

INBREEDING, OUTBREEDING, AND HETEROSIS IN THE YELLOW PITCHER PLANT, *SARRACENIA FLAVA* (SARRACENIACEAE), IN VIRGINIA¹

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The yellow pitcher plant, *Sarracenia flava*, is an insectivorous plant restricted to fire-maintained wetland ecosystems in southeastern Virginia. Only four natural sites remain in the state totaling fewer than 100 clumps. Plants from sites located in Dinwiddie, Greensville, Prince George, Sussex counties, and the city of Suffolk were tested for the effects of self-pollination, intrasite outcrossing, and intersite outcrossing on offspring quantity (total seed number and total seed mass) and offspring quality (average seed mass, germination, and growth).

Self-pollination resulted in significantly lower offspring quantity and quality. Total seed number and total seed mass for self-pollinated capsules were approximately one-fourth that of outcrossed capsules. Germination, survivorship, and growth over 5 yr were also significantly lower for offspring from self-pollinated capsules. Together, these results suggest strong inbreeding depression in this species.

Relative to offspring from intrasite crosses, offspring from intersite crosses were significantly larger after 5 yr of growth. This suggests that restoration efforts for Virginia *S. flava* will be most successful when plants from multiple sites are used.

Key words: carnivorous plant; inbreeding; outbreeding; pitcher plant; *Sarracenia*; Sarraceniaceae.

Inbreeding can occur in plants through either selfing or biparental inbreeding (Ellstrand and Elam, 1993). Because normally outcrossing species with consistently large population sizes accumulate many deleterious recessive alleles, such populations are potentially subject to intense inbreeding if population size suddenly declines. Small populations inherently suffer greater levels of inbreeding resulting in homozygosity and decreased mean population fitness known as inbreeding depression (e.g., Wright, 1977b; Shields, 1982; Lynch, 1989; Barrett and Kohn, 1991; Lynch, 1991; Ouborg, van Treuren, and van Damme, 1991; van Treuren et al., 1993; Newman and Pilson, 1997). Among plants, inbreeding depression may be manifest as reduction in seed set, total mass of seeds, average seed mass, percentage germination, survivorship, and/or growth (Lande and Schemske, 1985).

Increased offspring number and increased offspring fitness via heterosis are often considered to be two of the chief benefits of outcrossing (Williams, 1975; Maynard Smith, 1979; Schemske, 1983). Conversely, outcrossing can result in a fitness decline known as outbreeding depression (Templeton, 1986), particularly if there exists highly local adaptation within populations (Waser and Price, 1983, 1989; Svensson, 1988). Outbreeding depression has been found in a variety of plant species (Hickey and McNeilly, 1975; Turkington and Harper, 1979; Schemske, 1984; Waser and Price, 1985).

The relative magnitudes of inbreeding and outbreeding depression may be a crucial factor determining the outcome of attempts to reestablish populations of threatened or endangered species. If inbreeding depression is far stronger than outbreed-

ing depression, reestablishment of viable populations should be more likely if individuals from multiple populations are used; if the converse is true, success should be more likely if individuals from a single population are used.

The yellow pitcher plant, *Sarracenia flava* L., a rhizomatous perennial insectivorous pitcher plant restricted to acid seeps and wetland pine savannas of the southeastern United States, is listed as an S1 or extremely rare and critically imperiled species in Virginia by the Division of Natural Heritage (Killeffer, 1999). Historically, 17 populations of *S. flava* were known to exist in eight counties in the southeastern coastal plain of Virginia with three additional sites discovered during field work in the 1980s (Fig. 1) (Fernald, 1937a, b, 1939, 1947; Harper, 1904; Lewis, 1936; Sheridan, 1986, 1993, 1994). Today, there are only four known natural populations in Virginia totalling fewer than 100 clumps. Whether new *S. flava* populations should be established using progenitors from one or multiple populations will depend, in part, on the relative magnitudes of inbreeding and outbreeding depression within existing populations. Therefore, in this study, we asked the following questions: (1) Is there evidence of inbreeding depression and/or outbreeding depression among existing populations of *S. flava* in Virginia and, if so, what are the relative magnitudes of inbreeding and outbreeding depression? (2) Is inbreeding and/or outbreeding depression manifested as reduction in seed set, total mass of seeds, average seed mass, percentage germination, survivorship, and/or growth?

MATERIALS AND METHODS

Test plants were obtained between 1983 and 1989 either by collecting divisions of wild plants or by germinating seeds collected in the field (Shands only). The six populations used in this study are: Addison and Shands (Dinwiddie County), Dahlia (Greensville County), Sappony (Sussex County), Killy (Suffolk City), and Gary's Church (Prince George County); the latter two populations were subsequently extirpated during the study. Plants were maintained in railroad-tie beds at the Meadowview Biological Research Station

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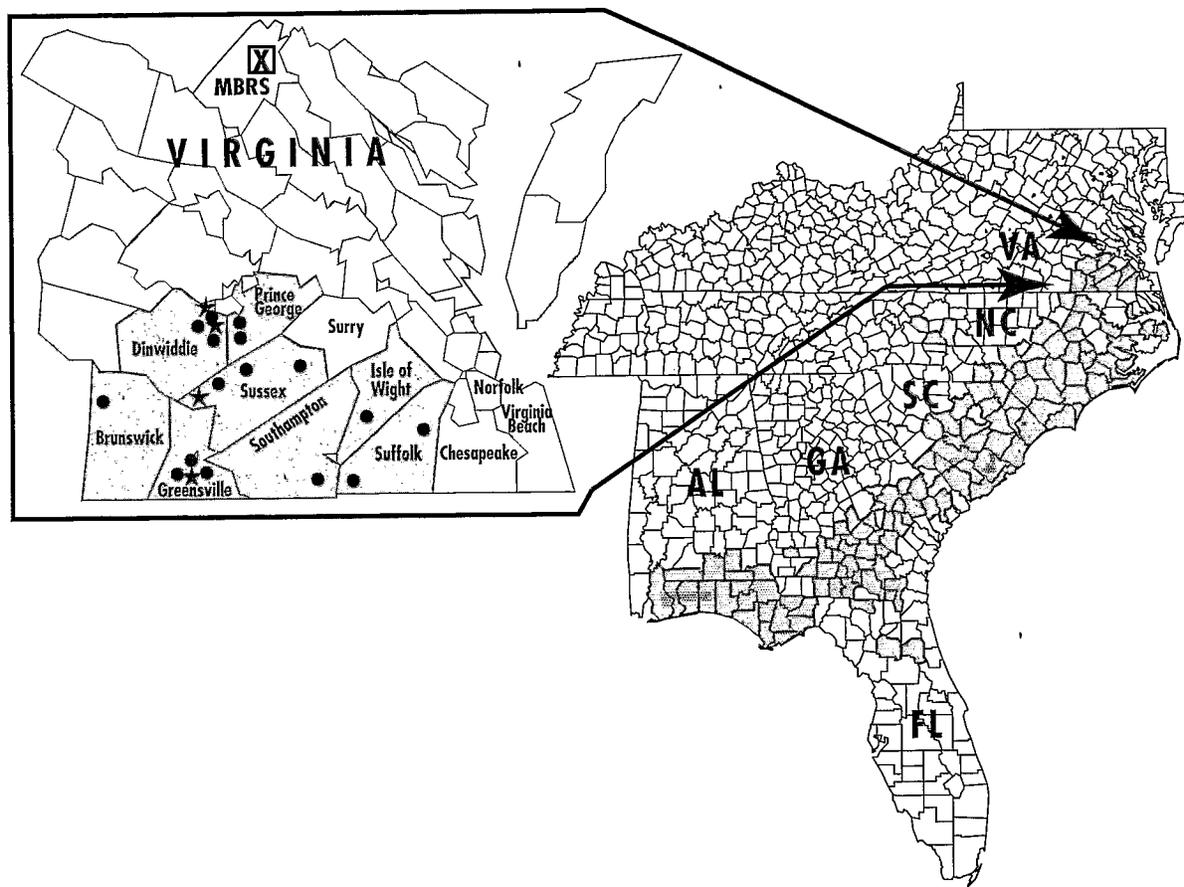


Fig. 1. Historical distribution of *Sarracenia flava*. Exploded area shows distribution in Virginia with stars as extant sites and solid circles as extirpated colonies. Meadowview Biological Research Station (MBRS) located by square with cross lines.

(MBRS) in Caroline County, Virginia. Beds were prepared in 1987 and measured 2.6×0.86 m. The inside of the bed was lined with (6 mil) polyethylene and filled to a depth of 20 cm with a premoistened 50/50 mix of sand and Canadian sphagnum peat moss. Beds were irrigated 15 min daily from May through September using water from Meadow Creek Pond. Annual burns were conducted each year in late winter to remove the previous season's growth and debris.

One week prior to the onset of blooming (typically the last week of April in Virginia), four randomly chosen flowers per test plant were individually covered with bags (Remay fabric—spun polypropylene), in order to prevent entry of pollinators (except 1994 where intersite crosses were not covered and 1996 when no intersite crosses were done). All other flowers produced by the plant were undisturbed. Twist ties were used to secure the bags to a bamboo pole inserted in the bed at the base of the plant. On each plant, the four bagged flowers were then randomly assigned to the four pollination treatments: control, self-pollination, intrasite cross, and intersite cross.

Pollinations were performed following the methods of Sheridan (1997). To accomplish each self-pollination, a toothpick was dipped in canola vegetable oil and pollen was scraped from the style umbrella and liberally applied to all five stigma tips of the same flower. Once the flower had been self-pollinated in this manner, the toothpick was used to perform an intrasite cross on an adjacent plant from the same population. In 1994, intersite crosses were performed on the Addison, Gary's Church, and Kilby sites by tapping pollen from all uncovered flowers into a common collection glass lightly coated with canola oil. The pollen slurry was then applied with a toothpick to an uncovered flower on each of the test plants from Addison, Gary's Church, and Kilby. Because intersite cross flowers were uncovered, it is possible that this treatment in 1994 included some self-pollination and intra-site pollination. This was not likely in 1995, since the flower selected for the intersite cross

was covered prior to blooming and pollen was obtained from a covered flower from a separate Virginia site. In 1995 the intersite treatment included crosses among Gary's Church \times Addison, Shands \times Addison, Sappony \times Gary's Church, Dahlia \times Shands, Kilby \times Dahlia, and Addison \times Sappony (in other words the pollen was not mixed as a common slurry in 1995). In each year, all crosses were performed in approximately equal numbers. During 1996, only self-pollinations and intrasite crosses were performed.

Bagging appeared to effectively limit natural pollination on control flowers; no seeds were produced by control flowers in 1994, a total of 26 seeds were produced by two clones in 1995, and a total of 264 seeds were produced by three clones in 1996. We consider this level of seed production by the controls minimal and attribute it to airborne pollen, incidental transmission by small ants capable of entering the bags, and/or self-pollination caused by the tilting of the flowers in late anthesis.

To determine the effect of pollination treatment on offspring quantity, seeds from experimental beds at MBRS were harvested in mid to late August of each year and stored at room temperature until capsules had dried. Seeds were then separated from capsular debris, and all inflated seeds were counted and weighed. Seeds were excluded if they lacked endosperm or were disfigured, <2 mm long, or flattened.

To determine the effect of pollination treatment on offspring quality, germination, survivorship, and growth, seedlings from the 1994 crosses were monitored over 5 yr. One hundred randomly selected seeds from each capsule produced from self-, intra-, and intersite pollination were sown on the surface of 7×7 cm pots containing a premoistened 50/50 peat-sand mix. Each pot received ten seeds. A total of 4680 seeds were sown (1380 self-pollinated, 1700 intrasite, 1600 intersite; the differences are due to the fact that some self-pollinated and intersite cross capsules did not produce 100 seeds). Pots were positioned randomly in irrigated plastic trays and placed at 7°C for 6

TABLE 1. Number, mass, germination, survivorship, and growth of seeds produced by *S. flava* individuals that received pollen from themselves (self), from a different individual within the same population (intrasite), or from an individual from a different population (intersite) during 1994. Means are given with standard deviations in parentheses. Means followed by the same letter are not significantly different at $P = 0.05$ by paired t tests. Sample sizes were 18 for total seed number, total seed mass, and average mass and 16 for percentage germination, survivorship, and maximum pitcher height.

Cross	Total seed no.	Total seed mass (mg)	Average seed mass (mg)	Germination (%)	Survivorship (%)	Maximum pitcher height 1997 (cm)	Maximum pitcher height 1999 (cm)
Self	165.3 a (121.3)	134.6 a (73.5)	0.634 a (0.108)	22.2 a (16.0)	21.4 a (19.9)	3.24 a (0.96)	13.44 a (7.32)
Intrasite	666.6 b (244.0)	423.3 b (149.7)	0.668 a (0.088)	42.6 b (14.8)	32.4 b (21.3)	4.06 b (1.25)	16.08 b (3.78)
Intersite	683.6 b (182.0)	470.0 b (110.5)	0.760 b (0.199)	44.0 b (15.1)	28.5 b (13.8)	5.13 c (1.82)	21.70 c (5.20)

wk. On 16 May, 1995 trays were moved to the Virginia Commonwealth University (VCU) greenhouse on a series of stacked racks, each with a bank of four fluorescent lights placed 13 cm from the top of the pots. Germination was recorded monthly from June to September. After seedlings had entered dormancy in the fall, trays were moved to MBRS and covered with a pine straw mulch to prevent freezing and desiccation. Mulch was removed in April 1996 and trays were covered by translucent fiberglass frames and misted daily. In the spring and summer of 1997, seedlings were maintained under full sun without fiberglass covers. Seedlings were repotted in the spring of 1998 into 14 × 11 cm pots. Germination and survivorship were measured each year through August 1999. The height of the largest pitcher per pot was measured each August from 1997 to 1999.

Paired t tests were used to determine the effect of pollination treatment on all measures of offspring quantity and quality; this analysis focused comparisons among capsules on the same plant receiving the three pollination treatments. For unknown reasons, reproduction of these *S. flava* populations was much more successful in 1994 and 1995 than in 1996. Therefore, analyses were conducted separately for each year. Capsules that were damaged by insects (~10% of all capsules) were not included in the analyses.

The relative fitness of self-pollinated vs. outcrossed plants in 1994 was calculated as in Schemske (1983). Briefly, means for total seed number, germination, survivorship, and growth of seeds from self-pollinated capsules were expressed as a proportion of the corresponding values observed for outcrossed capsules (e.g., mean seed number self-pollinated/mean seed number intrasite), then multiplied (e.g., proportion seed number × proportion germination, etc.) to give a single estimate of relative fitness.

RESULTS

During all three years, *Sarracenia flava* capsules that were self-pollinated produced significantly fewer seeds than capsules from intrasite crosses; reduction in seed set relative to intrasite crosses ranged from 65% in 1996 to 75% in 1994

TABLE 2. Number and mass of seeds produced by *S. flava* individuals that received pollen from themselves (self), from a different individual within the same population (intrasite), or from an individual from a different population (intersite) during 1995. Means are given with standard deviations in parentheses. Means followed by the same letter are not significantly different at $P = 0.05$ by paired t tests. Sample sizes were 35 for self vs. intrasite crosses, 27 for self vs. intersite crosses, and 29 for intrasite vs. intersite crosses.

Cross	Total seed no.	Total seed mass (mg)	Average seed mass (mg)
Self	214.8 a (180.0)	167.1 a (127.3)	0.693 a (0.178)
Intrasite	785.6 c (307.8)	540.0 b (245.6)	0.669 a (0.169)
Intersite	573.7 b (357.3)	457.0 b (300.3)	0.735 a (0.253)

(Tables 1–3). During the two years in which comparisons could be made, self-pollinated capsules also produced significantly fewer seeds than capsules from intersite crosses; reduction in seed set relative to intersite crosses was 76% in 1994 and 63% in 1995 (Tables 1 and 2). Capsules from intrasite crosses also produced significantly more seeds (26% more) than capsules from intersite crosses, but only in 1995 (Table 2).

Total seed mass was also significantly lower for selfed capsules than for intrasite capsules in all three years and was also significantly lower for selfed capsules than for intersite capsules in 1994 and 1995 (Tables 1–3). Total seed mass did not differ significantly between intra- and intersite capsules in either year (Tables 1 and 2).

Average seed mass did not differ significantly between selfed and intrasite capsules in any year, but was significantly lower for both treatments than for intersite capsules in 1994 (Tables 1–3). Average seed mass was not significantly correlated with total seed number for any treatment in any year.

Germination, survivorship, and growth were measured only for seeds produced during 1994. Seeds from self-pollinated capsules in 1994 germinated at a significantly lower rate than seeds from intrasite or intersite crosses (22 vs. 43% and 44%, respectively; Table 1). Moreover, survivorship through the summer of 1998 was also significantly lower for seeds from self-pollinated capsules than for seeds from intrasite or intersite crosses (21 vs. 32% and 29%, respectively; Table 1). In addition, growth over five years (as indicated by maximum pitcher height) was significantly lower for seeds from self-pollinated capsules than for seeds from intrasite or intersite crosses (13.4 vs. 16.1 and 21.7 cm, respectively; Table 1). Although only three plants produced flowers in the spring of 1999, all that did so were progeny from either intrasite (one plant) or intersite crosses (two plants).

Because both offspring quantity and quality were signifi-

TABLE 3. Number and mass of seeds produced by *S. flava* individuals that received pollen from themselves (self) or from a different individual within the same population (intrasite) during 1996. Means are given with standard deviations in parentheses. Means followed by the same letter are not significantly different at $P = 0.05$ by paired t tests ($N = 15$ for each comparison).

Cross	Total seed no.	Total seed mass (mg)	Average seed mass (mg)
Self	145.5 a (114.9)	113.3 a (86.6)	0.798 a (0.247)
Intrasite	418.5 b (290.4)	322.8 b (211.0)	0.744 a (0.128)

TABLE 4. Effects of self-pollination on relative fitness as determined by the ratio of self-pollination: outcross values for each life-history stage. Values are presented also for comparison of intrasite vs. intersite crosses.

Component	Cross		
	Self/Intrasite	Self/Intersite	Intrasite/ Intersite
I Seed number	0.248	0.242	0.975
II Germination	0.521	0.505	0.901
III Survivorship	0.660	0.751	1.137
IV Growth	0.836	0.619	0.741
Relative fitness	0.071	0.057	0.740
Total inbreeding depression	0.929	0.943	0.260

cantly adversely affected, the relative fitness of self-pollinated capsules was only 7% that of intrasite outcrossed capsules and only 6% that of intersite outcrossed capsules (Table 4).

Interestingly, we observed several differences between intrasite and intersite outcrossed capsules. During 1994, intersite crosses resulted in significantly heavier seeds than intrasite crosses. Moreover, seeds from intersite crosses produced the most vigorous seedlings; in August 1997 maximum pitcher height was significantly greater for seedlings from intersite crosses. This difference persisted through August 1999 (Table 1). Using 1994 capsules, relative fitness of intrasite crossed capsules was only 76% that of intersite crossed capsules (Table 4). However, this difference may not be consistent from year to year; in 1995, intersite capsules produced 27% fewer seeds than intra-site capsules (Table 1).

The effects of pollination treatment on all measures of offspring quantity and quality were consistent among sites in each of the three years.

DISCUSSION

Species that have long been obligate outcrossers often harbor so many recessive alleles that self-fertilization results in a great reduction in vigor at one or many life-history stages (Stebbins, 1974; Wright, 1977a; Schemske, 1983). The structure of *S. flava* flowers encourages cross pollination, which is accomplished primarily by queen *Bombus* bees (Schnell, 1976, 1983). Based on allozyme analysis, Godt and Hamrick (1996) determined that *Sarracenia jonesii* and *S. oreophila* are indeed highly outcrossed. These authors also lamented the lack of work on relative fitness of inbred and outcrossed *Sarracenia* progeny.

To our knowledge, this paper, based on our earlier abstract (Sheridan and Karowe, 1995), provides the first experimental evidence of extensive inbreeding depression in *Sarracenia*. Relative to outcrossed *S. flava* capsules on the same plant, self-pollinated capsules displayed reductions of 65–76% in total seed set and 63–71% in total seed mass. That reduced offspring quantity is due at least in part to inbreeding depression, rather than simply to partial self-incompatibility, is suggested by the corresponding decrease in offspring quality. Relative to seeds from intersite outcrossed capsules, seeds from self-pollinated capsules weighed, on average, 17% less. More importantly, relative to both types of outcrossed capsules, germination of seeds from self-pollinated capsules was reduced by 48–50%, survivorship was reduced by 25–34%, and growth over a 5-yr period was reduced by 16–38%.

If one accepts that the life history of an organism is a re-

flection of a cascade of molecular events mediated by the genome, then it is not surprising that inbreeding depression was manifest in several life-history stages in *S. flava*. In this study, the cumulative inbreeding depression for self-pollinated *S. flava* was 93% relative to intrasite crosses and 94% relative to intersite crosses. *Sarracenia flava* appears to be particularly vulnerable to inbreeding depression; Schemske (1983) reported figures as high as 56% in *Costus* spp. and Schoen (1983) as much as 44% inbreeding depression over the life cycle of *Gilia achilleifolia*.

Although we have not yet been able to evaluate flower, fruit, and seed production on the progeny from self-pollinated plants, other studies indicate a strong effect late in the plant's life cycle (Toppings, 1989; Dudash, 1990; Fenster, 1991). Inbreeding depression and heterosis may depend also on the environment, with the most pronounced effects occurring under stressful conditions (Parsons, 1971; Charlesworth and Charlesworth, 1987) or field conditions (Kohn, 1988; Dudash, 1990). If additional reductions in fitness for self-pollinated *S. flava* progeny occur in the reproductive phase and under field conditions, then selection against selfing would be even stronger.

In contrast to our results, North Carolina *S. flava* populations displayed no disadvantage of selfing vs. intrasite outcrossing in terms of seed set, seed size, or seed quality over 25 yr (Schnell, 1983). Further research on the regional nature of inbreeding depression in *S. flava* may therefore be warranted.

The 26% decrease in fitness of intrasite outcrosses relative to intersite outcrosses in 1994 may reflect past bottlenecks experienced by our study populations. All six populations used in this study (both the Gary's Church and Kilby site were extirpated during the course of this study) cover less than an acre, are isolated from each other, and have been small for a number of generations (Sheridan, personal observations). For instance, the Kilby population was historically isolated by at least 32 km from any other *S. flava* population and has been very small since the site was mined for clay in the 1950s. Plants in this site today may therefore be reasonably closely related; if so, intrasite pollination would result in biparental inbreeding.

Conservation—The results of this study provide useful, practical information to guide recovery efforts for Virginia *S. flava* populations. Initial recovery efforts with other rare pitcher plant species (e.g., *S. rubra* ssp. *jonesii*) have avoided mixing regional populations when either restoring extirpated sites or initiating new populations. However, Barrett and Kohn (1991) point out that “the attempt to preserve population differentiation may conflict with practices aimed at species preservation. . . in the long-term, species conservation is, in general, of greater importance. Attempts to preserve population distinctiveness should be undertaken only when they do not endanger species conservation.” Our data indicate that the most vigorous *S. flava* offspring are produced by intersite crosses. Therefore, conservation biologists working with rare pitcher plant species may find that the best approach for establishing vigorous pitcher plant colonies is to allow intersite crossing of regional populations. Godt and Hamrick (1999) commented on the need to maintain populations at census sizes to reduce the possibility of demographic extinction and encouraged the use of different source propagules for restoration. Our results support this approach.

Although a number of plant species maintain additional genetic variation in dormant root stocks or seeds (Ellstrand and Elam, 1993), which may prevent inbreeding depression, this is not the case with *S. flava* in Virginia. Although Folkerts (1992) reports growing-season dormancy of *Sarracenia* rhizomes, the senior author conducted a removal experiment with the forested, fire-suppressed *S. flava* population at Addison (Dinwiddie County) prior to the site being clear-cut. No evidence of a seed bank or dormant rhizomes resprouting was found up to four years after the clear-cut (Sheridan and Scholl, 1999). This suggests that the few remaining, depauperate Virginia *S. flava* populations are unlikely to harbor additional genetic reservoirs to prevent strong inbreeding depression.

Given the extensive habitat destruction of seepage wetlands in southeastern Virginia over the past 400 yr and the restricted size of the few remaining *S. flava* populations, an active program to restore this species is clearly warranted. Our results suggest that restoration efforts are most likely to succeed in areas with a large population of outcrossing pollinators (e.g., bumble bees), particularly if populations contain plants gathered from multiple existing sites. As little as a few pollen dispersal events per generation per population may suffice to maintain historic levels of gene flow (Ellstrand and Elam, 1993) and prevent inbreeding depression in these Virginia populations.

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