

AMERICAN JOURNAL OF Botany

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Reviewed work(s):

Source: *American Journal of Botany*, Vol. 76, No. 1 (Jan., 1989), pp. 67-73

Published by: [Botanical Society of America](#)

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PATTERNS OF FRUIT PRODUCTION IN A NEOTROPICAL ORCHID: POLLINATOR VS. RESOURCE LIMITATION¹

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ABSTRACT

Patterns of growth, and of flower and fruit production, were monitored over two years in a population of the orchid *Aspasia principissa* Reichb. f. in central Panama. Observations and experimental manipulations were used to determine the relative importance of pollinator and resource limitation on fruit production. Within a season, fruit production was limited by pollinator availability. Fruit set for hand-pollinated flowers was over six times greater than that for naturally pollinated flowers. However, in plants that produced more than one fruit, fruit size declined in subsequent fruits, indicating that resources could limit seed production within a season. Plants producing fruits in 1986, on average, produced smaller shoots and inflorescences in 1987 relative to plants that flowered but produced no fruit in 1986. Thus, plants are likely to be resource limited over their lifetimes. Most individuals of reproductive size (82.5%) did not produce fruit over a three-year period. The reproductive dominance of a few individuals in this population of *Aspasia principissa* may have important implications for understanding the population structure of the species and the high species diversity of orchids.

INVESTIGATIONS of breeding systems in plants often begin with the observation that more ovules and ovaries are produced than seeds or fruits. In the absence of herbivory, predation, or adverse conditions, it is often assumed that the availability of resources ultimately limits seed or fruit production (Lloyd, 1980; Stephenson, 1981). However, pollen or pollinator limitation has been demonstrated in a substantial number of cases and this source of low seed or fruit production may be common (Bierzychudek, 1981; Rathcke, 1983). Resource or pollen/pollinator limitation hypotheses are usually tested by comparing the seed or fruit set of flowers, inflorescences, or individual plants receiving supplemental hand pollination with those of open-pollinated counterparts within a season. Pollen or pollinator limitation are inferred if seed or fruit set are elevated by hand pollinations relative to natural pollinations. Conversely, if seed or fruit set cannot be elevated by hand pollinations, resources are presumed to limit the production of seeds or fruits. From this viewpoint, pollination and resource limitation are mutually exclusive ex-

planations of observed patterns of seed or fruit production.

Three important problems result when levels of fruit or seed set are used to test for pollinator limitation. First, increases in fruit or seed production by hand pollination may be offset by decreases in the quality of those fruits or seeds (Bawa and Webb, 1984). Second, increases in fruit production may be offset by a reduction in flower production (e.g., Alexander, 1987) or in the maturation of further fruits. In this regard the best studies of pollen limitation are those in which all flowers receive hand pollinations and total plant fecundity is monitored (Stephenson, 1981). Third, elevated fruit set in one year by hand pollination may come at the expense of future growth, reproduction, or survival, indicating that plants are resource limited over their lifetimes (Janzen et al., 1980; Montalvo and Ackerman, 1987). These considerations suggest that there is an interaction between resource and pollen/pollinator limitation. In the first two cases, pollen and resource limitation both affect reproduction *within* a given season. In the latter, plants might be pollen or pollinator limited within a season, but observations extended *between* seasons could indicate that plants are resource limited.

Recent studies have demonstrated that plants which are pollinator limited within a season may be resource limited over their lifetimes. Paige and Whitham (1987) have shown that some populations of normally semelparous *Ipomopsis aggregata* can be iteroparous at high elevations. The frequency of iteroparity in these

¹ Received for publication 17 February 1988; revision accepted 11 May 1988.

We thank Jim Ackerman, Ricardo Calvo, Lissy Coley, Phil DeVries, Vince Eckhart, Monica Geber, Richard Primack, Doug Schemske, and Nick Waser for comments on the manuscript. Facilities for this project were provided by the Smithsonian Tropical Research Institute. Support was provided by Smithsonian Predoctoral Fellowships awarded to both authors and NSF Grant BSR-8501246 to JKZ.

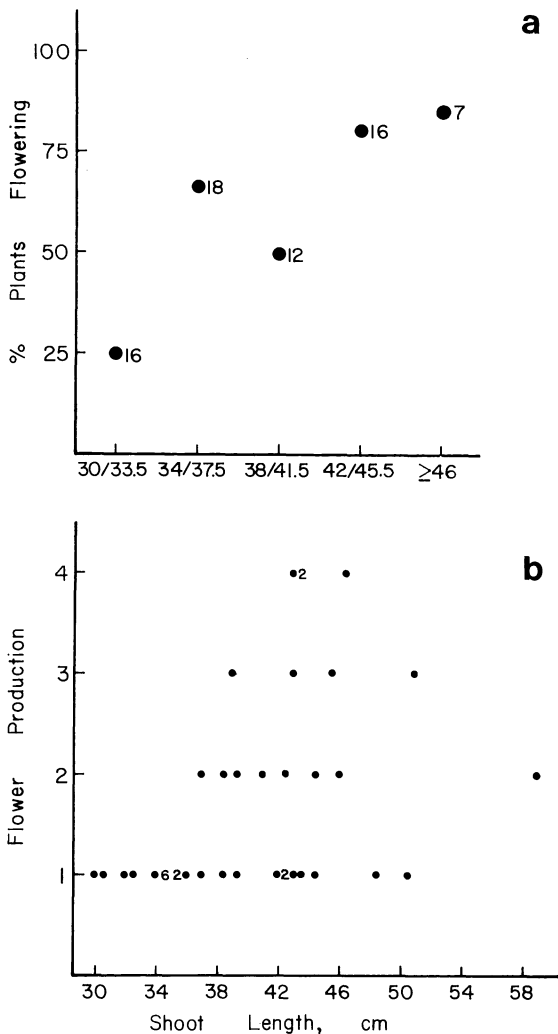


Fig. 1. a. The proportion of flowering plants in 1986 in groups of plants with different shoot lengths (Spearman rank correlation, $r_s = 0.90$, $P = 0.01$). Numbers adjacent to data points indicate the number of individuals in each size class. b. Flower production as a function of shoot length. Numbers indicated multiple data points.

populations is most common among those individuals with low fruit set, and fruit set in these individuals is limited by pollinator availability. In the neotropical orchid *Ionopsis utricularioides*, Montalvo and Ackerman (1987) provided evidence of pollinator limitation within a season, but pointed out that high fruit set in one year led to reduced growth and flowering in the following year, suggesting that reproduction in these plants is resource limited.

We report on the within- and between-year patterns of growth, and flower and fruit production in the orchid *Aspasia principissa*. We demonstrate that there is an interplay between

pollinator and resource limitation on fruit production and that this affects population structure. Finally, we discuss how these results may help to explain the extreme species diversity in the Orchidaceae.

MATERIALS AND METHODS—*Aspasia principissa* occurs in central and eastern Panama, primarily in the wettest forests of the region (Williams and Allen, 1980). Plants grow on tree trunks from near ground level to approximately 10 m in the lower portions of the forest canopy. Plant growth is sympodial; plants initiate a new shoot (leaves + pseudobulb) in March of every year and the new shoot matures by the following year. Flowers are produced in the late dry season (February–April) and the first month of the wet season (May) from the most recent, fully developed shoot. Plants usually produce one or occasionally two inflorescences, with up to six flowers per inflorescence. Inflorescence development is acropetalous, the first flower opening following the initiation of all buds, and individual flowers last from 1 to 7 weeks.

Aspasia principissa is pollinated by large euglossine bees in the genera *Eulaema* and *Exaerete* (Ackerman, 1983). Pollen is contained in two masses, pollinia, which are attached to the pollinator by a stipe and sticky viscidium. Pollinia, stipe, and viscidium together comprise the pollinarium, whose presence or absence in a flower is easily determined by close inspection. Flowers contain a long nectary-like structure but produce no nectar (Williams, 1974) and apparently attract pollinators by deceit, by resembling food flowers of the bee visitors.

Following deposition of a pollinium in the stigmatic cleft, swelling of the stigma occurs within 24 hr, precluding any subsequent insertion of pollinia (Zimmerman and Aide, personal observation). Hand pollinations demonstrated that *A. principissa* is self-compatible. Self pollinations ($N = 20$) produced an average fruit set of 60%, not significantly different ($G = 0.01$, $P > 0.9$) from that for cross pollination (61%, $N = 49$). The fruits are retained on the plants through the wet season until the following dry season, when fruit dehiscence occurs.

The study was conducted on Barro Colorado Island, a preserve of lowland, semideciduous, moist forest located in the Panama Canal in central Panama (see Croat, 1978; Leigh, Rand, and Windsor, 1982, for descriptions). In January 1986 we located over 200 reproductive sized individuals along or near existing trails. Plants within reach ($N = 69$) were tagged and the shoot (pseudobulb and leaf) length was

TABLE 1. Summary data for reproduction in unmanipulated plants of *A. principissa* on Barro Colorado Island, Panama, for two years. Data in parentheses represent percentages of previous column

Year	Plants	Flowering plants	Buds	Flowers	Fruits
1986	202	88 (43.6)	231	179 (77.5)	15 (8.4)
1987	175	63 (36.0)	155	131 (84.5)	14 (10.6)

measured to the nearest 0.5 cm. Individuals in the canopy ($N = 153$) were located by maps of their host tree canopy. All plants were checked for the presence of fruits from the previous year, 1985. Plants in the canopy were censused weekly, with binoculars, between 17 February and 26 May 1986 for the presences of flower buds, flowers, and fruits. For plants within reach, we also recorded the presence or absence of pollinaria. To increase levels of pollination, all flowers ($N = 33$) of twenty haphazardly selected plants were pollinated by hand.

In February 1987, we relocated the study plants and recorded the number of plants alive after one year. The lengths of the new shoots and the length of any fruit produced the previous year were measured for all tagged plants. All surviving plants were censused weekly between 19 February and 28 May 1987 for buds, flowers, fruit production, and, when possible, for pollinaria removal.

To investigate the effects of flower position and pollination intensity (number of flowers pollinated per inflorescence) on the abortion of pollinated flowers, hand pollinations and observed natural pollinations from both years were combined into a single data set.

RESULTS—Within-season patterns—Flowering: Only plants with shoots ≥ 30 cm in length flowered, and above this threshold, 43.6% and 36% of the plants flowered in 1986 and 1987, respectively (Table 1). The proportion of plants flowering increased with plant size (Fig. 1a) and larger plants produced more flowers (Fig. 1b; Spearman rank correlation, $r_s = 0.54$, $P < 0.001$).

Flowering plants aborted 15–23% of buds before flowers developed fully (Table 1). Aborted buds were almost always terminal ones and there was no difference in abortion rate between those inflorescences that did or did not initiate a fruit (1986: $G = 0.04$, $P = 0.88$; 1987: $G = 1.79$, $P = 0.26$).

Pollinaria removal—Of the flowers that could be closely observed ($N = 35$), 58.1% had pollinaria removed. A comparison of pollinaria removal among 1–3-flowered inflorescences showed that plants which produced more flowers had, on average, more pollinaria removed by pollinators (Table 2). However, the proportion of flowers with pollinaria removed did not change with inflorescence size ($G = 1.42$, $P = 0.49$).

Fruit production—Fruit set averaged 9.5% over the two study years (Table 1). Most plants setting fruit produced only a single fruit. Hand pollinations increased fruit set to 60.8%, about 6.4 times that observed for natural pollinations, indicating that fruit set was limited by pollen availability.

There was a nearly significant positive correlation of flower production with fruit production (Table 2; $r_s = 0.75$, $P = 0.075$) which resulted in a significant difference in the number of flowers that had been produced by fruiting and nonfruiting plants (Mann-Whitney U test; 1986: $P = 0.048$; 1987: $P = 0.035$). The proportion of flowers setting fruit among inflorescence size classes was not significantly different ($G = 2.21$, $P = 0.70$).

Length of the first initiated fruit on an infructescence was positively related with shoot size ($r^2 = 0.47$, $P = 0.005$) (Fig. 2b), but in plants that produced more than one fruit, fruit length declined in the subsequent fruits (Fig. 2a).

Fruit abortion—The failure of a pollinated flower to produce a fruit was independent of flower position. This was clear in two flowered inflorescences ($N = 16$, $G = 0.37$, $P = 0.59$).

TABLE 2. The effect of flower production on pollinaria removals and fruit production; data for 1986 and 1987 combined. In most cases, flower production equals inflorescence size, except for larger values, where production by two inflorescences on an individual have been combined

	Flower production (no. flowers)				
	1	2	3	4	5–7
Ave. no. pollinaria removed/inflor.	0.625	0.857	1.750	—	—
N	24	7	4	—	—
Ave. no. fruits/inflor.	0.103	0.222	0.333	0.222	0.333
N	68	36	27	9	9

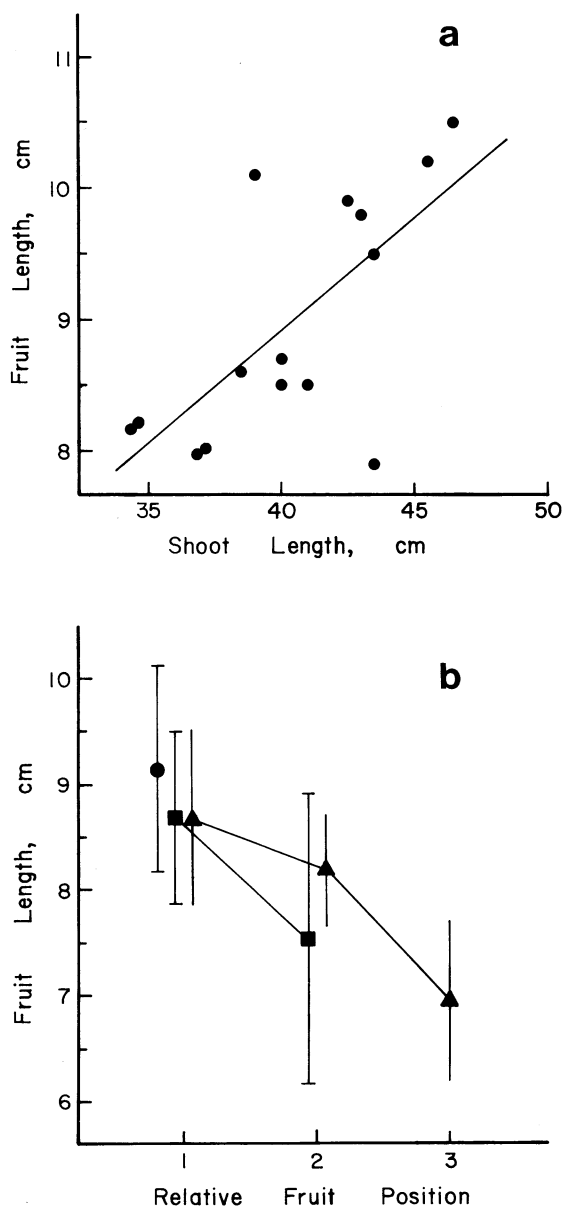


Fig. 2. **a.** Correlation between length (base of pedicel to base of column) of the first-produced fruit and shoot length; all plants combined. Regression line represents the equation $Y = 0.171X + 2.081$. **b.** Changes in fruit length as a result of changes in number of fruits/inflorescence; data for naturally and hand pollinated inflorescences combined (1986). Error bars for 1- ($N = 10$) and 2-fruited ($N = 4$) inflorescences are SD, while those for 3-fruited inflorescences ($N = 2$) are ranges. Subsequent fruit production did not affect the size of the first fruit produced (data for 2- and 3-fruited inflorescences combined, $P = 0.40$). Changes in fruit length between first- and second-produced fruits (2- and 3-fruited inflorescences combined) were always negative and were significant (paired t test, $P = 0.04$).

and, although data were less abundant, similar patterns were observed for 3- and 4-flowered inflorescences. There was also no difference in the proportion of fruits that were produced between inflorescences that had all or part of the flowers pollinated ($N = 60$, $G = 0.93$, $P = 0.42$).

Between-season patterns—Mortality: Over 10% of plants died between January 1986 and February 1987 (Table 3). Mortality was random with respect to a plant's reproductive status in 1986 (Table 3; $G = 0.20$, $P > 0.9$). Eighteen of 21 recorded deaths resulted from plants falling from their substrate, or plants falling with trees or limbs, while the remainder died in place from unknown causes.

Frequency of flowering—Forty-three percent of the plants did not flower during the two years of this study (Table 3). Of the plants that flowered, but did not set any fruit in 1986, 61.5% flowered again in 1987, while 69% of the plants that produced fruit in 1986, flowered again in 1987 (Table 3; $G = 0.28$, $P = 0.66$).

Effects of fruit production—Compared to flowering plants that did not set fruit, plants that produced fruits (natural and hand-pollinated plants combined) in 1986 showed a significant reduction in shoot length (Fig. 3; one-tailed t test, $P = 0.001$) and flower production (Fig. 3, $P = 0.002$) in 1987.

DISCUSSION—Pollinator limitation—Within a season, reproduction in *A. principissa* is limited by pollinator availability. When plants were pollinated by hand, fruit set increased over six-fold that observed for naturally pollinated plants. Approximately 60% of the flowers had pollinaria removed, indicating that a large proportion of flowers in the population were never visited by pollinators (deposition of pollinia was always accompanied by pollinaria removal). Pollinator scarcity may have led to the evolution of pollinator deceit in *A. principissa* as proposed for other orchid species (Ackerman, 1986a).

Larger inflorescences received more pollinator visits and produced more fruits than did smaller inflorescences. However, there was no evidence that male or female reproductive success increased disproportionately with the inflorescence size as observed for the orchid *Brassavola nodosa* (Schemske, 1980). This may have occurred in part because flower production and display were not tightly correlated due to the sequential development of *Aspasia* inflorescences.

TABLE 3. Transitions in reproductive status of *A. principissa* plants between 1986 and 1987. Data in parentheses are proportions of row totals

	1987				
	Nonflowering	Flowering	Fruiting	Dead	Total
1986					
Nonflowering	87 (76.3)	13 (11.4)	2 (1.8)	12 (10.5)	114 (100)
Flowering	25 (34.2)	32 (43.8)	8 (11.0)	8 (11.0)	73 (100)
Fruiting	4 (28.6)	6 (42.9)	3 (21.4)	1 (7.1)	14 (100)
Total	116	51	13	21	201

Other studies support the observation that reproduction in orchids is pollinator limited (Ivri and Dafni, 1977; Nilsson, 1978, 1980, 1981; Janzen et al., 1980; Schemske, 1980; Dieringer, 1982; Ackerman and Montero Oliver, 1985; Inoe, 1985; Barrett and Helenurm, 1987; Montalvo and Ackerman, 1987; Ackerman, in press; Calvo and Berry, unpublished data; Primack, unpublished data). Inoe (1985) demonstrated a lack of pollinator limitation of fruit set in one of two orchid species he studied.

Resource limitation—Plant size was an important determinant of reproductive performance. Large plants flowered more often, produced greater numbers of flowers, were pollinated more often and produced larger fruits than their smaller counterparts. The factors influencing plant size are unclear, although a reasonable set of hypotheses would consider long-term resource availability as a contributing factor. This variation in resource availability may be unique to the epiphytic habitat where nutrient availability would be expected to vary in time and space (Benzing, 1973). Plant size should also be affected by age and past history, particularly fruit production in past years.

Within a season, resources limited fruit quality. Abortion of flower buds and pollinated flowers were not affected by the production of fruits indicating that resource limitation was not involved in these "decisions." This is contrary to patterns reported by Ackerman (in press) and Montalvo and Ackerman (1987) in the orchids they studied (see also Colosi and Cavers, 1984; Alexander, 1987). However, if *A. principissa* set more than one fruit, subsequent fruits were smaller (Fig. 2b). Fruit size declined with increased fruit set and overpollination of inflorescences did not result in linear gains in reproductive success.

On average, *A. principissa* plants appear to be resource limited over their lifetimes. Fruit

production in one year caused a reduction in shoot size and flowering in the following year, although variation in this response among plants was evident (Fig. 3). Recent studies have found similar effects in other orchids (Ackerman and Montero Oliver, 1985; Montalvo and Ackerman, 1987; Ackerman, in press; Snow, personal communication; Primack, unpublished data). Just as pollinator limitation, within a season, may be common in orchids, long-term resource limitation in this group seems to be frequent as well.

Evolutionary consequences—The results of this and other studies have demonstrated that pollinator/resource limitation is not a dichotomy, but an interaction affecting lifetime reproductive success. Theoretical and empirical studies have suggested that there should be a trade-off between present reproduction and future growth, reproduction, or survival (Williams, 1966; Schaffer, 1974; Law, 1979). That orchids frequently express this trade-off may be linked to extreme pollinator limitation, especially in a few-flowered species such as *Aspasia*. Because the probability of fruit production in a given year is low, when pollinated, plants should be selected to forego some future reproductive opportunities in favor of present ones. The rarity of pollination events further suggests that plants should not abort pollinated flowers. In *A. principissa* plants aborted a significant proportion of pollinated flowers, but this abortion was not affected by flower position nor pollination intensity (see also Montalvo and Ackerman, 1987).

Summation of three years data (1985–1987) for fruit production indicated that 18% ($N = 32$) of reproductive sized individuals produced all the fruits in the population and few plants (8) produced fruits in more than one year of the study (e.g., see Table 3). The mortality data (Table 3) suggests that plants of reproductive size live on average for about ten years (as-

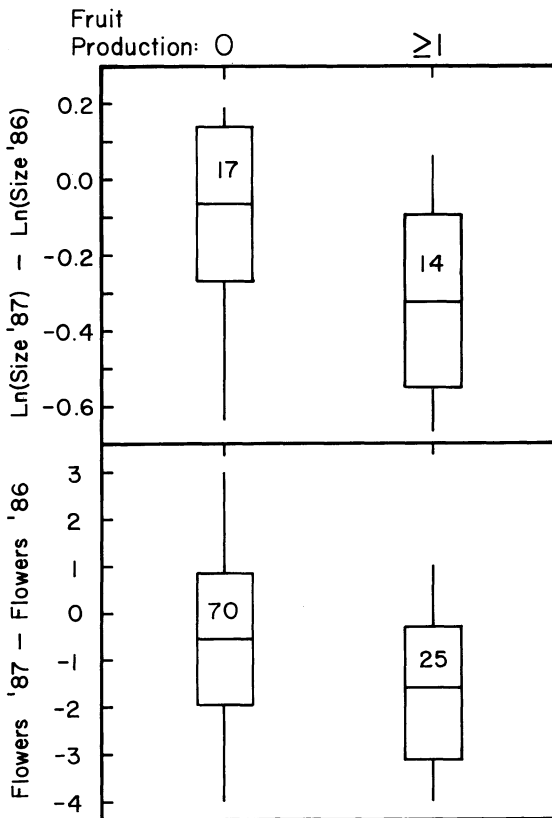


Fig. 3. Comparison of changes in plant size (shoot length, cm) and flower production for plants that produced fruits in 1986 (naturally and hand-pollinated plants) with those that did not. Differences in shoot length were calculated from \ln transformed data to provide near-normal distributions for the difference values.

suming mortality is random); therefore, three years of data should be a good estimate of the variation in lifetime reproductive output. The timing of pollen deposition and closing of the stigmatic cleft further stipulates that most fruits are single-fathered, indicating that paternal opportunities among plants are limited as well.

Patterns of speciation in orchids have often been linked to aspects of pollination and reproduction (Pijl and Dodson, 1966; Dressler, 1981; but see Benzing, 1981). If the reproductive patterns observed in *Aspasia* are similar in other orchids, as present evidence suggests, could this be a contributing factor in understanding the apparent rapid diversification of the Orchidaceae (Dressler, 1981)? Although genetic differences may be correlated with observed variation in fruit production in *Aspasia*, it is more likely this variation would affect a reduction in effective population size, leading to increased genetic drift. This would augment the effects of small (absolute) population sizes,

a common situation in epiphytic communities (Ackerman, 1986b; and references therein) and relatively short lifetimes, which limits opportunities for reproduction. Although the subject of a long-standing debate, many argue that genetic drift has an important role in determining rates of speciation (Wright, 1931; Lande, 1976; Kiester, Lande, and Schemske, 1984; Carson, 1985; and references therein) and the situation presented by epiphytic orchid populations would appear to present an extreme case. However, we emphasize the need for more empirical studies of the long-term demography of epiphytic orchid populations to determine the generality of our observations for *A. principissa* in Panama. Moreover, information on mating system, gene flow, and variance in family size is required to fully evaluate the degree to which reproductive patterns limit effective population size in orchids.

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