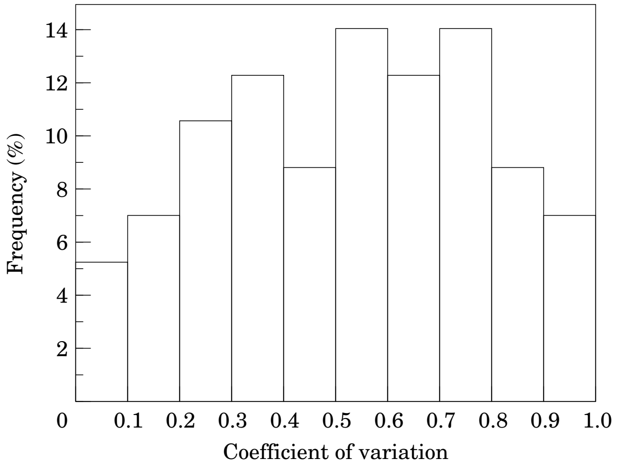

FIG. 2. Frequency distribution (%) of 58 coefficients of variation of metrics that describe nectar production.

seemingly typical. If this particular floral dimension has a mean of 10 mm and its distribution is normal, then only half of the flowers will have measurements within 1 mm of the mean, although approximately 95% of flowers will be expected to return a measurement within 3 mm of the mean. Are we surprised by the variability of these flowers, or by their invariability? The answer depends on our assumptions about the precision of the requirements for effective pollen transfer. One point is certain, natural selection can stabilize the evolution of flowers only if abnormal flowers are functionally inferior, but how can such performance differentials arise? Below, mechanisms are considered by which stabilizing selection can act on flowers.

STABILIZING INFLUENCES IN THE EVOLUTION OF FLOWERS

(*1*) *Mate matching: pollen exchange and the match between sexual architecture in conspecific flowers*

Ideas. Berg (1960) argued for the operation of stabilizing selection on floral morphology as follows. Pollen wastage can be reduced when deposition on the pollinator is focused on a site that is sheltered from the animal's grooming behaviours. However, precise localization of pollen is advantageous in promoting pollen exchange only if the male and female sexual parts of conspecific flowers all tend to contact the pollinator at the same specific site. The sexual parts of abnormal flowers will be less effective in contacting the most common site of pollen deposition and stabilizing selection will standardize sexual architecture by 'mate matching'.

Evidence. No experiments have directly tested the mate matching hypothesis. However, there are three lines of circumstantial support. First, evidence comes from studies of heterostylous species, which exhibit a polymorphism whereby anthers and stigmas are borne at differing heights in each morph. For example, distylous species exhibit 'reciprocal herkogamy' (Barrett, 1992) in which about half the plants typically have long styles and short stamens and the remainder have short styles and long stamens. Mating between dissimilar morphs is favoured (Lloyd and Webb, 1992; Harder and Barrett, 1996), presumably because pollinator contacts correspond between sexual organs of differing morphs. Thus, in homostylous species, pollen exchange may also be favoured by increased similarity in the location of male and female sexual parts.

However, these conclusions must be viewed with caution. First, the differences between distylous morphs are generally fairly large (Dulberger, 1992). If such large differences are necessary to achieve segregation in pollen placement, then, in homostylous species, selection will act against only very abnormal flowers. Second, selection for mate matching may not operate against all kinds of abnormalities because, even in distylous species, not all variation affects pollen exchange. For instance, Stone (1995) found that pollen from short stamens borne deep within the floral tube was preferentially transferred to short stigmas, but pollen presented at the mouth of the corolla was transferred equally to stigmas of both floral morphs.

A second source of evidence derives from consideration of heterospecific pollen transfer. When plant species share a pollinator, dissimilarities among species in floral morphology account for the differences in pollen placement on the pollinator (e.g. Sprague, 1962; Beattie, 1971; Levin and Berube, 1972; Stiles, 1975; Waser, 1978; Murcia and Feinsinger, 1996). Thus, it is postulated that heterospecific pollen exchange increases with the degree of similarity between flowers (Rathcke, 1983; Waser, 1983), although this is not yet supported by experiments. By extension, floral similarity may be said to favour pollen exchange in homostylous species also.

Third, the notion of mate matching also underpins one explanation for the evolution of secondary pollen presentation, which involves the transfer of pollen to a structure other than the thecae of the anthers prior to the arrival of pollinators (Yeo, 1993). In some species (e.g. some Campanulaceae) pollen is presented on the style. Stylar presentation may serve to match the sites of pollen presentation and reception and increase the chance of pollen reaching a conspecific stigma (Yeo, 1993). However, there are also many other functional explanations for secondary pollen presentation (Yeo, 1993; Cresswell, 1994).

(*2*) *Vector matching: pollen transfer and the structural match between flowers and their pollinators*

Ideas. Stabilizing selection can operate if the degree of pollen transfer depends on the mechanical fit between the animal vector and the flower's sexual parts (Wilson, 1995). In this case, the evolution of the flower stabilizes on a form that optimizes the mechanical fit.

Evidence. Of six experimental studies, four support the proposition that transfer of pollen between flower and pollinator is affected by flower form through vector matching. Nilsson (1988) found that shortening the floral tube of an orchid, *Platanthera bifolia* (Fig. 3A), reduced the likelihood that pollinia were transferred during the visit of a long-tongued moth. Similarly, Campbell, Waser and Price (1996) found that pollen export in *Ipomopsis aggregata* (Fig. 3B) was reduced when the hummingbird pollinators were

FIG. 3. Illustrations relating to experimental investigations of the relationship between flower form and pollen transfer. A, *Platenthera bifolia*, studied by Nilsson (1988), showing experimental constriction on a nectar spur; B, hummingbird-pollinated *Ipomopsis aggregata* studied by Campbell *et al.* (1996); C, cut flowers of *Impatiens pallida* (yellow, left) and *I. capensis* (orange, right), studied by Wilson and Thomson (1996); D, bumblebee species studied by Wilson and Thomson (1996) showing variation in size (left to right: workers of *Bombus impatiens*, *B. fervidus*, *B. vagans*).

prevented by a plastic shield from fully inserting their beaks into tubular flowers. In particular, Campbell *et al.* (1996) found that an alteration of just 2 mm in floral diameter greatly reduced pollen removal during a hummingbird visit. Wilson and Thomson's (1996) study of bumblebee-pollinated *Erythronium grandiflora* found that stigma exsertion related to pollen import, which possibly resulted from vector matching. Somewhat discordant support for vector matching emerges from Wilson and Thomson's (1996) study of bumblebee-pollinated *Impatiens pallida* (Fig. 3C), in which pollen export varied with certain floral dimensions, but pollen transfer did not vary among bumblebee species that showed consistent differences in size and tongue length (Fig. 3D). In conflict with the vector matching hypothesis are the results of Wilson (1995), who found that manipulations of the dimensions of the tubular corolla in *Impatiens pallida* and *I. capensis* (Fig. 3C) flowers generally did not influence pollen transfer by bumblebees. Similarly, Cresswell and Galen (1991) found little difference in pollen transfer in single visits by bumblebees to different sized flowers of *Polemonium viscosum*.

The match of flower and pollinator is the basis of the recognition of floral 'syndromes' (van der Pijl, 1961), which link types of flowers with particular types of pollinator (e.g. 'bee flowers', 'moth flowers', etc.). It may be objected that plants are actually visited by more kinds of pollinator than their syndrome classification may suggest (Knuth, 1908; Waser *et al.*, 1996), in which case vector matching will not be a potent stabilizing mechanism when the suite of pollinators contains different body shapes. Stebbins (1970) has responded by proposing that '… the characteristics of the flower will be molded by those pollinators that visit it most frequently and effectively …', which he terms the 'most effective pollinator principle'. However, a study by Fenster (1991) undermines the generality of this principle. Fenster reasoned that the length of a flower's corolla tube will restrict accessibility by pollinators such that the shortest tubes will attract the highest pollinator diversity. In a survey of hummingbird-pollinated species in the neotropics, Fenster (1991) found the lowest variation in dimensions in flowers with the longest corollas. Since natural selection erodes variation, Fenster's result implies that selection for vector matching is likely to be most stringent only when pollinator diversity is low.

(3) Forager attraction

Ideas. A flower's sexual capacity is likely to be limited by the availability of pollinators acting through male function (Stanton, 1994) if not always through female function (Bierzychudek, 1981; Haig and Westoby, 1988; Bell and Cresswell, 1998). There is extensive evidence that pollinators such as social bees (Hodges, 1985; Schmid-Hempel, 1987; Cresswell, 1990) and hummingbirds (Pyke, 1978; Montgomerie, Eadie and Harder, 1984) are sensitive to foraging economics and can discriminate among intraspecific variants based on rather subtle criteria (Galen and Newport, 1987; Cresswell and Robertson, 1994). Variant flowers that advertise a reduced uptake rate will be discriminated against by economically sensitive pollinators, resulting in stabilizing selection focused on the optimally rewarding form of flower.

Evidence. Møller (1995) found that, in pairwise choices, bumblebees preferred the flower of *Epilobium angustifolium* with the highest bilateral symmetry. Nectar production was also greater in more nearly symmetrical flowers. Thus, pollinator preference could stabilize the evolution of floral symmetry. Similarly, flower colour may be stabilized because foragers prefer a floral colour scheme that maximizes the clarity of nectar guides, which reduces reward extraction time (Waser and Price, 1983). More generally, the existence of an optimally rewarding form of flower is not so easily guaranteed. For instance, it has been found that pollinators discriminate against flowers with smaller corollas (Bell, 1985; Galen and Newport, 1987; Strauss, Conner and Rush, 1996), presumably because, on average, smaller flowers contain smaller rewards (Cresswell and Galen, 1991), but discrimination against unusually large flowers has not been reported. However, it is possible to construct a scenario whereby stabilizing selection could arise. Suppose that increased corolla size signals both an increased amount of nectar and increased depth of the floral tube, which could either increase the amount of time that it takes a forager to extract the reward (Harder, 1983) or decrease the amount of nectar accessible to the forager. Under these seemingly restrictive conditions, economically sensitive foragers would discriminate in favour of an intermediate corolla size.

A further stabilizing mechanism may result from pollinator ethology whereby pollinators become neurobehaviourally fixated on particular floral cues and so avoid abnormal variants (Wilson and Stine, 1996).

(4) Probe duration

Ideas. Potentially, pollen transfer can increase with the amount of time that the pollinator spends in probing the flower. For stabilizing selection to operate, the advantages of increased probe time must be balanced by concomitant fitness costs. For example, the plant may be selected to produce flowers with larger rewards whose extraction increases probe time, but the pollinators' response to large rewards may be to probe more flowers on the plant, producing increased geitonogamy and pollen discounting (Klinkhamer and de Jong, 1993). Similarly, the plant may be selected to increase probe duration by making rewards less accessible, but pollinator limitation may result if economically sensitive pollinators discriminate against flowers where reward extraction takes longest.

Evidence. Many studies have found that pollinators spend more time in a flower with a large nectar reward and, as a result, pollen transfer at the flower increases (Galen and Plowright, 1985; Thomson, 1986; Galen and Stanton, 1989; but see Mitchell and Waser, 1992). Hodges (1995) offers tentative evidence that stabilizing selection may act on nectar production in *Mirabilis multiflora* because the level of deleterious self-pollination increases with nectar levels. No study has yet demonstrated nectar-independent effects of flower structure on probe duration.

(5) Visitor restriction

Ideas. Stabilizing selection could focus on a flower form that conferred optimal pollen transfer because it attracted visits from the greatest diversity of pollinators. Potentially, such a situation would result if abnormal flowers had rewards that were less accessible to certain pollinator species, who avoided these variants to the detriment of the plants' reproduction.

Evidence. There is no direct evidence that intraspecific flower variants experience differences in the species composition of their pollinator faunas, although the existence of a relationship between floral morphology and pollinator composition is widely accepted in the context of interspecific variation (e.g. Van der Pijl, 1961).

(6) Pollination at the whole-plant level

Ideas. Pollinators often probe more than one flower during a visit to an individual plant. Flower structure is likely to affect the pattern of within-plant pollen carry-over and, consequently, the degree of geitonogamy and pollen discounting, which may have a deleterious effect on pollination performance (Robertson, 1992; de Jong, Waser and Klinkhamer, 1993; Harder and Barrett, 1996). Potentially, stabilizing selection could maintain a floral form that confers optimal performance by maximizing pollen transfer at the individual flower and minimizing geitonogamy for the multi-flowered 'pollination unit'.

Evidence. As yet, there is little experimental evidence that the morphology of individual flowers affects performance at the whole-plant level. Contrary to the proposed stabilizing mechanism, Waser and Price (1984) suggest that selection may operate to maintain within-plant variation among flowers in order to extend pollen carry-over and ameliorate geitonogamy.

(7) The role of limited resources

Ideas. Increased biomass allocation to floral parts may improve the pollen transfer attained by a single flower, but also divert resources away from other fitness-related sinks. Therefore, stabilizing selection will cause evolutionary convergence on an optimal allocation pattern.

Evidence. Limits to resource allocation must necessarily exist, but it is not possible that resource limitation can, by itself, stabilize the form of individual flowers. The modular construction of plants means that individuals could be selected for reduced flower number and reallocation of the extra resources among the remaining flowers. Thus, resource limitation may impose constraints on overall reproductive allocation, but not on the distribution of biomass among and within individual flowers.

FUNCTIONALLY NEUTRAL IDEAS FOR THE INVARIABILITY OF FLOWERS

(*8*) *Genetic homogeneity*

Ideas. Flowers are relatively constant because of the homogeneity of the genes that control flower morphology.

Evidence. The position that genetic homogeneity maintains floral constancy is untenable. Floral variation is known to have a heritable basis in many species (Mitchell and Shaw, 1993; Robertson, Diaz and Macnair, 1994; Campbell, 1996; Galen, 1996). Moreover, even meristic characters such as the numbers of flower parts, which are usually relatively invariable, have been shown to have an underlying genetic heterogeneity (Huether, 1968).

(*9*) *Developmental integration*

Ideas. Flower structure is stabilized because genetic changes that alter flower development are eliminated by selection because of their deleterious effects on other plant traits. This mechanism evokes the viewpoint of Gould and Lewontin (1978), which presents the organism as an 'integrated whole' and 'replete with constraints'. For example, to explain the invariability of flowers, Stebbins (1974) postulates a 'genic balance or equilibrium that for some unknown reason is adaptive and is maintained by natural selection'.

Evidence. Stebbins (1974) supports his proposed 'genic balance' by reference to Huether's (1968, 1969) studies of *Linanthus androsaceus*, which found that compared to normal pentamerous plants, abnormal, non-pentamerous plants were 'weak and slow growing'. Plausibly, developmental integration could constrain major changes in flower development concerning meristic characters or homeosis, which involves changes in the identity of floral parts. However, it seems unnecessary to accept that similar constraints act on minor quantitative changes in continuous characters, such as floral dimensions.

Primack (1987) has shown that phenotypic correlations exist between attributes of flowers, fruits and seeds. If developmental integration is strong, then flowers could be constrained by stabilizing selection acting at the dispersal stage of the life cycle.

CONCLUSION

In the decade since the publication of Endler's (1986) seminal book on natural selection, pollination biologists have demonstrated the action of natural selection on flowers in the wild (Campbell, 1989; Galen, 1989; Schemske and Horvitz, 1989; Conner *et al*., 1996). However, it is directional selection that has been revealed and little consideration has been given to mechanisms that stabilize the evolution of flowers. A survey of intraspecific variation in flowers reveals patterns that are consistent with the assertion that pollination performance constrains certain aspects of flower structure. This review has introduced six ways that the evolution of flowers could be stabilized by pollinator-mediated selection. The list could probably be extended by considering the relationship between herkogamy and autogamy and the potential for seasonal shifts in the direction of selection (Schemske and Horvitz, 1989). In theory, the mechanisms that I have described are not mutually exclusive and, in reality, even the functional and functionally neutral mechanisms will probably be found to co-operate. Further work is required to identify the actual mechanisms by which selection stabilizes the evolution of flowers. With luck, the next decade will be as fruitful for pollination biologists as the last one has been.

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APPENDIX 1

Studies that contributed coefficients of variation and identification of the plant species concerned. The kind of data contributed by each study is identified in the column headed 'Data category' as follows: 'a' indicates advertising, 'b' indicates biomass, 'g' indicates gender, 'm' indicates meristic, 'n' indicates nectar, 'p' indicates pollen grain volume, 's' indicates sexual dimensions, 't' indicates stigmatic area, 'v' indicates vector matching. For a fuller listing of the contents of these functionally-related categories, see Table 1. '*' indicates that the data was obtained from Briggs and Walters (1984).

Study	Species	Family	Data category
Ågren & Schemske, 1995	*Begonia semiovata*	Begoniaceae	a b m
Aizen & Raffaele, 1996	*Alstroemeria aurea*	Alstroemeriaceae	g n p v
Andersson, 1996	*Crepis tectorum*	Asteraceae	v
Arroyo & Dafni, 1995	*Narcissus tazetta*	Amaryllidaceae	a n v
Barrett *et al.*, 1996	*Narcissus assoanus*	Amaryllidaceae	s
	Narcissus calcicola	Amaryllidaceae	s
	Narcissus cuatrecasasii	Amaryllidaceae	s
	Narcissus gaditanus	Amaryllidaceae	s
	Narcissus papyraceous	Amaryllidaceae	s
	Narcissus rupicola	Amaryllidaceae	s
Belaoussoff & Shore, 1995	*Turnera ulmifolia*	Turneraceae	a b s
Brunet, 1996	*Aquilegia caerulea*	Ranunculaceae	g m
Campbell, 1989	*Ipomopsis aggregata*	Polemoniacea	a s v
Carr & Fenster, 1994	*Mimulus guttatus*	Scrophulariaceae	a s v
	Mimulus micranthus	Scrophulariaceae	a s v
Conner *et al.*, 1996	*Raphanus raphanistrum*	Brassicaceae	a g s
Cresswell & Robertson, 1994	*Campanula rotundifolia*	Campanulaceae	v
Cruden *et al.*, 1984	*Monarda fistulosa*	Lamiaceae	n
De Vries, 1894*	*Caltha palustris*	Ranunculaceae	m
	Potentilla anserina	Rosaceae	m
Delesalle & Mazer, 1995	*Spergularia marina*	Caryophyllaceae	a g m p
Elmqvist *et al.*, 1993	*Silene dioica*	Caryophyllaceae	a g s
Galen *et al.*, 1987	*Polemonium viscosum*	Polemoniaceae	a v
Gilbert *et al.*, 1991	*Cerinthe major*	Boraginaceae	n
Gregor, 1938*	*Plantago maritima*	Plantaginaceae	s
Harder & Cruzan, 1990	*Arctostaphylos uva-ursi*	Ericaceae	n v
	Chamaedaphne calyculata	Ericaceae	n v
	Gaylussacia baccata	Ericaceae	n v
	Gaylussacia frondosa	Ericaceae	n v
	Leucanthoe racemosa	Ericaceae	n v
	Lyonia mariana	Ericaceae	n v
	Vaccinium corymbosum	Ericaceae	n v
	Vaccinium pallidum	Ericaceae	n v
	Astragalus americanus	Fabaceae	n v
	Astragalus dasyglottis	Fabaceae	n v
	Hedysarum alpinum	Fabaceae	n v
	Lathyrus ochroleucus	Fabaceae	n v
	Oxytropis monticola	Fabaceae	n v
	Oxytropis sericea	Fabaceae	n v
	Oxytropis splendens	Fabaceae	n v
Herrera & Soriguer, 1983	*Helleborus foetidus*	Ranunculaceae	m
Herrera, 1995	*Lavendula latifolia*	Lamiaceae	a v
Herrera, 1996	*Narcissus cuatrecasasii*	Amaryllidaceae	v
	Anchusa azurea	Boraginaceae	v
	Anchusa undulata	Boraginaceae	v
	Cerinthe major	Boraginaceae	v
	Lithodora fruticosa	Boraginaceae	v
	Trachelium caeruleum	Campanulaceae	v
	Lonicera arborea	Caprifoliaceae	v
	Lonicera etrusca	Caprifoliaceae	v
	Lonicera implexa	Caprifoliaceae	v
	Lonicera splendida	Caprifoliaceae	v
	Saponaria ocymoides	Caryophyllaceae	v

APPENDIX 1 (*cont.*)

Study	Species	Family	Data category
	Silene colorata	Caryophyllaceae	v
	Silene lasiostyla	Caryophyllaceae	v
	Silene legionensis	Caryophyllaceae	v
	Silene vulgaris	Caryophyllaceae	v
	Coris monspeliensis	Coridaceae	v
	Mucizonia hispida	Crassulaceae	v
	Pistorinia hispanica	Crassulaceae	v
	Scabiosa turolensis	Dipsacaceae	v
	Acinos alpinus	Lamiaceae	v
	Ballota hirsuta	Lamiaceae	v
	Calamintha sylvatica	Lamiaceae	v
	Cleonia lusitanica	Lamiaceae	v
	Lavendula stoechas	Lamiaceae	v
	Marrubium supinum	Lamiaceae	v
	Origanum virens	Lamiaceae	v
	Phlomis lychnitis	Lamiaceae	v
	Phlomis purpurea	Lamiaceae	v
	Prunella hyssopifolia	Lamiaceae	v
	Prunella laciniata	Lamiaceae	v
	Prunella vulgaris	Lamiaceae	v
	Rosmarinus officinalis	Lamiaceae	v
	Salvia argentea	Lamiaceae	v
	Salvia blancoana	Lamiaceae	v
	Salvia verbenaca	Lamiaceae	v
	Satureja intricata	Lamiaceae	v
	Sideritis arborescens	Lamiaceae	v
	Sideritis incana	Lamiaceae	v
	Teucrium rotundifolium	Lamiaceae	v
	Teucrium webbianum	Lamiaceae	v
	Thymus orospedanus	Lamiaceae	v
	Pinguicula vallisnerifolia	Lentibulariaceae	v
	Dipcadi serotinum	Liliaceae	v
	Muscari comosum	Liliaceae	v
	Jasminum fruticans	Oleaceae	v
	Dactylorhiza elata	Orchidaceae	v
	Polygala boissieri	Polygalaceae	v
	Primula vulgaris	Primulaceae	v
	Chaenorhinum sylvaticum	Scrophulariaceae	v
	Linaria aeruginea	Scrophulariaceae	v
	Linaria anticaria	Scrophulariaceae	v
	Linaria viscosa	Scrophulariaceae	v
	Daphne gnidium	Thymelaeaceae	v
	Daphne laureola	Thymelaeaceae	v
	Fedia cornucopiae	Valerianaceae	v
	Viola cazorlensis	Violaceae	v
Inoue *et al*., 1996	*Campanula microdonta*	Campanulaceae	a g v
	Campanula panctata	Campanulaceae	a g v
Jennions, 1996	*Microloma calycinum*	Asclepiadaceae	a
	Chrysanthemoides monilifera	Asteraceae	a
	Tecomaria capensis	Bignoniaceae	a
	Heliophila africana	Brassicaceae	a
	Cyphia volubilis	Campanulaceae	a
	Wahlenbergia annularis	Campanulaceae	a
	Lebeckia sericea	Fabaceae	a
	Pelargonium fruticosum	Geraniaceae	a
	Chasmanthe floribunda	Iridaceae	a
	Lapeirousia arenicola	Iridaceae	a
	Albuca cooperi	Liliaceae	a
	Oxalis purpurea	Oxalidaceae	a
	Polygala myrtifolia	Polygalaceae	a
	Solanum burchellii	Solanaceae	a
	Strelizia reginae	Streliziaceae	a
	Cyanella orchidiformis	Tecophilaeaceae	a
Johnston, 1991	*Lobelia cardinalis*	Lobeliaceae	s
	Lobelia siphilitica	Lobeliaceae	s
Kang & Primack, 1991	*Chelidonium majus*	Papaveracea	a
Ludwig, 1901*	*Ranunculus ficaria*	Ranunculaceae	m

APPENDIX 1 (*cont.*)

Study	Species	Family	Data category
Macnair & Cumbes, 1989	*Mimulus cupriphilus*	Scrophulariaceae	a s v
	Mimulus guttatus	Scrophulariaceae	a s v
Marden, 1984	*Impatiens capensis*	Balsaminaceae	n
Marshall *et al*., 1985	*Sesbania drummondii*	Fabaceae	g
	Sesbania macrocarpa	Fabaceae	g
	Sesbania vesicaria	Fabaceae	g
Mazer & Hultgard, 1993	*Primula farinosa*	Primulaceae	a g p v
	Primula scandinavica	Primulaceae	a g p v
	Primula scotica	Primulaceae	a g p v
	Primula stricta	Primulaceae	a g p v
Mazer & Schick, 1991	*Raphanus sativus*	Brassicaceae	a g p
Mazer, 1992	*Raphanus sativus*	Brassicaceae	a g p
Mitchell, 1994	*Ipomopsis aggregata*	Polemoniaceae	a n v
Mossop *et al*., 1994	*Mimulus guttatus*	Scrophulariaceae	a b g
Murcia & Feinsinger, 1996	*Didpiptera iopus*	Acanthaceae	g s t v
	Hansteinia blepharorachis	Acanthaceae	g s t v
	Satyria warszewiczii	Ericaceae	g s t v
	Besleria triflora	Gesneriaceae	g s t v
	Cephaelis elata	Rubiaceae	g s t v
	Palicourea lasiorrachis	Rubiaceae	g s t v
Parker *et al*., 1995	*Epilobium angustifolium*	Onagraceae	b g
	Epilobium ciliatum	Onagraceae	b g
Pleasants & Chapin, 1983	*Ascelpias grandifolia*	Asclepiadaceae	g n
Pleasants, 1983	*Ipomopsis aggregata*	Polemoniaceae	n
Pledge, 1898*	*Ranunculus repens*	Ranunculaceae	m
Real & Rathcke, 1988	*Kalmia latifolia*	Ericaceae	n
Rodriguez-Robles *et al*. 1992	*Comparrettia falcata*	Orchidaceae	v
Schemske & Horvitz, 1989	*Calathea ovandensis*	Marantaceae	v
Schlichting & Levin, 1984	*Phlox cuspidata*	Polemoniaceae	a v
	Phlox drummondii	Polemoniaceae	a v
	Phlox roemeriana	Polemoniaceae	a v
Sherry & Lord, 1996	*Clarkia tembloriensis*	Onagraceae	a s
Southwick & Southwick, 1983	*Asclepias syriaca*	Asclepiadaceae	n
Stanton & Preston, 1988	*Raphanus sativus*	Brassicaceae	a b g n p s
Stöcklin & Favre, 1994	*Epilobium dodonaei*	Onagraceae	g
	Epilobium fleischeri	Onagraceae	g
Svensson & Persson, 1994	*Spergularia salina*	Caryophyllaceae	g
Svensson, 1990	*Scleranthus annuus*	Caryophyllaceae	g
Waser & Price, 1984	*Ipomopsis aggregata*	Polemoniaceae	a s v
Widen & Andersson, 1992	*Senecio integrifolius*	Compositae	a s v
Zimmerman & Pyke, 1986	*Polemonium foliosissimum*	Polemoniaceae	n

APPENDIX 2

Studies that contributed data to the literature survey.

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