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SELF-COMPATIBILITY IN DISTYLOUS *CRYPTANTHA FLAVA* (BORAGINACEAE)

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SUMMARY

The seed production of hand pollinated flowers indicates that distylous *Cryptantha flava* (A. Nels.) Payson is both intramorph and self-compatible. In addition, there is no inhibition of pollen tube growth following either intramorph or self-pollinations. Despite the potential for crosses between individuals of the same style length and thus the production of unequal morph ratios, pins and thrums occur in equal numbers in natural populations.

Key words: Heterostyly, self-compatibility, *Cryptantha flava*, Boraginaceae.

INTRODUCTION

Most heterostylous species have an incompatibility system which insures that only crosses between morphs produce seed (Darwin, 1877; Vuilleumier, 1967). The few self-compatible heterostylous species are thought to be derived from self-incompatible heterostylous ancestors (Baker, 1966; Yeo, 1975; Ganders, 1979). The only genus in which all distylous species are known to be self-compatible is *Amsinckia* (Boraginaceae) (Ray & Chisaki, 1957a; Ganders, 1979). Compatibility systems in the nine or so distylous species of *Cryptantha* section *Oreocarya* (Boraginaceae), (Higgins, 1971), from which *Amsinckia* is thought to have evolved (Ray & Chisaki, 1957b), have never been investigated. This paper examines the breeding system of the morphologically distylous *Cryptantha flava* (A. Nels.) Payson and reports the proportions of pins and thrums found in natural populations of this species.

MATERIALS AND METHODS

Description of species

C. flava is an herbaceous perennial that occurs throughout much of the arid Colorado Plateau of eastern Utah and parts of adjoining states. Depending on the geographical location and season, flowering begins in early to late May and continues for four or five weeks. Inflorescences of usually 45 to 55 flowers are produced from basal rosettes borne at the ends of a branched woody caudex. The yellow corolla is approx. 1 cm in diameter with a tube of about 1 cm in length. The distance from the top of the anthers to the base of the ovary is 6.20 ± 0.08 (SE) mm for the pin morph and 9.70 ± 0.19 (SE) mm for the thrum morph. The distance from the stigma to the base of the ovary is 9.20 ± 0.18 (SE) mm for the pin morph and 5.40 ± 0.17 (SE) mm for the thrum (Casper, 1983). Other details of floral morphology and pollen production in pins and thrums are described in Casper (1983). Anthophorid bees are the most common floral visitors (Casper, 1983). Usually only one seed (nutlet) is produced per flower although all four ovules may initiate embryos (Casper & Wiens 1981; Casper, 1983).

Plants reach the flowering stage only after several years in the field, but one-year-old plants grown in the greenhouse will flower following vernalization. Inflorescences on greenhouse plants typically consist of fewer flowers than those in the field, and the flowering period in the greenhouse is considerably shorter.

Tests for incompatibility

Hand pollinations to test for incompatibility were conducted in a single population located in Steinaker State Park near Vernal, Utah and in the greenhouse with plants grown from seed collected in four different populations. In the field crosses, inflorescences were covered with fine mesh nylon to exclude insects. Two to ten flowers on each inflorescence were pollinated with either self-, intramorph, or intermorph pollen. Flowers within an inflorescence received the same treatment. For interplant crosses, thrums were first emasculated by severing the corolla tube just below the attachment of the anthers. Pins were not emasculated since the style protrudes approx. 3 mm above the anthers. A portion of the flowers receiving intramorph or intermorph pollen were collected 2, 7, 8 or 24 h after pollination, preserved in FAA, and examined for pollen tube growth in the styles using fluorescence microscopy (Currier, 1957; Weller & Ornduff, 1979). The remaining flowers were collected upon maturity and examined for nutlet production.

The four source populations for the greenhouse plants are geographically separated by at least 75 km. All interplant pollinations were performed between individuals from the same population but different progeny groups. Except for flowers that were to be self-pollinated, the flowers of both morphs were emasculated in late bud and pollinated on the second day of floral anthesis. The self-pollination category includes some flowers that received pollen from other flowers on the same plant. Several flowers of each pollination treatment were collected two days following pollination and examined for pollen tube growth as before. Seed set was determined for the remaining flowers.

Morph ratios

Sixteen populations located throughout eastern Utah were analyzed for ratios of floral morphs. In some populations, every flowering individual encountered while walking a transect through the population was included until a predetermined sample size of 100 or 150 was obtained. In others, all flowering individuals were scored in two 1 × 50 m belt transect. In some smaller populations, all of the flowering individuals were scored.

RESULTS

Incompatibility

It is clear from the amount of seed (nutlet) production following hand pollinations in the field (Table 1) and greenhouse (Table 2) that *C. flava* is both intramorph and self-compatible. Self-, intramorph, and intermorph pollinations result in about the same seed set under a particular growth regime. The low seed production of self-pollinated pins in the greenhouse is an exception. Self-pollination of pins in the field, however, did not produce this same low seed set relative to intramorph and intermorph pollinations. As is typical for this species, most hand pollinated and insect pollinated flowers in the field matured only one of the four ovules. The production of more than one seed per flower was more common under greenhouse conditions, but still only 25% of all ovules matured. Some of the

Table 1. *Seed production of field crosses, P = pin, T = thrum*

Type of cross	(No. of individuals, No. of flowers)	Mean No. of seeds per flower
Intermorph		
P × T	(16, 58)	0.70
T × P	(12, 34)	0.85
Intramorph		
P × P	(9, 53)	0.62
T × T	(7, 40)	0.93
Self		
P	(11, 74)	0.72
T	(17, 139)	0.76
Natural Pollinators		
P	(6, 300)	0.94
T	(6, 300)	1.19
Untreated		
P	(16, 224)	0.08
T	(16, 242)	0.22

Table 2. *Seed production of greenhouse crosses, P = pin, T = thrum*

Type of cross	(No. of individuals, No. of flowers)	Mean No. of seeds per flower
Intermorph		
P × T	(12, 58)	1.00
T × P	(11, 42)	1.62
Intramorph		
P × P	(11, 53)	1.15
T × T	(10, 58)	1.17
Self		
P	(9, 77)	0.57
T	(9, 58)	1.07
Untreated		
P	(7, 175)	0.01
T	(7, 175)	0.00

untreated flowers under exclosures in the field, particularly thrums, produced seed, but of the 350 untreated flowers from the greenhouse experiment that were examined, only one produced a mature nutlet.

Examination of pistils revealed no general inhibition of pollen tube growth either on the stigma or in the style following self- or intramorph pollinations. Pollen tubes had not reached the base of the style in any of the pistils collected in the field, but there were no apparent differences either in pollen tube number or length following intramorph ($n = 32$) and intermorph ($n = 39$) pollinations. In the greenhouse crosses collected 2 days after pollination, pollen tubes could be traced to the base of the style. Again, there were no differences in the general appearance of pollen tubes following self-pollinations ($n = 41$), intramorph crosses ($n = 30$) or intermorph crosses ($n = 46$). In seven of the styles collected from the greenhouse, one or two pollen tubes appeared to have been arrested in their growth and exhibited

enlarged fluorescing tips. Six of these were the products of intermorph crosses; only one was the result of an intramorph cross. A few styles from all pollination treatments exhibited no pollen tubes at all, but apparently these resulted from inadequate pollination.

Morph ratios

As determined by a G-test for goodness of fit, the morph ratios are homogeneous among the 13 populations (Table 3) and do not deviate significantly from 1:1 (Table 4).

Table 3. *Proportions of pins and thrums in natural populations*

(Each of the 16 samples is from a different population)

Year sampled	County	Pins	Thrums	Total	Ratio P/T
1980	Emery, UT	63	87	150	0.72
	Uintah, UT	38	33	71†	1.15
	Uintah, UT	36	33	69†	0.94
1981	Uintah, UT	41	59	100	0.69
	Duchesne, UT	47	53	100	0.89
	Uintah, UT	11	13	24	0.85
	Uintah, UT	49	51	100	0.96
	Duchesne, UT	18	32	50*	0.56
1983	Carbon, UT	45	55	100†	0.82
	Emery, UT	79	71	150	1.11
	Grand, UT	77	73	150	1.05
	Grand, UT	24	23	47*	1.04
	Montezuma, CO	52	48	100	1.08
	San Juan, UT	22	29	51†	0.76
	San Juan, UT	61	52	113†	1.17
Grand, UT	51	48	99†	1.06	

* Entire population sampled.

† Population sampled by belt transect method.

Table 4. *G-test statistics for goodness of fit to a 1:1 ratio for data in Table 3*

d.f.	G-statistic	Significance
16	Total = 15.81982	ns
15	Heterogeneity = 14.38404	ns
1	Pooled = 1.43578	ns

DISCUSSION

Like the distylous species of closely-related *Amsinckia*, *C. flava* is intramorph and self-compatible. As would be expected from the arrangement of floral parts, the species does not appear to be autogamous. A fairly high proportion of untreated thrum flowers under exclosures in the field did produce seed, but this did not occur in the greenhouse. Thrums under exclosures may have selfed as the result of the nylon netting rubbing against the inflorescences. The results also suggest that the

low seed production in *C. flava* is not a consequence of any post-fertilization incompatibility reaction (cf. Crowe, 1971). Other work demonstrates that some of the embryos that would normally fail to mature in naturally pollinated flowers of *C. flava* are capable of developing (Casper, 1985).

Both from studies of other taxa and from theoretical considerations (Baker, 1966; Charlesworth & Charlesworth, 1979), it seems likely that self-compatible but morphologically heterostylous species have usually evolved from heterostylous species that have the sporophytic incompatibility system. One or more of the other eight distylous species of *Cryptantha* may prove to be self-incompatible and thus a possible extant progenitor of this group, but preliminary data show that at least one other species, *C. flavoculata*, (A. Nels.) Payson is also self-compatible. As noted by Yeo (1975) and Ganders (1979), distylous species that exhibit self- and intramorph incompatibility do occur in other genera in the Boraginaceae. At least two distylous members of the Boraginaceae, *Anchusa hybrida* Ten. (Dulberger, 1970) and *Anchusa officinalis* L. (Phillip & Schou, 1981), are known to be intramorph compatible, but self-incompatible.

Despite the absence of an incompatibility system in *C. flava*, pins and thrum still occur in equal numbers in natural populations. In species in which only crosses between morphs are possible, the genetics of the distylous system maintains a 1:1 ratio of pins and thrums. The morphological characteristics and incompatible types are normally controlled by a supergene complex that behaves as a single locus with one dominant and one recessive allele (Ganders, 1979). In most species, thrums are heterozygous and pins are homozygous recessive (Ganders, 1979). The absence of an incompatibility system in *C. flava* means that intermorph crosses are not strictly enforced and that equal numbers of the two morphs should not necessarily occur.

Unfortunately, the pollen grains of pins and thrums in *C. flava* are not dimorphic as they are in many distylous species (Ganders, 1979), making it impossible to determine the proportion of intramorph pollen on naturally pollinated stigmas. In species in which the pollen of pins and thrums can be distinguished, the stigmas of both morphs usually accumulate considerable intramorph pollen; pins typically have more pollen and usually a higher proportion of intramorph pollen than thrums (Ganders, 1979). Assuming that some intramorph pollen flow takes place in *C. flava*, it is surprising that a 1:1 ratio of pins and thrums occurs consistently in natural populations.

Weller & Ornduff (1974) propose that a cryptic incompatibility system regulates morph ratios in the distylous annual *Amsinckia grandiflora* Kleeb. They found that fewer pollen tubes reach the base of the style following illegitimate crosses (intramorph or self-pollinations) than following legitimate crosses. They claim that such a system could explain the equal numbers of pins and thrums often found in the single natural population of this species even though a large proportion of illegitimate pollinations usually occur. Carey and Ganders (unpublished data cited in Ganders, 1979), however, failed to find this cryptic incompatibility in *A. grandiflora* or other distylous species in the genus. From the results of the pollen tube growth studies reported here, it appears that cryptic incompatibility does not operate in *C. flava*.

An alternative means by which morph ratios could be controlled in self-compatible distylous species is through selective abortion of embryos. Consistent with this interpretation is the finding that the progeny of naturally pollinated thrum flowers in *A. grandiflora* contain an excess of pins (Weller & Ornduff, 1977). Either

the thrum allele is selected against during the meiotic event that gives rise to the embryo sac or embryos carrying the thrum allele are selectively eliminated (Weller & Ornduff, 1977). The latter is particularly likely because *A. grandiflora* exhibits a consistently low seed set similar to that in *C. flava*. Thrum × thrum hand pollinations in *A. grandiflora* also yield more pins than predicted based on the genetics of the system (Weller & Ornduff, 1977; Ganders, 1979). Ganders (1979) presents data which suggest that the thrum allele may also be selected against in the female parent in two other distylous species of *Amsinckia*.

Regulation of morph ratios other than through the strict genetics of an incompatibility system is predicted under the models of sex (energy) allocation (Casper & Charnov, 1982; Taylor, 1984). The genetic control of distyly in *C. flava* and the possibility that selective elimination of embryos controls morph ratios in this species is currently being investigated.

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