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Bulletin of the Torrey Botanical Club, Volume 123, Issue 1 (Jan. - Mar., 1996), 34-40.

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Bulletin of the Torrey Botanical Club
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More flowers or new cladodes? Environmental correlates and biological consequences of sexual reproduction in a Sonoran Desert prickly pear cactus, *Opuntia engelmannii*

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BOWERS, JANICE E. (U.S. Geological Survey, 1675 W. Anklam Road, Tucson, AZ 85745). More flowers or new cladodes? Environmental correlates and biological consequences of sexual reproduction in a Sonoran Desert prickly pear cactus, *Opuntia engelmannii*. Bull. Torrey Bot. Club 123: 34–40. 1996.—Should a platyopuntia expend all areolar meristems in flower production, no new cladodes could be produced, and further reproductive effort and vegetative growth would cease. To investigate the trade-off between flower and cladode production, the numbers of flowers, fruits, and cladodes were monitored for 4 years on 30 *Opuntia engelmannii* Salm-Dyck plants on Tumamoc Hill, Tucson, Arizona. Plant size controlled the number of flowers initiated each spring. The proportion of flowers that developed (i.e., did not abort) was perhaps determined by December–February rainfall in the months before bloom, with more being developed in the wettest years. Models based on different ratios of initiated cladodes to initiated flowers demonstrated that continued high investment in flowers and fruits would eventually terminate reproduction altogether; therefore periods of high sexual reproduction should alternate with periods of high vegetative growth. In the first 3 years of this study, the ratio of new cladodes to initiated flowers was low, showing a high investment in sexual reproduction. As suggested by the model, the population recouped this investment in the fourth year, when the number of new cladodes was nearly 3 times the 1992–1994 mean, and the number of initiated flowers was only 73% of the 3-year mean.

Key words: flower production, fruit production, resource allocation, Sonoran Desert, *Opuntia engelmannii*.

In the Cactaceae, flowers and apical growth originate in specialized axillary buds, the areolar meristems; a meristem can produce either a flower or a cladode, but once it has done so, that meristem cannot be used again (Gibson and Nobel 1986). In many cacti, flowers appear on meristems produced a year or two earlier (subapical meristems); thus reproductive effort in one year depends partly on vegetative growth in the preceding years. For such species, which include the columnar cacti *Carnegiea gigantea* (Engelm.) Britt. & Rose and *Ferocactus wislizenii* (Engelm.) Britt. & Rose, expending all areolar meristems on flower production in one year would not preclude further apical growth the following year. For platyopuntias, which produce most of their flowers and new cladodes from meristems located largely on the upper edge of mature cladodes, this is not the case. If all areolar meristems were to be expended in flower production, no new cladodes could be produced and further reproductive effort and vegetative growth would cease. To survive, therefore, pla-

tyopuntias must maintain a balance between vegetative gains and reproductive output.

Resource allocation in the Cactaceae has been studied at the physiological level (e.g., Nobel 1988), but the specific trade-off between sexual reproduction and vegetative growth has received little attention. For cacti that bloom only once a year and only for a short time, resource allocation is in part a matter of timing. *Carnegiea gigantea* usually flowers 1–2 months before apical growth is initiated (Hastings 1961). As much as 50% of the potential stem growth of a 4- to 5-m-high plant is diverted into reproduction each year (Steenbergh and Lowe 1977), which shows the extent to which the flowers successfully preempt plant resources. In the platyopuntias, many of which produce flowers and new cladodes more or less simultaneously, competition between flowers and cladodes for plant resources might also be intense. Even if this is not the case, the “choice” to produce a new cladode instead of a flower is by default the “choice” to postpone sexual reproduction in favor of having a greater number of areolar meristems the following year.

In general, the amount of photosynthate available for allocation to reproduction and growth increases with plant size. In columnar cacti such as *Carnegiea gigantea* and *Stenocereus thurberi*

¹ Steven P. McLaughlin, Mark A. Dimmitt, and two anonymous reviewers read the manuscript and made many helpful comments.

Received April 17, 1995, and in revised form July 31, 1995.

(Engelm.) Buxb., a common measure of size is plant height, and plant height in turn is a good predictor of reproductive effort and vegetative growth (Steenbergh and Lowe 1977, 1983; Parker 1987, 1988). It is not known if this is also the case for platyopuntias, or whether the number of cladodes would better predict flower and new cladode production.

The goal of this study was to determine the environmental controls of flower and cladode production in a common platyopuntia, *Opuntia engelmannii* Salm-Dyck., and to model the relative proportions of flowers and cladodes needed in successive years to ensure continued reproductive and vegetative growth. Specific questions asked were: 1) Does flower production vary from year to year; 2) How do reproductive and vegetative capacity change with plant size; 3) In a given year, what determines how many flowers and cladodes will be initiated; and 4) Do flowers and new cladodes compete for plant resources?

Methods. **STUDY AREA.** The Tumamoc Hill study site (32°13'N, 111°05'W) is at 814 m above sea level on a gently sloping bench with a northeast aspect. Tumamoc Hill, an outlier of the Tucson Mountains, Pima County, Arizona, has a maximum elevation of 948 m and a basal elevation of 703 m. The rocky, basaltic-andesitic slopes are dominated by *Cercidium microphyllum* (Torr.) Rose & Johnst., *Carnegiea gigantea*, *Larrea tridentata* (DC.) Cov., *Fouquieria splendens* Engelm., *Ambrosia deltoidea* (A. Gray) Payne, *Opuntia engelmannii*, and other woody plants characteristic of the Arizona Upland division of the Sonoran Desert. Annual rainfall averages 250 mm, almost half of which falls during July, August, and September. Maximum temperatures in summer frequently exceed 40°C. Minimum temperatures rarely drop below -6°C in winter. Although freezing nights can be common in winter, daytime temperatures always rise above 0°C.

PLANT SAMPLING. A group of 30 *Opuntia* plants was selected in March 1992 by walking across a gentle, north-facing slope and tagging cacti as they were encountered until there were approximately equal numbers of plants in each of four size classes (1-10 cladodes, 11-30 cladodes, 31-50 cladodes, and >50 cladodes). Plant size (number of cladodes at the start of the growing season) was determined for each. The first 17 plants encountered were monitored in-

tensively to determine whether production of flowers, fruits, and new cladodes changed as active cladodes aged from year to year. The other 13 plants provided supplementary information on the relation between production and plant size.

For each of the 13 plants in the second group, the number of cladode buds, flower buds, flowers, fruits, and new cladodes was recorded every week from the initial appearance of buds in early March to the ripening of fruits in mid-July. As buds matured into flowers and flowers ripened into fruits, a strict accounting of gains and losses was kept for each plant to minimize the risk of double-counting from week to week. Fruits were considered "set" when petals had abscised and ovaries appeared plump. Flower buds, flowers, and immature fruits were classified as aborted when they shriveled or abscised. Due to heavy predation, presumably by peccaries, coyotes, and rodents, it was not possible to obtain meaningful counts of ripe fruits; therefore, number of fruits set was used in the data analyses. The same plants were censused again in the spring and summer of 1993, 1994, and 1995.

On each of the 17 plants selected for cladode-by-cladode monitoring, every cladode that produced buds was numbered consecutively with a marking pen. Throughout the 1992 growing season, production of cladode buds, flower buds, flowers, fruits, and cladodes was recorded for each numbered cladode on a weekly basis. Again, a balance sheet was employed to tally gains and losses. Plant height was measured in March 1992. In 1993 and 1994, the monitoring process was repeated, numbering new cladodes in such a way as to distinguish them from those of previous years. In 1993 individual flowers were marked with the week of anthesis (first, second, third, etc.). When number of fruits appeared to be at a maximum for the entire population, a census was made to determine how many fruits were produced from flowers of the first week, how many from the second week, and so forth. In 1995, buds, flowers, and new cladodes were counted weekly for these 17 plants on an individual basis but not on a cladode-by-cladode basis.

To determine whether cladode production diverted resources from flower and fruit production, all newly developing cladodes were removed from 10 *Opuntia* plants in April 1992. (These plants were not in the group of 30 described above.) Each treated plant was matched with a control that had approximately the same

Table 1. Results of the linear regressions. Plant size was expressed as the number of cladodes at the start of the growing season. Regressions of plant height used 1992 data. In all other regressions, the variables represent 4-year means (1992–1995).

Independent variable	Dependent variable	R^2	Sample size
Plant height (cm)	Flowers initiated	0.48 ^a	15
Plant height (cm)	Cladodes initiated	0.53 ^a	15
Plant size	Plant height (cm)	0.75 ^b	15
Plant size	Flowers initiated	0.90 ^b	26
Plant size	Flowers developed	0.83 ^b	26
Plant size	Fruits initiated	0.83 ^b	26
Plant size	Fruits developed	0.79 ^b	26
Plant size	Cladodes initiated	0.83 ^b	26
Plant size	Cladodes developed	0.83 ^b	26
Plant size	Percent aborted flowers	0.03 ^c	26

^a $P < 0.005$.

^b $P < 0.001$.

^c $P > 0.375$.

number of cladodes. No cladodes were removed from the controls. Every week during the growing season, number of buds, flowers, fruits, and new cladodes was recorded for treated plants and controls.

DATA ANALYSIS. The 4-year average was calculated for number of flowers, fruits, and cladodes initiated, and for number of flowers, fruits, and cladodes developed. Developed flowers were defined as those remaining after abortion of flower buds and open flowers. All ovaries that set fruit were considered to be developed fruits. Developed cladodes were defined as those that remained as of the sixth week of observation, at which time they were fully expanded and had lost their ephemeral leaves. Flower success, fruit success, and cladode success were calculated as the ratio of the number of parts that developed to the number that were initiated. Four plants that died or became moribund during the study were omitted from these calculations and from the following analyses.

To examine the relationship between plant size and reproductive effort, average number of old cladodes during 4 years was used as the independent variable in linear regressions against number of flowers (initiated or developed), number of fruits (initiated or set), and flower success. Number of old cladodes was also used as the independent variable in linear regressions against number of new cladodes and number of meristems used per cladode. Plant height was regressed against number of flowers and cladodes initiated in 1992 and against number of old cladodes in 1992. Analysis of variance was used to determine if number of cladodes or flowers differed significantly among years. A paired *t*-

test was used to examine the difference between the 10 treated plants (new cladodes removed) and their controls.

Results. Plants ranged in height from 16.5 cm to 157 cm. Plant size, that is, number of cladodes at the start of the growing season, and plant height were highly correlated (Table 1). Linear regression demonstrated that plant height was not as predictive of flower production as plant size (Table 1). Plant size was also a better predictor than plant height of new cladode production (Table 1). A high proportion of the variance in new cladode, flower, and fruit production was explained by plant size (Table 1). The proportion of flowers aborted in a given year was not related to plant size (Table 1). On average, 14% of flower buds aborted before anthesis each year.

Analysis of variance showed that plant size did not change significantly during the 4 years of this study ($F = 0.242$, $P > 0.80$), nor were there significant differences among years in aborted flowers and flower buds ($F = 1.333$, $P > 0.20$), initiated flowers ($F = 0.695$, $P > 0.50$), developed flowers ($F = 1.507$, $P > 0.20$), initiated fruits ($F = 1.50$, $P > 0.20$), and developed fruits ($F = 1.468$, $P > 0.20$) (Table 2). Flower and cladode success (number developed/number initiated) were significantly lower in 1994 than in the other three years (flower success: $F = 11.313$, $P < 0.001$; cladode success: $F = 19.136$, $P < 0.001$) (Fig. 1). Fruit success in 1995 was significantly higher than in 1992, 1993, and 1994 ($F = 8.40$, $P < 0.001$) (Fig. 1). At peak flower, most cladodes in the population produced only a few flowers (Fig. 2). Week of anthesis had little effect on proportion of fruits

Table 2. Annual production of flowers, fruits, and cladodes for 26 *Opuntia engelmannii* plants.

	1992 Mean (SE)	1993 Mean (SE)	1994 Mean (SE)	1995 Mean (SE)	4-Year average (SE)
Old cladodes	31.5 (5.78)	36.0 (6.24)	37.6 (6.44)	38.2 (6.25)	35.8 (6.15)
Cladodes initiated	6.7 (1.01)	5.7 (1.22)	10.9 (2.15)	23.9 (4.04)	11.8 (1.70)
Cladodes developed	6.2 (0.94)	4.5 (1.14)	4.9 (1.27)	22.3 (3.95)	9.5 (1.47)
Flowers initiated	42.3 (12.60)	42.6 (12.21)	28.8 (6.59)	27.6 (16.05)	35.4 (8.83)
Flowers developed	34.7 (10.57)	28.1 (8.49)	13.0 (3.43)	23.7 (5.26)	24.8 (6.26)
Fruits initiated	34.7 (10.55)	27.8 (8.51)	12.9 (3.45)	23.5 (5.22)	24.7 (6.24)
Fruits developed	22.4 (8.13)	17.7 (6.15)	6.8 (2.29)	21.0 (5.05)	17.0 (4.70)

set. All flowers that opened during the first week set fruits. For flowers of the second through fifth weeks, the ratio of fruits set to flowers initiated was 0.87, 0.76, 0.71, and 0.80, respectively.

Cladodes of different ages varied consider-

ably in flower production. No cladodes produced flowers or new cladodes before the age of ca. 1 year. At peak flower on April 17, 1994, 71% of all flowers occurred on 1- or 2-year-old cladodes. Older cladodes accounted for the remain-

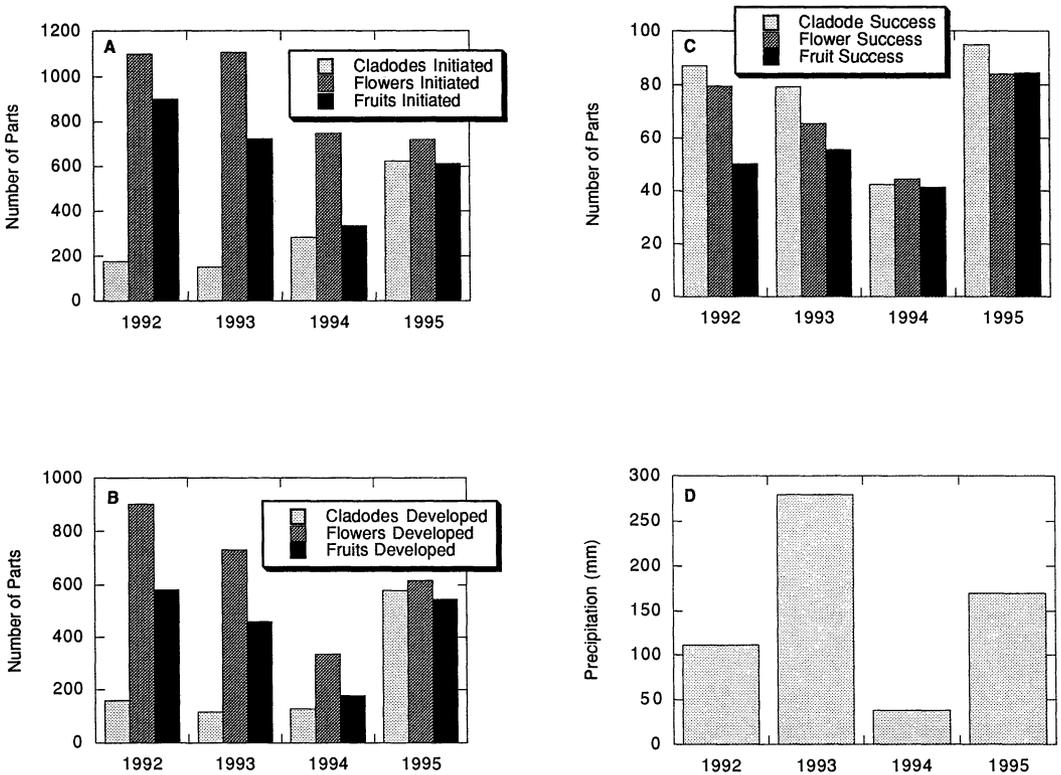


Fig. 1. A. Numbers of flowers, fruits, and cladodes initiated in 4 consecutive years. B. Numbers of flowers, fruits, and cladodes developed in 4 consecutive years. C. Flower, fruit, and cladode success in 4 consecutive years. Success was calculated as the ratio of number developed to number initiated. D. December–February precipitation in 4 consecutive years.

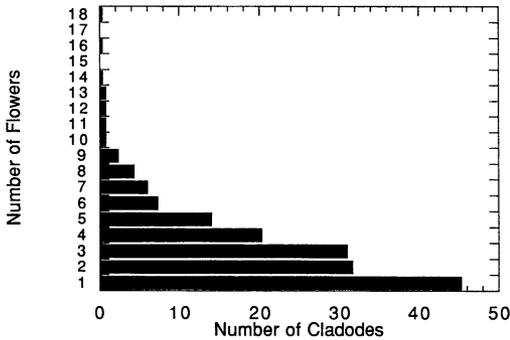


Fig. 2. Frequency distribution of number of flowers per pad at peak flower. Values represent 3-year mean of 12 individuals (1992–1994).

ing 29%. In 1994, the average number of flowers produced on 1-year-old cladodes was 4.4, on 2-year-old cladodes, 2.3. The average number of meristems put into production (including flowers and new cladodes) per cladode per year was rather low (Fig. 3). For the 17 plants that were monitored on a cladode-by-cladode basis, the number of meristems “used” per cladode increased with plant size (Fig. 3) ($R^2 = 0.59$, $P < 0.001$).

In the cladode-removal experiment, 57% of the initiated flowers on treated plants set fruits. Forty-two percent of initiated flowers set fruits on the control plants. The difference was not significant ($t = 1.434$, $P > 0.18$). Before cladode removal, the number of original cladodes did not differ significantly between treated plants and controls ($t = 0.667$, $P > 0.51$). It cannot be shown that flowers and new cladodes compete for plant resources.

Discussion. One key to understanding inter-annual variation in flower and cladode numbers in *Opuntia engelmannii* is the environmental or biological triggers for bud production. Because the number of flowers initiated did not differ significantly among the 4 years of this study, it would seem that intrinsic rather than extrinsic factors control the initial number of flower buds. The most likely is plant size; number of old cladodes and number of flowers initiated are highly correlated.

Two observations suggest that extrinsic rather than intrinsic factors control flower bud and flower abortion. First, the proportion of aborted flower buds and flowers was not related to plant size. Second, in some species, open flowers abort because they function as pollen donors (for reviews, see Sutherland and Delph 1984; Suth-

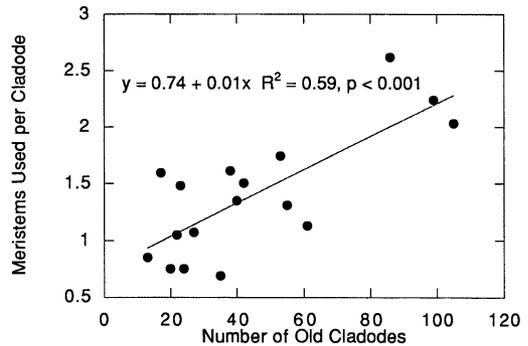


Fig. 3. Number of meristems used as a function of plant size. Values represent 3-year mean of 17 individuals (1992–1994).

erland 1986) or because of inadequate pollination, but in this study, flower buds commonly abscised before either pollen donation or pollination was possible. This suggests that the plants assessed at an early phenological stage whether the current environment could provide enough resources to develop all buds initiated.

Because agronomic work on *Opuntia ficus-indica* (L.) Miller has shown that flower and fruit production respond positively to supplementary irrigation (Barbera et al. 1992), it seemed possible that soil moisture might determine the proportion of *O. engelmannii* flowers that can develop. In the 4 years of this study, flower and cladode success did not vary significantly in the 3 wet years (1991–92, 1992–93, and 1994–95), but in the single dry year (1993–94), both were significantly lowered. Fruit success was significantly higher in 1995 than in the other years, perhaps because predation by lepidopteran larvae was negligible in 1995.

From the limited data available, December–February rainfall seems to be critical in determining flower and cladode success. Unpublished field notes document notably poor flower of *Opuntia engelmannii* on Tumamoc Hill in the springs of 1986 and 1989 (pers. observ.). In 1986, 1989, and 1994, Dec.–Feb. rain was 53.2 mm, 19.6 mm, and 37.9 mm, respectively. In 1992, 1993, and 1995, years of good spring flower, Dec.–Feb. rain was 111.3 mm, 279.2 mm, and 170 mm, all substantial increases. These comparisons emphasize the extent to which cacti depend upon moisture of the current growing season.

In sum, it appears that plant size controls the number of flowers initiated and that Dec.–Feb. rainfall affects the proportion of flowers that can develop. Burgess and Shmida (1988) have point-

ed out that cacti and other succulents are rare in extremely arid regions. Most occur in warm semideserts where annual precipitation ranges from 150–400 mm (Burgess and Shmida 1988). The distribution of *Opuntia engelmannii* at the upper margins of the Sonoran Desert and the lower margins of desert grassland suggests a reliance on moister climates within a generally arid region (Turner et al. 1995). The need for extra moisture to maintain an adequate reproductive level might explain in part why this is the case.

Whether a meristem produces a flower rather than a cladode or vice versa is a problem in resource allocation. Because the areolar meristems of *Opuntia engelmannii* and other platyopuntias are apical rather than subapical, too large an investment in sexual reproduction would bring all cladode production to a halt, and, conversely, an overemphasis on vegetative growth could eventually reduce sexual reproduction to the point where populations could no longer replace themselves. The fact that *Opuntia engelmannii* continues to exist as a sexually reproducing species indicates that the plants adjust the relative proportions of new cladodes and flowers from year to year. Various ratios of productivity bear this out. For instance, the annual ratio of cladode buds to flower buds was 0.16 and 0.14 in 1992 and 1993, both years of relatively high flower production, whereas in 1994 and 1995, years of lower flower production, the ratios were 0.41 and 0.87. The proportion of new cladodes relative to plant size also varied, from 0.16 in 1993 to 0.63 in 1995.

The short-term effects of different new-cladode-to-flower ratios were modeled for *Opuntia* no. 23, a large and productive plant. The new-cladode-to-flower ratios used were the average 1992–1993 ratio (0.15) and the 1994 ratio (0.41). By projecting these ratios for several consecutive years into the future, it was possible to determine the effect of each ratio when it was repeated year after year.

The model plant chosen averaged 123 cladodes in size and produced an average of 33 new cladodes annually. In year₀, this plant was assumed to have at its disposal 33 meristematically active cladodes from previous years. It was further assumed that in each model year, this plant “used” 3 meristems on every active cladode, a reasonable estimate for a plant of this size (Fig. 3). The total number of meristems used in year₀, therefore, was 99. Assuming a new-cladode-to-flower ratio of 0.15, 84 of these meristems were

Table 3a. The effect of a 0.15 new-cladode-to-flower ratio on numbers of cladodes and flowers produced on a large *Opuntia engelmannii* plant. The individual is assumed to be 123 cladodes in size and to produce 33 new cladodes in year₀. In each successive year, every new cladode puts 3 meristems into flower and cladode production according to the proportions dictated by the 0.15 ratio. The number of new cladodes produced in one year become the number available for flower and cladode production in the following year.

	New cladodes produced	Total meristems produced	Meristems devoted to flower production	Meristems devoted to cladode production
Year ₀	33	99	84	15
Year ₁	15	45	38	7
Year ₂	7	21	18	3
Year ₃	3	9	8	1
Year ₄	1	3	3	0

devoted to flowers that year, and only 15 were used for new cladodes. In year₁, these 15 meristematically active cladodes produced 45 new meristems, of which 7 went to new cladodes and 38 went to flower production, as dictated by the 0.15 ratio. In successive years, the number of new cladodes added annually continued to decrease, steadily lowering the number of meristems available for either flowers or new cladodes (Table 3a). By year₄, the plant had no active meristems left. Thus, the short-term effect of a low new-cladode-to-flower ratio was to deprive the plant of future opportunities for vegetative growth and sexual reproduction alike.

Table 3b shows the effects of a new-cladode-to-flower ratio of 0.41 for the same plant. Under this scenario, the number of new cladodes in-

Table 3b. The effect of a 0.41 new-cladode-to-flower ratio on numbers of cladodes and flowers produced on a large *Opuntia engelmannii* plant. The individual is assumed to be 123 cladodes in size and to produce 33 new cladodes in year₀. In each successive year, every new cladode puts 3 meristems into flower and cladode production according to the proportions dictated by the 0.41 ratio. The number of new cladodes produced in one year become the number available for flower and cladode production in the following year.

	New cladodes produced	Total meristems produced	Meristems devoted to flower production	Meristems devoted to cladode production
Year ₀	33	99	58	41
Year ₁	41	123	73	50
Year ₂	50	150	88	62
Year ₃	62	186	110	76
Year ₄	76	228	166	116
Year ₅	116	348	205	143

creased every year. This resulted in an ever-larger supply of meristems, which in turn allowed continued production of both flowers and new cladodes (Table 3b). Obviously, if the 1995 ratio (0.87) had been used instead, the supply of meristems would have increased even more.

The models demonstrate that continued high investment in flowers and fruits would eventually terminate reproduction altogether, therefore periods of high sexual reproduction should alternate with periods of high vegetative growth. On the basis of 4 years of data, it appears that this is indeed the case. In 1992, 1993, and 1994, flower production greatly exceeded cladode production. For the population to maintain its reproductive capacity, this situation had to be reversed eventually, which is what happened in 1995, when the number of new cladodes was nearly 3 times the 1992–1994 mean, and the number of initiated flowers was only 73% of the 3-year mean. The alternation between periods of high flower and cladode success did not seem to be correlated with precipitation (Fig. 1). Additional years of observation are needed to clarify the role of climate, if any.

The physiological process that allows annual adjustment of cladode and flower production is unknown. Presumably, the plants can assess the type of structure needed based on resource expenditure in the previous year. This process may be analogous to the ability of certain monoecious species such as *Atriplex canescens* (Pursh) Nutt. to alter the ratio of male to female flowers on a single plant and in a given population based on seed production of the previous year (McArthur and Freeman 1982).

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