HETEROSTYLY, HOMOSTYLY, AND FECUNDITY IN AMSINCKIA SPECTABILIS (BORAGINACEAE)

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Amsinckia is a small genus of Boraginaceae consisting of 10–15 species found primarily in California but occurring naturally north to British Columbia, south to Baja California, east to Utah, and disjunctly in southern South America. Weedy members of the genus have been introduced to Europe, South Africa, central and eastern North America, Alaska and the Yukon, and Australia. Five of the species in the genus are, at least in part, heterostylous, with populations that consist of plants with "pin" flowers, with long styles and short stamens, and "thrum" flowers, with short styles and long stamens. Heterostylous taxa of *Amsinckia* are all endemic to California. They appear to be edaphic endemics, restricted to slopes of loose shaly fragments in the South Coast Ranges, except *A. spectabilis* F. & M., which is restricted to stabilized sand dunes and coastal bluffs. Three of the heterostylous taxa, *A. vernicosa* H. & A. var. *furcata* (Suksd.) Hoov. in Jeps., *A. grandiflora* Kleeb. ex Gray, and *A. douglasiana* A. DC., exhibit a pronounced pollen dimorphism, with thrum pollen larger than pin pollen, and also possess thrum flowers that are larger than pin flowers. *Amsinckia lunaris* Macbr. exhibits a peculiar type of heterostyly with a variety of stamen and style length combinations and anthers inserted at two levels in the corolla (Ray and Chisaki, 1957a). All heterostylous taxa in this genus are self-compatible (Ray and Chisaki, 1957a; Ganders, unpublished).

The remaining species of *Amsinckia,* including all the widespread, weedy taxa, are homostylous, with anthers and stigma positioned at the same level in the corolla. Morphological, ecogeographical, and cytogenetic evidence indicates the homostylous taxa have been derived from heterostylous taxa, which are primitive in this genus. Conspecific homostylous and heterostylous populations occur in *A. spectabilis* and have also been reported in *A. vernicosa* var. *furcata* and *A. lunaris* (Ray and Chisaki, 1957a, 1957b).

Homostyly in Amsinckia spectabilis

The distribution of distylous and homostylous plants in *A. spectabilis* populations is unusual. Populations may be exclusively distylous, exclusively homostylous or contain pins, thrums, and homostyles. Furthermore, in mixed populations of distylous and homostylous plants, there is considerable variation in the degree of heterostyly among different plants, that is, the distance separating anthers and stigmas in flowers may vary. There is virtually a complete gradient from pins to homostyles to thrums (fig. 1).

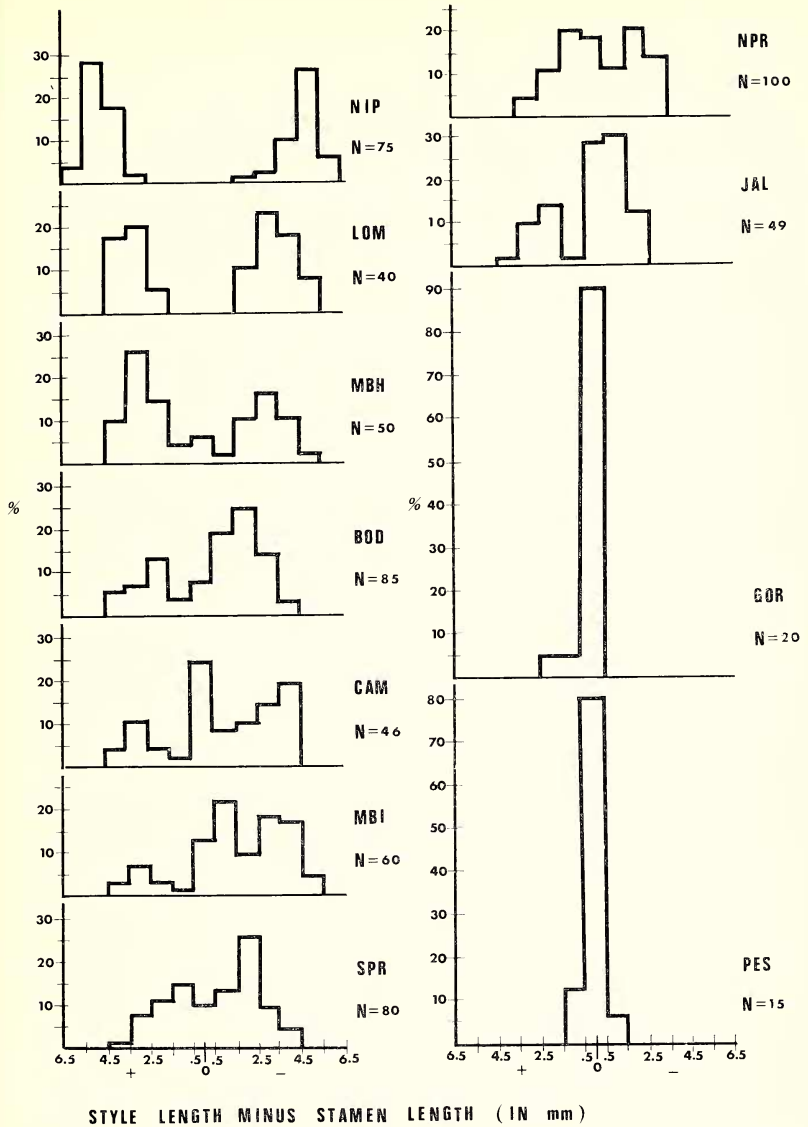

FIG. 1. Percentage frequency of stigma-anther separation classes in populations of *Amsinckia spectabilis* in California. Long styled flowers (pins) are to the left of 0 and short styled flowers (thrums) are to the right of 0. Locations of populations: (distylous populations) NIP—Nipomo, San Luis Obispo Co.; LOM—Lompoc, Santa Barbara Co.; (mixed populations) MBH—Henrietta Street, south side of Morro Bay, San Luis Obispo Co.; BOD—Bodega Bay, Sonoma Co.; CAM—Cambria, San Luis Obispo Co.; MBI—Inyo Street, south side of Morro Bay, San Luis Obispo Co.; SPR—South Point Reyes Beach, Marin Co.; NPR—North Point Reyes Beach, Marin Co.; JAL—Jalama Beach, Santa Barbara Co.; (homostylous populations) GOR—Goat Rock State Beach, Sonoma Co.; PES—Pescadero State Beach, San Mateo Co. N = sample size; one flower per plant was measured.

Unfortunately the genetics of this situation is not yet known. Ray and Chisaki (1957a) reported that a thrum × homostyle cross gave approximately a 1:1 ratio of thrums and homostyles in the progeny. Such a result is compatible with the interpretation that the homostyle allele represents a crossover of the *Primula* type, where thrum is dominant to pin. If this is so, it seems likely that other genes and possibly environmental factors are modifying the expression of the heterostyly alleles to produce the variation in degree of heterostyly found in these populations.

In mixed populations interbreeding between distylous and homostylous plants undoubtedly occurs; progeny from naturally pollinated homostyles contains pins and thrums. It is possible that these populations are evolving toward homostyly, but it is also possible that mixed populations have reached an equilibrium among the forms. Darwin (1877) grew seeds of *A. spectabilis* after Asa Gray suggested that several species in the genus were heterostylous, but because he found such a range of stamen and style lengths Darwin concluded that *A. spectabilis* was merely variable. Although prior to the work of Hoover (in Jepson, 1943) and Ray and Chisaki (1957a) the taxonomy of *Amsinckia* was hopelessly confused, there is no doubt that Darwin's plants were actually *A. spectabilis* var. *spectabilis,* since it is the only taxon in the genus that exhibits this type of variation. Darwin's record proves that such mixed populations have persisted for at least a century.

Homostylous and mixed populations and strictly distylous populations of *A. spectabilis* differ in several other morphological features and also in geographical range and are best considered infraspecifically distinct. Plants from the distylous populations [*A. spectabilis* var. *microcarpa* (Greene) Jeps. & Hoov.] have all five calyx lobes free to the base, have small mericarps (nutlets) 1.25–1.75 mm long, and the bifurcations of the cotyledons are flat and spreading. Distylous populations are restricted to Late Pleistocene sand dunes (the Orcutt Sand) in southern San Luis Obispo County and northern Santa Barbara County, California. *Amsinckia spectabilis* var. *spectabilis* consists of homostylous and mixed populations, two or three of the adaxial calyx lobes are fused one-half or more of their length, the nutlets are larger (1.75–2.33 mm long), and the bifurcations of the cotyledons are clavate and recurved. Flowers in this variety tend to be smaller and the plants tend to be more spreading in habit, branching from the base. *Amsinckia spectabilis* var. *spectabilis* is strictly coastal in distribution and ranges interruptedly from Guadalupe Island off Baja California to the Queen Charlotte Islands in British Columbia. The two varieties are interfertile and intergrade on the south side of Morro Bay, San Luis Obispo County, California. These populations, arbitrarily referred to var. *microcarpa,* may contain homostyles (fig. 1) and some plants with fused calyx lobes or a spreading habit. They retain the nutlet and cotyledon characteristics of var. *microcarpa.*

Mixed populations of *A. spectabilis* var. *spectabilis* occur only in Marin, Sonoma, San Luis Obispo, and Santa Barbara Counties. Strictly homostylous populations range north and south of the mixed populations

in Marin and Sonoma Counties, California (see fig. 1), and at least formerly they ranged south of the mixed populations in Santa Barbara County. Only homostyles occur outside of California. The homostylous populations in central California are small and the beaches where they occur have only small areas of suitable sandy habitats. On the other hand, the mixed populations are large and occur at Point Reyes and Bodega Bay where there are large areas of stabilized sand dunes. It might be noted that there are areas of apparently suitable sand dunes, such as at the mouth of Salmon Creek, Sonoma County, where the species has not been found.

Geographic distribution of mixed and homostylous populations strongly suggests that (1) homostylous populations were derived by colonization from mixed populations and (2) pins and thrums were selectively eliminated from the small founder populations. If monomorphic populations were derived solely by genetic drift in founder populations, monomorphic pin or thrum populations would also be expected, but they do not occur.

It seems reasonable to hypothesize that large mixed populations are sufficiently conspicuous to attract large numbers of pollinators, so that pins, thrums, and homostyles will all exhibit a high rate of seed set. In very small founding populations pollinator visits to flowers will be erratic and suboptimal for full seed set. If homostyles, because their anthers and stigmas are in close proximity, are capable of significantly higher rates of autogamous seed set than are pins and thrums, they will be at a great selective advantage. In small founding populations, homostyles will replace pins and thrums.

Materials and Methods

To test the validity of this hypothesis, autogamous seed set by the three forms was measured on plants grown in growth chambers. Pollinators were excluded, but the ventilation system of the growth chambers provided considerable air circulation, simulating the effect wind might have in nature in shaking pollen from anthers within flowers.

Seed set was measured on inflorescences collected from several large and medium sized natural populations where pollinators were presumably abundant. Inflorescences were collected from 13 pin and 21 thrum plants at Lompoc; 3 pins, 4 thrums, and 1 homostyle at Morro Bay; 13 pins, 5 thrums, and 28 homostyles at Jalama Beach; 3 pins, 8 thrums, and 7 homostyles at Cambria; 4 pins, 2 thrums, and 9 homostyles at North Point Reyes Beach; and 15 homostyles at Pescadero State Beach. For seed set measurements, homostyles were defined as plants with flowers in which the distance from the center of the anthers to the stigma was 1.5 mm or less. Only one very small mixed population was found during this study, at Atascadero State Beach on Morro Bay in San Luis Obispo County. The population consisted of nine plants in 1971, but seed set data were not obtained that year. In 1972, when seed set was measured, the population consisted of only two plants, one pin and one homostyle.

Results

In growth chambers, thrums set 196 out of 1680 possible seeds autogamously (11.7 %). Pin flowers set 458 out of 4524 possible seeds (10.1 %). The difference between autogamous seed set in pins and thrums is not significant ($\chi^2 = 3.09$, $P > .05$). Homostylous flowers set 293 out of 352 possible seeds autogamously (83.2 %). Thus, without pollinator visits, homostylous plants set eight times as many seeds as pins or thrums.

Natural seed set was high (80 % or higher) in all forms in large populations (Table 1). In the distylous population at Lompoc and the mixed populations at Jalama Beach and Morro Bay there was a significant difference in seed set among the forms. Only at Morro Bay, how-

Table 1. Seed Set by Different Flower Forms in Natural Populations of Amsinckia spectabilis.

	Pin	Thrum	Homostyle
Lompoc, Santa Barbara Co. (var. *microcarpa*)			
seed set	1430	2092	
seed failed	78	248	
total	1508	2340	
percent seed set	94.8	89.4	
$\chi^2 = 34.12$; $P < 0.001$			
Morro Bay, San Luis Obispo Co. (intermediate between var. *microcarpa* and var. *spectabilis*)			
seed set	382	572	226
seed failed	82	144	26
total	464	716	252
percent seed set	82.3	79.9	89.7
$\chi^2 = 12.33$; $P < 0.003$			
Jalama Beach, Santa Barbara Co. (var. *spectabilis*)			
seed set	752	238	1446
seed failed	44	6	46
total	796	244	1492
percent seed set	94.5	97.5	96.9
$\chi^2 = 9.82$; $P < 0.01$			
Cambria, San Luis Obispo Co. (var. *spectabilis*)			
seed set	221	841	503
seed failed	23	71	33
total	244	912	536
percent seed set	90.6	92.2	93.8
$\chi^2 = 2.22$; $P > 0.1$			
North Pt. Reyes Beach, Marin Co. (var. *spectabilis*)			
seed set	699	354	1270
seed failed	69	30	126
total	768	384	1396
percent seed set	91.0	92.2	91.0
$\chi^2 = 0.58$; $P > 0.7$			
Pescadero State Beach, San Mateo Co. (var. *spectabilis*)			
seed set			1226
seed failed			50
total			1276
percent seed set			96.1

ever, were homostyles at an advantage over the other two forms. This population was smaller than other mixed populations studied, occurring in a vacant lot at a housing development in Cuesta-by-the-Sea. It appears that in large natural populations pollinators are sufficiently abundant that all forms have a high rate of seed set.

In 1972, the Atascadero State Beach population consisted of one pin and one homostyle. Population size was probably limited by the small area of suitable habitat, by human disturbance, and by abnormally low rainfall in 1972. Nevertheless, the population simulates a small founder population. On inflorescences collected, the homostyle set 30 out of 32 possible seeds (93.8 %) whereas the pin plant set 76 out of 136 possible seeds (only 55.9 %). The difference is statistically significant ($z = 3.99$, $P < .002$).

Discussions and Conclusions

In large populations where pollinators would be expected to find it advantageous to exploit *A. spectabilis,* all three forms have very high seed set. Under such conditions homostyles do not have a significant advantage in fecundity over the other two forms. Homostyles, however, are capable of a much higher level of autogamous seed set. Under conditions where pollinator activity is erratic or suboptimal, such as may occur in small populations, homostyles will be at a strong selective advantage.

These conclusions suggest the following model to account for the establishment and geographical distribution of homostylous populations. The model is necessarily a simplification in that it ignores the variation in degree of homostyly.

Small founder populations derived from mixed populations, either in nearby habitats of limited carrying capacity (due to the small extent of open, stabilized, sandy areas), or in distant habitats where long distance dispersal results in few colonizers, will evolve quickly toward complete homostyly. If, however, a founder population in a habitat of large carrying capacity increases in size quickly enough, pins and thrums may not be eliminated before the selective advantage of homostyly disappears. Also, if the founder population is near enough to a mixed source population so that dispersal is more or less continuous, migration will slow the elimination of distylous plants giving the founder population more time to reach the population size at which the selective advantage of homostyly disappears. Geographic distribution of suitable habitats for *A. spectabilis* is linear and patchy. One would expect populations distant from mixed source populations, where the migration rate is very low (probably close to zero), to be homostylous. Populations established nearby mixed source populations, however, would be expected to remain mixed, if habitat size is large and particularly if migration is also relatively high. Nearby founder populations in small habitats, where population size cannot become large, would be expected to become homo-

stylous unless the migration rate were extremely high, which would be the case only if the habitats were adjacent. The model is consistent with the known distribution of population types.

This means that over short periods of a few generations, population size determines the selective value of homostyly. After populations have reached carrying capacity, habitat size, by setting the upper limit to population size, determines the selective value of homostyly.

Finally, selection for autogamy in founding populations seems to be a sufficient explanation for the distribution pattern of populations in this species. It is unnecessary to postulate that autogamy is advantageous because it preserves certain closely-adapted genotypes—the "fitness" hypothesis first advocated by Mather (1943). This concurs with recent studies of the evolution of autogamy in other annual genera (Lloyd, 1965; Arroyo, 1973). These studies also support the view that autogamy is selected primarily under conditions of unreliable or inefficient pollinator availability.

Literature Cited

Arroyo, M. T. K. 1973. Chiasma frequency evidence on the evolution of autogamy in *Limnanthes floccosa* (Limnanthaceae). Evolution 27:679–688.

Darwin, C. 1877. The different forms of flowers on plants of the same species. John Murray, London.

Jepson, W. L. 1943. *Amsinckia.* Flora of California 3(2):318–327.

Lloyd, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). Contr. Gray Herb. 195:3–134.

Mather, K. 1943. Polygenic inheritance and natural selection. Biol. Rev. Cambridge Phil. Soc. 18:32–64.

Ray, P. M. and H. F. Chisaki. 1957a. Studies on *Amsinckia* I. A synopsis of the genus with a study of heterostyly in it. Amer. J. Bot. 44:529–536.

———. 1957b. Studies on *Amsinckia* II. Relationships among the primitive species. Amer. J. Bot. 44:537–544.

NOTES AND NEWS

Ranunculus flagelliformis Discovered in the Galápagos Islands.—No member of the Ranunculaceae had been reported from the Galápagos Islands by the end of 1970. Then, in June 1971, Paul A. Colvinaux and Charles Racine from Ohio State University discovered plants of a semi-aquatic *Ranunculus* near the summit of Mount Crocker on Isla Santa Cruz. Upon return to Ohio, Colinvaux sent me a sheet of the material and a slide bearing a preparation of its pollen.

An appeal was made to Daniel Weber, who was searching for orchids in the Galápagos Islands at the time, requesting that he look for good specimens of the *Ranunculus* around the higher flanks of Mount Crocker. He replied that he had already collected buttercups in that area during the previous February and forwarded a duplicate sheet of his specimens.