

Why Do Flowers Vary?

The functional ecology of variation in flower size and form within natural plant populations

Candace Galen

The remarkable diversity of flowers has a profound impact on humankind. Flower diversity inspires masterpieces of art and literature, fuels highway beautification schemes, gives amateur gardeners moments of great joy and pride, and nurtures industries of bulb growers, seed companies, and horticultural supply houses. Botanists, for their part, have pondered the processes driving diversification in flower form for over two centuries (Sprengel [1793] 1972). Nearly all botanists give animal pollinators credit for the vast smorgasbord of flower shapes and sizes observed in nature. This conclusion is intuitively satisfying in that pollinators have the motive (energy and nutrition gain) and the means (via pollen transfer, a key step in plant sexual reproduction) to exert selection on the floral features of their host plants. Moreover, the taxonomic diversity of pollinators (insects, rodents, lizards, fish, primates, and birds) accommodates a tremendous range of morphology, sensory modality, and behavior to match the variation in flower form.

Phylogenetic studies have suggested that the acquisition of key floral characters, such as the spurs of columbine flowers, which foster interactions with novel kinds of pollinators, can launch the adaptive ra-

Flowers and the organs that compose them fulfill a number of ecological functions over their lifetimes

diation of flowering plant groups (Armbruster 1996, Hodges 1997). Ultimately, the process of diversification in flower form among species or genera of plants must be fueled by genetic variation in floral traits at the intraspecific level. Indeed, within species and even populations, individual plants vary widely in flower size and form, and much of this variation appears to have a heritable basis (Mitchell and Shaw 1992, Anderson and Widén 1993, Fenster and Ritland 1994, Young et al. 1994, Campbell 1996, Galen 1996a). Are pollinators the sole driving force behind such variation? New evidence suggests that selection on flower form and size is a more pluralistic process, involving not only pollinators but also enemies and even aspects of the plant's abiotic environment. Indeed, several recent studies have taken issue with the notion that divergence in flower form solely reflects diversifying selection by pollinators (Wilson 1995, Conner and Rush 1996, Mitchell et al. 1998).

In this article, I advocate a more holistic view of the ecology of flower size and shape based on the general premise that the morphological fea-

tures of an organism are subject to multiple and conflicting selection pressures. Specifically, I consider why pollinator-mediated selection does not fully explain variation in flower size within and among plant populations, drawing mainly from my studies of floral evolution in the alpine skipper, *Polemonium viscosum*. When possible, I also draw on findings from other species to illustrate the general conditions under which ecological forces other than pollinators may drive the evolution of flower morphology.

In particular, I emphasize two neglected aspects of the functional ecology of flowers that bear on the evolution of flower size and form: interactions of plants with flower enemies and resource costs associated with floral display. My focus is on flower size in particular, although many of the points made in this article should also apply to the evolution of flower shape. Because my intent is to bring up new perspectives on the functional ecology of flowers, topics that have historically received more attention are not reviewed here. Two such topics that deserve special mention are the role of genetic constraints in the evolution of flower form and the interplay between mating system evolution and flower morphology.

Questioning the primacy of pollinators

The process of pollinator-driven diversification in flower form is one of evolutionary specialization. Plant populations or subpopulations are thought to diverge over time in re-

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sponse to directional selection from alternative kinds of pollinators. Although many examples support the view that pollinator-mediated selection accounts for divergence in flower size or shape among geographically isolated populations (e.g., Miller 1981, Robertson and Wyatt 1990, Johnson and Steiner 1997), it is less clear that pollinators effectively promote floral divergence within populations. Individual plants that make up populations are seldom visited by a single species of pollinator. Rather, different kinds of animals with overlapping preferences but variable mechanical attributes as pollinators often service the same individuals. For example, hummingbirds and bumblebees visit and effectively pollinate individuals of the scarlet gilia, *Ipomopsis aggregata* (Waser et al. 1996).

In this ecological context, natural selection may favor generalization in floral adaptations that affect pollination efficiency, rather than specialization on alternative pollinating agents. Generalization may also be favored if relative abundances of effective pollinators vary from year to year and from patch to patch within habitat mosaics (Herrera 1996). In the face of such temporal variation in the pollinator pool, specialization becomes an evolutionarily risky strategy. It follows that pollinator-mediated selection on flower form may promote character divergence within plant populations less often than anticipated, given the centrality of pollination to the process of sexual reproduction.

When alternative kinds of flower visitors differ consistently in their contributions to plant pollination, a hierarchy of pollination effectiveness results that reflects differences in visitation frequency, mechanical fit, or behavior among visitors (Schemske and Horvitz 1984, Stanton et al. 1991, Conner et al. 1996). Under this scenario, specialization on the most effective pollinator is possible and may lead to diversification in flower traits among isolated populations. However, preferences of related or even phylogenetically distant pollinators often converge in relation to flower shape or size. For example, both small bees and syrphid flies prefer larger flowers of *Raphanus raphanistrum* (wild rad-

ish; Conner and Rush 1996). Similarly, Wilson and Thomson (1996) found no differences in selection on several aspects of flower morphology in jewelweed (*Impatiens pallida*) when pollinated by bumblebees with marked differences in tongue length and body size. Convergence in floral preference implies that similar floral traits will be favored in populations or among plants serviced by different kinds of animals.

Finally, changes in flower form may have less influence on the precision of pollen transfer than was once thought (e.g., Stebbins 1974, Nilsson 1988). For example, Wilson (1995) modified flower form in bumblebee-pollinated *Impatiens* by trimming vestibules on some flowers and gluing pleats into vestibules on others; he observed no effect on either pollen removal from anthers or pollen deposition on the stigmas. Wilson's findings imply that effective pollination may proceed despite a remarkable amount of "play" in flower architecture. Indeed, recent studies of hummingbird-pollinated *Impatiens* suggest that flower mobility—the movement of flowers in response to contact with hummingbird pollinators—may have a greater impact on pollination success than corolla dimension (Hurlbert et al. 1996). Taken together, these aspects of plant–pollinator interactions shed light on why pollinator diversity often provides an incomplete explanation for the evolutionary divergence of flower size or form within and even among nearby plant populations.

Dual roles: Conflict and the evolution of flower form

An alternative approach to understanding the ecological forces that maintain variation in flower size and form within plant populations follows from two fundamental observations on floral biology. First, flowers and the organs that compose them fulfill a number of ecological functions over their lifetimes. Whereas attracting pollinators is clearly a part of the "job description" for flowers of animal-pollinated plants, other, possibly conflicting functions are well known. For example, Grant (1950) and Stebbins (1970) both described the evolution of flower form as a

process of adaptive compromise between effective pollination and ovule protection. Historically, these conflicting functions have been assigned to different flower parts, with the calyx, or sepals, accorded a major role in protection and the corolla, or petals, the major attractive role.

It turns out, however, that plants are seldom so tidy. In paintbrushes (*Castilleja* spp.), flower bracts have the major attractive function. In the rose family, fusion of calyx, corolla, and stamen bases gives rise to the hypanthium, an organ that surrounds the ovaries and is thought to protect them from herbivory (Grant 1950, Simpson 1998). In grapes, the corolla encloses and protects the developing bud but is shed as the flower opens. In grasses, the entire perianth (i.e., petals and sepals collectively) is modified to form the lodicule, a knoblike organ that aids in flower expansion.

These examples show that characteristics of corollas as well as calyces and other flower parts may have not only attractive functions but also defensive roles. If the abundance of flower enemies varies across a plant's habitat, then conflicting selection pressures related to floral attractiveness and defense may maintain variation in the shape and size of flowers and floral organs. I call this idea the "escape hypothesis" because it postulates that natural selection for escape from enemies plays a role in floral evolution. Such enemies include disparate kinds of visitors, such as nectar or pollen robbers, flower herbivores, ovule predators, and fungal parasites.

A second aspect of floral biology is the inherent resource cost of flowers to the plant. Floral organs draw carbon, nutrients, and water from the vegetative portion of the plant, not only during their initial growth and expansion, but continuously over the flower's life span. In extremely resource limited environments, resource allocation to floral display can be costly in terms of future growth and survival. For example, in *Agave deserti*, a succulent plant of desert habitats, diversion of water from leaves to inflorescences during flowering contributes to the death of the vegetative plant after a single episode of reproduction (Nobel 1977).

Even under less extreme conditions,

flowers of different sizes or shapes vary in resource cost; such costs may affect plant reproductive success. For example, in *Sidalcea oregana*, corollas account for 40% of nitrogen budgeted to reproduction (Ashman 1994). This species exhibits gynodioecy, a sex polymorphism in which females and hermaphrodites coexist within populations. In *S. oregana*, flowers of hermaphrodites are larger than those of females. Because of their larger flowers, absolute nitrogen investment by hermaphrodites in corollas is greater than that by females, even though plants of the two morphs allocate similar proportions of nitrogen to flower production (Stanton and Galloway 1990, Ashman 1994). Moreover, the two morphs differ in the amount of nitrogen that can be recovered from senescing corollas and used for other functions after flowering. On average, more than twice as much nitrogen is recovered from the corollas of small-flowered female plants than from the corollas of larger-flowered hermaphrodites (Ashman 1994, see also Hemborg 1998). It follows that hermaphrodites experience a dual cost of corolla size compared to females, first in initial nitrogen investment and second in the amount of recoverable nitrogen.

Although in this article I focus primarily on variation in flower size within plant populations, it is possible that the shape as well as the size of flowers affects their cost in terms of limited resources. For example, tubular flowers may allow for greater light interception by subtending bracts or leaves than more rotate, or saucer-shaped, flowers. When the flower shape or size that optimizes pollinator attractiveness differs from the shape or size that optimizes resource economy, conflicting selection pressures may favor divergence in flower form within populations in relation to underlying variation in resource availability among microhabitats or across habitat gradients. I refer to this idea as the “resource-cost hypothesis.”

Floral variation in *Polemonium viscosum*

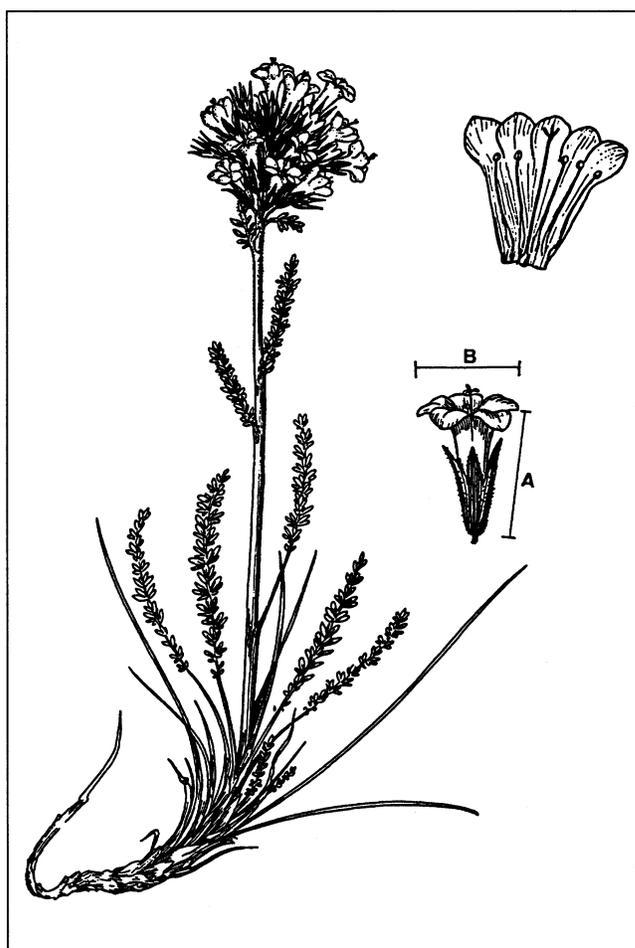
To address alternative functional explanations for the maintenance of

Figure 1. The alpine skypilot, *Polemonium viscosum*. Brackets on lower inset show (A) corolla length and (B) corolla flare. Upper inset shows arrangement of stamens and style within the corolla tube. Drawings reprinted from Davidson (1950) and used with permission.

variation in flower size within populations, I have conducted long-term studies of floral variation in an alpine wildflower species, *P. viscosum* (Figure 1). Plants of *P. viscosum* occur from timberline (approximately 3000–3500 m) to the high summits (approximately 4000 m) of the Rocky Mountains. Differentiation in flower size is evident across this elevational range, with corollas of plants near timberline (krummholz habitat) approximately 10% smaller than corollas of plants on the higher tundra slopes (Galen et al. 1987).

Genetic studies have shown that variation in corolla flare and corolla length (the distance separating the tips of opposite petal lobes and the distance from the base of the corolla to the petal lobes, respectively; Figure 1) within populations of the alpine skypilot has a heritable basis. In one krummholz location, for example, genetic differences among individuals accounted for an estimated 20–100% of variation in corolla length and 36–100% of variation in corolla length (Galen 1996b). The two traits also show a strong positive genetically based correlation, such that a given increase in corolla length is accompanied by a more modest increase in corolla flare (Candace Galen, unpublished data). This allometric relationship is manifest in the funnel-form shape of the corolla.

Plants of the alpine skypilot are self-incompatible and depend completely on insect visitors for effective



pollination and outcrossing (Galen and Kevan 1980). Although the insect visitors of skypilot flowers include bumblebees, solitary bees, flies, and, occasionally, hawkmoths, most pollination is accomplished by bumblebees. For example, on Pennsylvania Mountain, Colorado, a location that is near the geographic center of the species' range, pollination by bumblebees (mainly queens of *Bombus kirbyellus*) accounts for approximately 50% of seed set by plants in the krummholz and 95% of seed set by plants at higher elevations on the tundra slopes (Galen 1996b).

Bumblebees preferentially visit plants with large, long-tubed, broadly flared corollas, bypassing neighboring individuals with smaller corollas (Galen and Newport 1987). Indeed, selection exerted on flower size by bumblebees is sufficient to explain the evolution of large, broadly flared flowers in high-tundra skypilots (Galen 1996a). But why, in the same population, do plants with smaller flowers predominate near timberline, where bumble-

bee pollination still accounts for more than half of the seed set by individuals? Although the decrease in flower size at lower elevations could simply reflect the reduced importance of bumblebees as pollinators, other explanations must also be considered. Perhaps, for example, plants with less conspicuous flowers have functional advantages near timberline that compensate for their reduced attractiveness to pollinators. Both the escape hypothesis and the resource-cost hypothesis could potentially provide insights into the nature of these advantages.

The escape hypothesis: skypilot flowers and ants. The escape hypothesis predicts that “less attractive” floral morphologies will be maintained within plant populations if they allow plants to remain hidden or protected from flower enemies. Such enemies could include pre-dispersal seed or ovule predators (Hainsworth et al. 1984, Campbell 1991, Brody 1992, Kudoh and Whigham 1998), nectar robbers and nectar thieves (Roubik 1982, Norment 1988, Prys-Jones and Willmer 1992, Irwin and Brody 1998), fungal parasites (Elmqvist et al. 1993, Shykoff and Bucheli 1995), and flower herbivores (Spira and Pollak 1986, Lohman et al. 1996). The main villain for flowers of *P. viscosum* is *Formica neorufibarbus gelida* (Hymenoptera: Formicidae), a common ant of alpine habitats in the southwestern United States (Gregg 1963). Ants enter skypilot flowers through the corolla mouth, crawl to the base of the corolla tube, and sever the style when foraging at the glandular nectar disk surrounding the base of the ovary. Flowers in which the style has been severed by ants rarely set seed (Galen 1983). When ants are abundant, excluding them from a plant’s flowers can enhance average seed production by as much as 45% (Galen 1999). For skypilot plants, the threat of ant damage is greatest in the krummholz; at very high elevations, ant abundance

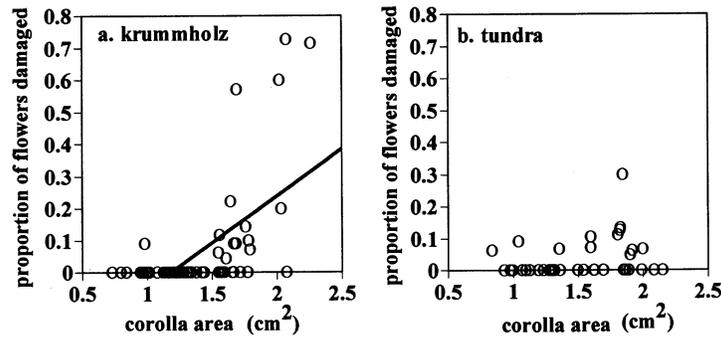


Figure 2. Relationship between the proportion of flowers per plant of alpine skypilot damaged by nectar-thieving ants and corolla area in two habitats on Pennsylvania Mountain, Colorado. Flowering plants in krummholz (a) and tundra (b) habitats were surveyed for ant damage in 1997. The slope of the best-fit line is significantly different from zero for krummholz plants ($P < 0.0001$, $n = 54$) but not for tundra plants ($P = 0.16$, $n = 35$).

drops markedly due to nest-site limitation (Gregg 1963, Puterbaugh 1998).

To determine whether skypilot plants with smaller flowers might be less susceptible to ant damage than nearby individuals with large flowers, I measured corolla surface area of flowers on 54 randomly chosen plants at approximately 3500 m in the krummholz and 35 randomly chosen plants at approximately 3700 m on the tundra slopes of Pennsylvania Mountain in 1997. I surveyed the same plants at 2-day intervals throughout flowering to determine the proportion of flowers that were damaged by ants (i.e., with styles severed) on each individual.

In the krummholz habitat, the proportion of flowers damaged by ants increased significantly with corolla size, in agreement with predictions of the escape hypothesis. At this low-elevation site, plants with small corollas showed negligible rates of damage, but on neighboring individuals with the largest corollas, nearly 75% of flowers were damaged (Figure 2a). Corolla size explained 40% of the variation in ant damage rate among krummholz plants ($F_{1,52} = 34.65$, $P \leq 0.0001$). However, on the tundra slopes, where ants are less common, the escape hypothesis was not supported. Corolla size of tundra skypilots explained only 6% of the variation among plants in flower damage ($F_{1,33} = 2.01$, $P = 0.16$; Figure 2b). In this higher-elevation habitat, levels of ant damage were relatively low, regard-

less of corolla size. For *P. viscosum*, therefore, it appears that the risks associated with the presentation of large, showy flowers vary within populations in relation to enemy abundance. This kind of fine-grained spatial variation in risks and benefits could contribute to the maintenance of variation in corolla size within natural plant populations.

The escape hypothesis assumes that flower choices of pollinators and enemies converge.

Under what conditions might this assumption hold? In the case of skypilot flowers, bumblebees and ants both forage for a similar reward—nectar—and share sensory modalities inherited from a common Hymenopteran ancestor. A plausible assumption, then, is that ant enemies have the energetic incentive and sensory capability to track reward availability using floral advertisements adapted for attraction of bumblebee pollinators. Because corolla size is positively correlated with nectar production rate in *P. viscosum*, it provides a visible cue to hidden nectar stocks for both kinds of visitors (Cresswell and Galen 1991). Indeed, correlations between flower size and nectar quantity characterize plants of many animal-pollinated species (reviewed by Delph 1996), providing cues that can be used by nectar thieves or robbers as well as legitimate pollinators.

When enemies are not mobile over plant-to-plant distances, pollinators may provide a convenient vector, intimately linking the processes of pollination and parasitism (e.g., Shykoff and Bucheli 1995). For example, the incidence of fungal infection correlates with bumblebee pollinator preference in populations of *Dianthus silvester* (Shykoff et al. 1997). Conversely, in interactions involving pre-dispersal seed predators, pollination directly affects host-plant quality for enemies. In such cases, selection may favor enemies whose host preference converges on the floral preference of pollinators,

because well-pollinated flowers provide greater food reserves than poorly pollinated ones. One of the best-studied interactions of this kind concerns hummingbird pollinators and Dipteran seed predators of *I. aggregata*. Both hummingbirds and flies discriminate among plants of *I. aggregata* on the basis of flower size (Brody 1992). Large flowers may have more ovules than small ones, and hummingbird preference ensures that a greater proportion of these ovules will develop into seed provisions for fly larvae.

The diverse behavioral mechanisms unifying the flower choice of pollinators and enemies suggest that the conflicting selection pressures of pollinator attraction and enemy avoidance, which are central to the escape hypothesis, may be widespread in animal-pollinated plant populations. Spatial models that explicitly incorporate enemy and mutualist abundances to predict variable selection on flower size would be valuable in exploring the generality of this idea. Another promising approach is illustrated by recent studies that contrast flower predator-mediated selection on sex morphs of dioecious or gynodioecious plant species (Puterbaugh 1998). For example, the escape hypothesis predicts that males, freed from selection for ovule protection, should show more exaggerated responses to pollinator-mediated selection on flower size than females of the same species. This idea offers an attractive hypothesis for the trend of greater allocation to corolla size in male flowers than female flowers of unisexual animal-pollinated plants, although alternative explanations for this trend are in no short supply (Delph 1996).

The resource-cost hypothesis: sky-pilot flowers and water use. The resource-cost hypothesis predicts that insofar as less conspicuous, smaller flowers require a lesser investment of essential resources from the plant than large, showy flowers, reduced flower size will be advantageous

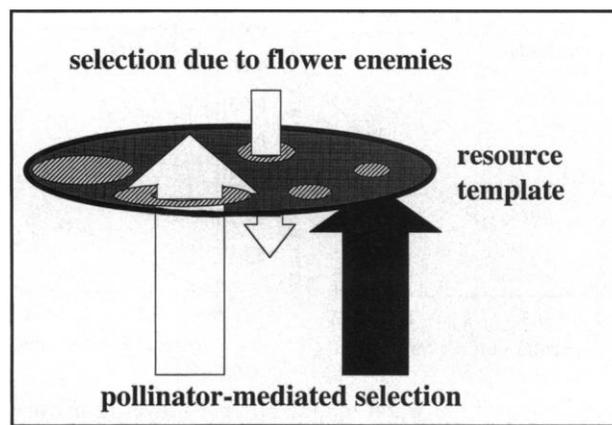


Figure 3. Model showing how environmental forces may interact to influence the adaptive evolution of flower size. Possible (open arrows) and impossible (solid arrows) modes of flower evolution based on resource availability are indicated. Directions of arrows indicate increases (upward) or decreases (downward) in flower size. Evolution of small flowers may occur in patches of low (small ovals) or high (large ovals) resource availability. Pollinators exert selection for increased flower size in all patches, but such selection is constrained under low-resource conditions. Where high-resource conditions prevail during flowering, flower size may increase evolutionarily in response to pollinator-mediated selection.

under resource-poor conditions. For example, for plants that, like *P. viscosum*, flower repeatedly over their lifetimes, pollinator-mediated selection should drive the evolution of large flower size if individuals have the resources to produce and maintain such flowers without compromising future survival and reproduction. Because resource heterogeneity within plant populations is a ubiquitous phenomenon (e.g., Bell and Lechowicz 1991, Reader and Bonser 1993, Stanton et al. 1994), the resource-cost hypothesis may have general applicability to the maintenance of genetic variation in flower size at the population scale. According to this hypothesis, resource heterogeneity acts as a selective template, allowing plants to respond evolutionarily to pollinator-mediated selection for large, showy flowers in areas of resource abundance but selecting against such responses in areas where resources are scarce (Figure 3).

Individuals may also adjust to differences in resource status through plastic changes in allocation to flowering. For example, flower size in alpine sky-pilot increases over the first several years of an individual's

lifetime, as the plant grows in vegetative size (Galen 1996b). In other species, plants show reductions in corolla size after foliage is removed by herbivores (e.g., wild radish; Strauss et al. 1996). Such plastic adjustment of floral traits represents an alternative strategy for coping with resource heterogeneity that is distinct from the adaptive genetic response predicted by the resource-cost hypothesis.

A test of the resource-cost hypothesis must first elucidate whether the production or maintenance of large, showy flowers requires an increased investment of resources compared to investment in smaller, less conspicuous flowers. Although this assumption is intuitively appealing, evidence for it is often equivocal. For example, photosynthetic flower organs, including sepals, petals, and even pistils,

contribute directly to energy for reproduction in several species (e.g., strawberry [*Fragaria virginiana*], Jurik 1985; orange [*Citrus sinensis*], Vu et al. 1985; petunia [*Petunia hybrida*], Weiss et al. 1990; buttercup [*Ranunculus adoneus*], Galen et al. 1993; white campion [*Silene latifolia*], Laporte and Delph 1996; and orchids [*Spiranthes cernua*], Antlfinger and Wendel 1997), reducing the demand for photosynthate from vegetative organs. In such species, increases in the photosynthetic capacity of flower parts could compensate for respiration by the larger attractive organs, if organ sizes scale allometrically (Galen et al. 1993). Nutrients allocated to flower tissues may be resorbed when organs senesce, again reducing the cost of floral structures on a whole-plant basis (Ashman 1994). The cost of investment in floral attractiveness is clearly "currency," or resource, dependent and should be greatest for resources that can be neither manufactured in nor resorbed from flower parts. Water represents the quintessential resource of this kind. Not surprisingly, water loss through flower transpiration has been implicated as a major cost of reproduction in arid

habitats (Nobel 1977).

In the alpine habitat of *P. viscosum*, water availability serves as a potent limiting factor for plant growth (Peterson and Billings 1982, Enquist and Ebersole 1994). To address whether large, showy flowers require more water over their lifetimes than smaller ones, I performed a simple potometer experiment (Galen et al. 1999). Immature flowering stems were excised from plants in the field and placed into test tubes filled with water to a constant volume. A stopper tightly fitted around each flowering stem minimized water

loss aside from that drawn into the inflorescence. Subtending leaves were trimmed, as were the buds, to provide a constant number of five flowers on each stem. Cut pedicel surfaces were coated with petroleum jelly to minimize the effects of trimming on water loss.

Depletion of water in the tubes was then monitored under laboratory conditions for inflorescences during bud expansion and again at female receptivity, when most of flower growth has been completed. Linear regression was used to test whether the amount of water taken up by developing buds was related to the volume of the fully expanded corollas. Here, volume was used as a proxy for corolla size because organs grow in three dimensions. Corolla surface area was used in a similar regression analysis of water uptake by receptive flowers. (Corolla dimensions were analyzed because the corolla represents the attractive portion of the flower.) Corolla size was found to strongly influence water uptake by inflorescences, explaining approximately 60% of the variation in rates of water removal from tubes during each phase of flower development (Figure 4; Galen et al. 1999). These laboratory results suggest that increases in corolla size may incur physiological costs for skypilot plants flowering under dry conditions. However, for

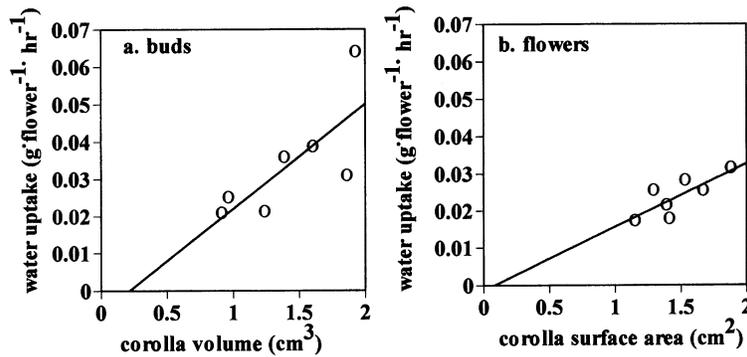


Figure 4. Relationship of water uptake rate per flower to mature corolla size of *Polemonium viscosum* as measured for inflorescence stems inserted into sealed tubes of water under laboratory conditions in 1997. Water uptake rates at the time of bud expansion are plotted as a function of corolla volume (a), and water uptake rates for inflorescences composed of fully expanded flowers are plotted as a function of corolla surface area (b). Best-fit regression lines are shown ($n = 7$ plants, $P < 0.05$ for both stages of flower development). From Galen et al. (1999). These results suggest that plants with large flowers use more water during bud expansion and flower maintenance than plants with smaller flowers.

more meaningful comparisons of the cost of large versus small flowers, the water relations of intact plants should be studied in their natural environments.

In the Rocky Mountains, precipitation over the course of the growing season follows a strong seasonal rhythm, with drought conditions prevailing during June and monsoon rains bringing extensive moisture in July and early August (Oberbauer and Billings 1981, Enquist and Ebersole 1994). Afternoon showers during the monsoon season reduce evapotranspiration and insolation, ameliorating water stress for alpine plants (Peterson and Billings 1982). At the field site on Pennsylvania Mountain, average precipitation during July is more than twice that in June (Western Regional Climate Center data from Leadville, Colorado, 1948–1997; National Climatic Data Center 1998). Flowering of skypilot plants on Pennsylvania Mountain takes place in early to mid-June in the krummholz (approximately 3500 m), whereas higher on the tundra slopes (approximately 3700–4000 m) flowering begins in July, concomitantly with seasonal monsoon rains.

Because plants in krummholz and tundra habitats differ in the synchrony of flower presentation with resource (water) availability, it is possible to test whether, as the resource-cost hypothesis predicts, the physiological cost

leaf cells enhance the tendency of water to remain within the leaf rather than diffusing to the atmosphere. If reproduction places a demand on the water balance of the plant, then leaf water potentials should drop (i.e., become more negative) during flowering or fruit set as water is diverted from vegetative to reproductive structures. As leaf water potential drops, stomatal closure occurs to maintain leaf turgor, and carbon assimilation ceases. For example, in the common alpine plant, *Acomastylis rossii*, rates of photosynthesis drop by 40% as leaf water potential declines from -0.8 MPa to -2.1 MPa (Bliss 1985).

By measuring leaf water potentials for krummholz *P. viscosum* flowering during the dry early portion of the summer and for tundra plants flowering during wetter mid-summer conditions, it was possible to ascertain the extent to which water stress incurred by vegetative organs during flowering differs between the two habitats. As expected from seasonal precipitation patterns, results for 1997 and 1998 showed that, on average, leaf water potentials tended to be more negative for krummholz plants, which flowered in June, than tundra plants, which flowered in July (Figure 5; $P < 0.08$). However, the degree to which water stress differed between habitats depended strongly on the time of day ($P \leq 0.01$).

Before dawn, when leaf water potentials are at equilibrium with soil water potentials, little water stress was evident for krummholz or tundra plants over the 2-year study. In both years, mean pre-dawn water potentials were above -0.55 and did not differ significantly between sites (Figure 5). This result suggests that, despite seasonal rainfall differences, soils in both habitats supply water at similar rates to flowering skylpilots.

However, over the course of the morning, as leaf stomata opened to support photosynthesis, water potentials dropped to more negative values for plants flowering in the krummholz than those flowering on the tundra (Figure 5; $P \leq 0.0001$). For example, in 1998, midday leaf water potentials averaged -0.86 ± 0.33 MPa (SD; $n = 10$) for krummholz plants in June and -0.61 ± 0.22 (SD; $n = 10$) for tundra plants in July.

This result is consistent with the idea that the monsoon precipitation pattern ameliorates water stress in skylpilots mainly by increasing atmospheric humidity and reducing midday evaporative demand on vegetative tissues. Similar findings have been reported for a number of other Rocky Mountain plant species that co-occur with skylpilots (Ehleringer and Miller 1975, Peterson and Billings 1982).

According to the resource-cost hypothesis, the same increase in corolla size should incur a greater physiological cost in the krummholz, where flowering plants are more water stressed, than on the higher tundra slopes. In 1998, I collected additional information to determine how flower size variation in each population affected the level of water stress experienced by vegetative organs. In the krummholz, midday leaf water potentials depended strongly on corolla surface area (Pearson's correlation coefficient, $r = -0.85$, $n = 10$, $P < 0.002$). The negative slope of this relationship (Figure 6) suggests that under dry conditions, the vegetative organs of plants diverting water to

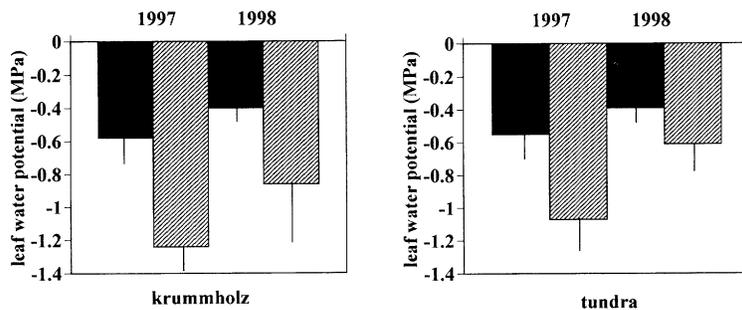


Figure 5. Average leaf water potentials (ψ_l) for flowering *Polemonium viscosum* in June (krummholz) and July (tundra). Brackets show one standard deviation. In 1997 and 1998, 15 and 10 plants, respectively, were measured in each site both before dawn (solid bars) and at midday (hatched bars). In both years, differences in average leaf water potentials between sites were significant at midday ($P < 0.0001$; planned contrasts following analysis of variance) but not before dawn.

maintain large, showy flowers experience greater water stress than the vegetative organs of neighboring plants with smaller flowers. For tundra plants flowering after the onset of the monsoon rains, no such cost was revealed (Figure 6; $r = 0.08$, $n = 10$, ns). Other factors undoubtedly differ between the two habitats that could influence the relationship between flower size and water stress, including plant community composition and vegetation cover. However, seasonal drought provides the most parsimonious explanation for the negative relationship between flower size and plant water status in the krummholz.

These findings support one aspect of the resource-cost hypothesis: small, less conspicuous flowers indeed reduce the physiological stress associated with reproduction in times of resource shortage. The findings also shed new light on the smaller corolla size of *P. viscosum* near timberline: Under the dry conditions associated with the earlier flowering schedule of krummholz plants, smaller corollas may render plants less vulnerable, not only to flower enemies, but also to water stress during flowering (Figure 3). These advantages of reduced corolla size, coupled with the availability of alternative insect pollinators at low elevations, may help to offset the disadvantage that small-flowered skylpilots incur in attracting pollinating bumblebees.

A definitive test of the resource-cost hypothesis must also assess the demographic consequences of produc-

ing large, showy flowers under resource-poor conditions. The hypothesis predicts that when resources are in low supply, stress associated with the production and maintenance of attractive flowers will bring about reductions in survival or reproduction. For example, Campbell (1997) found a negative genetic correlation between corolla width and survival rate in *I. aggregata*. This result suggests that a resource-based tradeoff between

allocation to pollinator attraction and survival plays a role in the evolution of corolla size in this species.

In skylpilots, the demographic consequences predicted by the resource-cost model could be studied by subjecting randomly chosen plants to either low or high resource availability during flowering and monitoring their future survival and reproduction. We are conducting a field experiment of this kind with skylpilot plants, watering individuals differentially to approximate average rainfall schedules during either June (dry) or July (wet) on Pennsylvania Mountain. If the resource-cost hypothesis is correct, then the relationship between flower size and future fitness components should depend strongly on water availability, with a negative relationship manifest under the drought treatment. This prediction assumes that plants in low and high watering treatments are of a similar initial stage in terms of vegetative size and age. Otherwise, variation in flower size with stage could mask genetically based differences in flower size among individuals and limit the ability to detect a demographic cost of floral allocation.

Above the population scale, the resource-cost hypothesis for the maintenance of genetic variation in flower size is amenable to comparative approaches that contrast the floral traits of sister species or subspecies that occupy xeric and mesic habitats (i.e., eastern and western slopes of the Continental Divide). The hypothesis that resource heterogeneity provides a template mediating the effi-

cacy of pollinator-mediated selection on flower size would be supported if lineages characterized by small, inconspicuous flowers were found to occupy habitats in which plants typically experience resource stress during flowering. In skip pilot populations distributed longitudinally along the Rocky Mountains, flower size decreases from north to south along a gradient of increasing aridity from northern Colorado to Arizona (Galen et al. 1987). Similarly, populations of *Clarkia xantiana* (a wildflower of the southern Sierra Nevada)

in hotter, more arid habitats have smaller flowers that are more likely to self-pollinate than those of populations in more mesic habitats (Eckhart et al. 1998, Runions and Geber 1998). Such an association of small flower size and drought is also found in a number of other annual plant species, in which it correlates with differences in mating system between populations of arid and mesic habitats (Guerrant 1989). Although other hypotheses cannot be ruled out, these geographic patterns suggest that among geographically isolated populations, the maintenance of variation in flower form and size is tied to resource heterogeneity.

A new holistic framework for the evolution of flower form

It is not surprising that plant reproductive ecologists have, until recently, had a narrow view of floral evolution, focusing almost exclusively on the process of pollination. Pollination is, after all, an event unique to flowers and one that defines the flowering plants or angiosperms as a group. But focusing narrowly on sexual functions of flowers and on the role of pollinators in mediating sexual reproduction has two shortcomings. This focus overlooks both other important functions of floral organs and the physiological integration of flowers with the vegetative body of the plant.

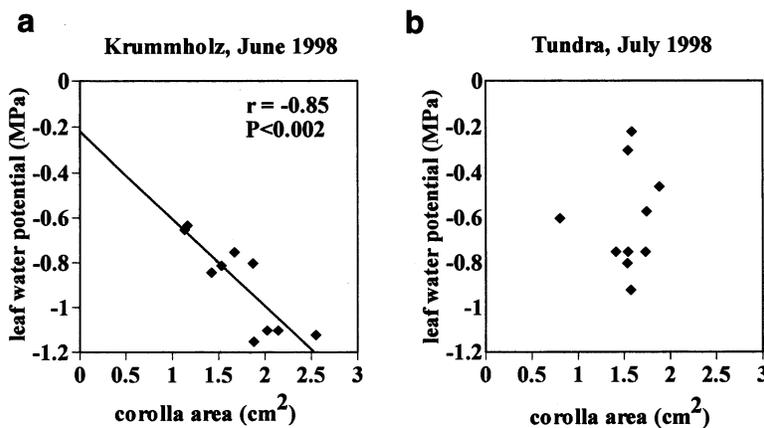


Figure 6. Relationship of midday leaf water potential to corolla surface area for plants of *Polemonium viscosum*. Plants flowering in krummholz (a) and tundra (b) habitats were measured during the summer of 1998. Leaf water potential showed a significant relationship to corolla surface area in the krummholz habitat (regression line shown; $P < 0.002$, $n = 10$) but not in the tundra habitat (ns, $n = 10$).

Scientists studying the functional ecology of plant secondary chemistry came to a similar juncture 20 years ago, when the diversity of secondary chemicals was viewed only in relation to herbivore pressure (apparency theory; Feeny 1976, Rhoades and Cates 1976). Plant secondary chemistry was thought to reflect the ease with which plants could be found by herbivorous insects. Variation among habitats in the availability of resources such as carbon or nitrogen, which are the building blocks of secondary defenses, was ignored. Apparency theory nicely predicts interspecific variation in secondary chemistry in some plant communities but falls short of explaining patterns in others (Howe and Westley 1988). A sea change in that discipline occurred when Coley (1983) and Coley et al. (1985) published papers that emphasized theoretical and empirical connections between plant secondary chemistry and resource availability. In showing how plant defenses might evolve in relation to underlying resources as well as herbivore pressure, Coley's work provided a powerful springboard for understanding plant chemical diversification. Similarly, our understanding of floral evolution can benefit from a more holistic approach to flower function that incorporates not only plant-pollinator relationships but also resource requirements for flower development and maintenance.

Clearly, hypotheses about the functional significance of floral variation are not mutually exclusive; as illuminated by studies of *P. viscosum*, multiple ecological forces may act on flowers simultaneously. Pollinators, enemies, and resource heterogeneity appear to operate simultaneously in exerting selection on flower size and shape in this system and in at least one other system that has received comparable long-term study (*I. aggregata*; Brody 1992, Campbell 1997). Recently, O'Connell and Johnston (1998) also

reported that the magnitude of selection on flower size from insect pollinators varies markedly among microhabitats in a population of the pink lady's slipper orchid, *Cypripedium acaule*. Although still few in number, these examples point to the need for a more pluralistic view of natural selection on floral traits.

There are promising signs that plant reproductive ecologists are embracing broader new perspectives: Recently, an issue of *Ecology* spotlighted connections between pollination and herbivory (Strauss and Armbruster 1997). Such studies may provide an ideal arena for addressing the resource-cost hypothesis because herbivores, by selectively reducing leaf area, essentially create resource (photosynthate) heterogeneity within plant populations. The abiotic environment is also gaining recognition as a source of selection on reproductive traits. For example, studies on the correlated evolution of physiological and reproductive characters are bringing new light to bear on the evolution of gender differences, no small part of which involves changes in flower morphology (Laporte and Delph 1996, Dawson et al. 1998, Dawson and Geber 1999).

In this article, I have suggested that resource availability may influence the efficacy of pollinator-mediated selection in bringing about increases in flower size. An alternative

and little-explored way in which the abiotic environment may affect the evolution of flower size or shape is as a force of natural selection on the developmental processes that underlie the growth and differentiation of flowers. For example, small flowers may reflect a history of selection for abbreviated development time under growing seasons characterized by rapidly deteriorating environmental conditions (Geurrant 1989, Eckhart et al. 1998, Runions and Geber 1998). By resolving how abiotic stress, as a source of selection on developmental processes, affects the evolution of flower shape and size, such new research may illuminate not only why, but how, flowers come to vary.

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