

## Factors limiting fecundity of the tropical tree *Ipomoea wolcottiana* (Convolvulaceae) in a Mexican tropical dry forest

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**ABSTRACT.** To explain very low fruit production in the tropical tree *Ipomoea wolcottiana* (Convolvulaceae), experiments and observations are presented regarding hypotheses that fecundity is limited by foliar herbivory, low soil phosphorus, inadequate cross-pollination, low rates of pollinator visitors, and parasitism of flower buds. A 2 × 2 factorial experiment was undertaken in two consecutive years which included control of herbivores with contact and systemic insecticides and addition of phosphorus. Phosphorus application in the second year increased the number of inflorescences and flowers by 200%, and the initiation of fruits by 400%. No response was observed for the number of mature fruits. Herbivore control and the addition of phosphorus increased seed weight by 22% in the first year, but could not be measured in the second year. Hand-pollination experiments increased the fruit set by 58% in the first year and by 75% in the second. Observations on visits to the flowers showed a six-fold difference between years in rates of pollinator visits. Parasitism of flower buds was 18% in the first year and 33% in the second. Several of the differences between years probably resulted from lesser and desynchronized flowering, due to heavy unseasonal rains in the second year. The differences in floral visitation and predation of floral buds were reflected in open fruit production: 16% in the first year and 6% in the second. All the factors investigated have important effects on the fecundity of *I. wolcottiana*. From the evolutionary point of view, the results suggest a complex interaction among selective forces which interact with the reproductive system. The theories of sexual selection and bet-hedging are the most plausible alternatives for explaining high levels of floral abortion in this species.

**KEY WORDS:** bet-hedging, herbivory, México, pollination, reproductive success, resource limitation, sexual selection, tropical trees

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## INTRODUCTION

In many hermaphroditic plant species it is commonly observed that the proportions of ovaries which form fruits and of ovules which form seeds are very low (Charlesworth 1989, Stephenson 1981, Sutherland 1986). There is also great variation among species in their degree of reproductive success (Herrera 1991, Wiens 1984). Proximal or ecological hypotheses have been proposed to explain the high levels of abortion of sexual reproductive structures (i.e. flowers, ovaries, fruits and seeds) and the limitation of fecundity in these plants. The main hypotheses are resource limitation (Janzen *et al.* 1980, Ackerman & Montalvo 1990); predation of flowers, fruits and seeds (Heithaus *et al.* 1982); lack of effective pollination (Bierzychudek 1981); and some environmental effects such as the water availability and level of nutrients in the soil (Ayre & Whelan 1989, Vaughton 1991).

Another series of hypotheses considers ultimate or evolutionary causes, based on the idea that the apparent overproduction of ovules and flowers is an adaptive response to various selective pressures (Lloyd 1980, Stephenson 1981). The pollinator-attraction hypothesis states that greater floral display increases both the rate of visitation and the amount of pollen received per-flower (Schemske 1980). The sexual selection hypothesis states that increased numbers of flowers serve the male function of pollen donation more than the female function of seed maturation (Willson 1979), although male competition may also increase the opportunities for selective abortion of genetically inferior seeds (Bawa & Webb 1984, Stephenson & Bertin 1983). Finally, the 'bet-hedging' hypothesis considers that high production of ovules and flowers allows plants to take advantage of unpredictable increases in resources or variation in other limiting factors (Ayre & Whelan 1989, Koslowski & Stearns 1989).

Regarding the ecological hypotheses, empirical and experimental evidence, and theory, indicate that various factors may act together to determine fecundity, although not necessarily at the same level of response (Copland & Whelan 1989, Haig & Westoby 1988). In spite of such evidence, there have been few experimental evaluations in natural conditions of more than one factor at a time, or their temporal variation. Moreover, most studies have focused on herbs or shrubs, and very few on tropical trees (Bullock & Bawa 1981, House 1992, Koptur 1984), although different life forms are likely to show many differences in reproductive strategies (Ramírez 1993).

Here we report the results of a 2-y study designed to evaluate ecological factors that might affect low fruit production in a population of the tropical tree *Ipomoea wolcottiana* Rose (Convolvulaceae). We considered several potential causes for low female success in this species: low levels of available phosphorus in the soil of the study site (Lerdau *et al.* 1991), high levels of herbivory on the leaves (Fillip *et al.* 1995), high levels of parasitism of the flower buds (V. Parra-Tabla & S. H. Bullock, *pers. obs.*), and the low effectiveness of pollinators

(Bullock *et al.* 1987). We evaluated all these potential causes and discuss the implications of our results for the evolutionary hypotheses.

#### METHODS

##### *Study site and species*

The study was conducted at Estación de Biología Chamela, a facility of the Universidad Nacional Autónoma de México located near the Pacific coast in the state of Jalisco (105°03'W, 19°30'N) at elevations between 30 and 110 m. Average total annual rainfall at the site was 707 mm (1977–1988), with 80% falling between July and October. Mean annual temperature was 24.9 °C. Vegetation of the site is predominantly tropical deciduous forest (Lott *et al.* 1987).

At Chamela, *Ipomoea wolcottiana* grows to heights of > 12 m, but is only common in areas of natural or human disturbance. It flowers in the dry season, usually in January–February, while leafless. Unusual rains in these months can desynchronize the population and reduce overall flowering (Bullock & Solís-Magallanes 1990), as occurred in 1992 during this study. The trees have large white self-incompatible flowers. Anthesis of most flowers usually starts at midnight and they remain open until noon; during anthesis flowers produce pollen and have receptive stigmas for *c.* 12 h (Bullock *et al.* 1987). Although flowers contain four ovules, only three seeds develop to maturity within the dry dehiscent fruits (Bullock *et al.* 1987).

##### *Herbivory and addition of phosphorus*

A factorial experiment was designed to evaluate the separate and joint effects of foliar herbivory and increased soil fertility on plant production. With and without treatments were established in each case: applications of insecticide and addition of phosphorus. Forty trees were marked along trails and roadways in the Estación de Biología, and 10 trees were assigned at random to each treatment. The selection criteria included similarity of conditions of slope and tree size. We used the same trees in both years. The trees were marked for repeated measurements of trunk diameter (DBH), which were used to calculate an index of relative growth rate ( $[\text{final DBH} - \text{initial DBH}] / \text{initial DBH}$ ). There were no significant differences among treatments in initial DBH (ANOVA,  $F = 0.38$ ;  $df = 3, 36$ ;  $P > 0.5$ ).

Ten branches of each tree were marked at different levels of the crown and the following variables were registered in each branch: number of inflorescences, number of flowers, number of fruits initiated and number of mature fruits. A weekly check of branches was carried out throughout the flowering and fruiting seasons of 1991 and 1992.

Seed weight was also measured in the first year, based on individually weighed seeds of 15–30 mature fruits per tree. Fruiting was too sparse in the second year to give an adequate sample size.

Foliar herbivory was controlled by the combined use of two types of insecticide: Metasistox®, an intralaminar or systemic insecticide that eliminates leaf miners, and Folidol®, a contact insecticide that acts on lepidopteran larvae. Fifteen ml of each insecticide were diluted in 10 l of water and sprayed on the marked branches at intervals of 20–25 d when the trees had leaves (between July and November 1990 and 1991). To evaluate the effectiveness of this method, herbivory was recorded on either at least 100 leaves or all the remaining leaves of each tree (less than 100) at the end of the rainy season. Herbivore damage was visually estimated as holes, spots, bites and other superficially evident physical disruption. A single observer recorded damage using the following categories: 0, no damage; 1,  $\leq 5\%$  of leaf area damaged or removed; 2, 6–10; 3, 11–25; 4, 26–50; 5, 51–75; and 6, 76–100%. An index of damage (ID) was calculated as:  $ID = [(\sum n_i)(n_i)]/N$  where  $n_i$  = number of leaves in damage category  $i$  and  $N$  = number of leaves sampled.

The addition of phosphorus was made once at the beginning of each rainy season (1990 and 1991). Superfosfato Triple FERTIMEX® was applied in dry form to the soil surface within a radius of *c.* 2.5 m around the trunk at the rate of 500 g per tree, equivalent to *c.* 255 kg ha<sup>-1</sup>. Previous experiments with superphosphate at Chamela showed that an addition of 250 kg ha<sup>-1</sup> increased available phosphorus by more than a factor of three (Jaramillo & Maass 1993). We did not select nitrogen or potassium as potential experimental variables as previous observations have shown that these nutrients are in high quantities in the study site (Jaramillo & Sanford 1995).

#### *Manual pollination experiment*

Limitation of matured fruit production by compatible pollination was evaluated with a manual pollination experiment. Twenty flowers were marked on each of five selected trees. Marked flowers were distributed among three branches, half were pollinated by hand with pollen from at least three distant trees, and the other 10 were left for open pollination. Hand-pollinated flowers were bagged to exclude subsequent visitors. All the flowers/fruits were observed weekly until abortion or maturation. Although this experiment was carried out in both years, it was not possible to use more than two of the same individuals due to the disruption of normal phenology by unusual rains in the second year. This experiment and the following observations were made on different trees to those used for the herbivory and phosphorus-addition experiment.

#### *Rate of flower visitation*

The number of visits per flower was counted during the peak of the flowering period in both years. On five consecutive days two trees were observed per day (10 trees in total), alternately for 15 min, with 5 min between periods, between 06h00 and 13h00. Since preliminary observations after 2200 h on three nights yielded only two visits, nocturnal observations were discontinued and were not

used in calculating floral visitation rates. Total and legitimate visits (i.e. involving contact with the reproductive structures) of 8–10 closely selected flowers, were counted from observation at a distance of <1 m mounted on a 3-m ladder so that the observer stood *c.* 5 m high. The close proximity did not distract or make the bees go further away. Different trees were used each day. Trees were chosen taking into account their relative isolation (to avoid attraction of visitors by neighbours), similarity in number of flowers and accessibility of the branches. Observations were made in January of the first year (1991), and in March of the second year (1992), when flowering occurred.

#### *Parasitism of flower buds*

Parasitism of flower buds by insect larvae was estimated from 100 buds taken from each of 10 trees chosen at random. Different trees were used in the two years. The buds were fixed in formalin-acetic acid-alcohol (3:1:1) and later dissected under a microscope (10 $\times$ ), noting the presence or absence of larvae.

## RESULTS

#### *Herbivory and addition of phosphorus*

Herbivory on leaves was significantly reduced with the use of insecticides, with and without phosphorus addition, in 1991 and 1992; the index of damage was *c.* 6-fold less in sprayed trees (Table 1).

Table 1. Indices of *Ipomoea wolcottiana* leaf damage (mean  $\pm$  SE) in a tropical dry forest of Chamela, western México. The z-value is presented for comparison between treatments using the normal approximation of the Mann-Whitney U-test (Zar 1984).

	n	Year	
		1990	1991
Trees with insecticides	20	0.033 $\pm$ 0.0055	0.0365 $\pm$ 0.0058
Trees without insecticides	20	0.199 $\pm$ 0.0085	0.191 $\pm$ 0.0064
z		3.87 P < 0.01	3.86 P < 0.01

Treatments affected measures of fecundity in different ways in the two years (Table 2). In 1991, significant effects of control of herbivory and phosphorus addition and their interaction were detected only in seed weight. The interaction between these factors increased seed weight by 22.5% (Figure 1). In 1992, the addition of phosphorus increased the total number of inflorescences and flowers more than 2-fold, and the total number of initiated fruits 4-fold (Figure 2). Control of herbivory in 1992 increased the total number of flowers more than 2-fold (Figure 2). No significant effects on the total number of mature fruits (Table 2, Figure 2) or relative growth in DBH in either year were detected (Table 2).

#### *Experimental pollination*

There were significant differences between manual pollination and open pollination in both years (Table 3). The mean increase in fruits matured was

Table 2. Variance-ratio (F) statistics from factorial analysis of variance for the addition of phosphorus and control of leaf herbivory with insecticide in *Ipomoea wolcottiana* in a tropical dry forest of Chamela, western México. (Df = 1, 36 for each factor in all cases.)

Variable	Year	Factors		
		Phosphorus	Insecticide	Interaction
Relative trunk diameter growth rate (cm)	1991	1.5	0.5	2.01
	1992	0.5	0.9	0.4
Seed weight (mg)	1991	8.8***	16.6***	22.3***
	1992	–	–	–
Number of inflorescences	1991	1.5	0.50	2.01
	1992	8.8***	0.94	0.01
Number of flowers	1991	1.84	1.62	0.49
	1992	5.26**	4.13*	0.31
Number of initiated fruits	1991	0.46	0.67	1.37
	1992	4.9**	1.5	2.74
Number of mature fruits	1991	1.86	1.67	0.5
	1992	0.53	1.52	0.02

\*P = 0.05, \*\*P < 0.025, \*\*\*P < 0.01

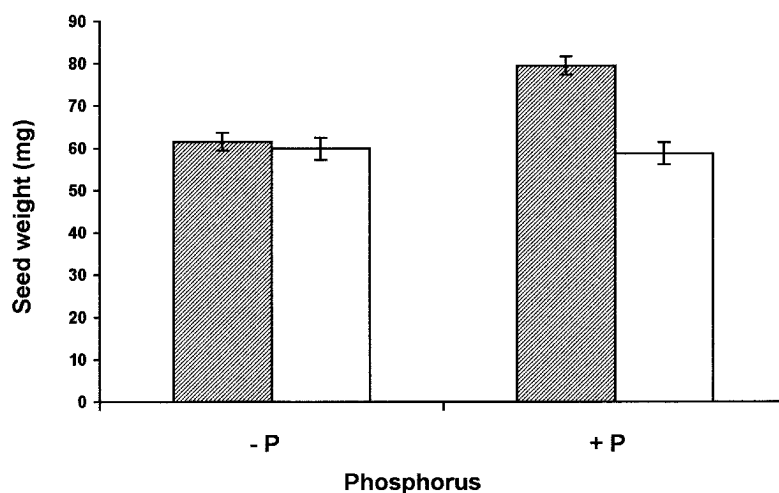


Figure 1. Seed weight variation (mg) of *Ipomoea wolcottiana* in a tropical dry forest of Chamela, western México, with addition of phosphorus and control of leaf herbivory with insecticides. Means  $\pm$  SE are presented. Open bars, no insecticide; hatched bars, treatment with insecticide. (See Table 2 for statistics.)

58% in the first year and 75% in the second. Also, there was a significant difference between years in the production of fruits by open pollination ( $t = 3.16$ ,  $df = 18$ ,  $P < 0.01$ ), with the first year exceeding the second by over 70.5% (Table 3).

#### *Rate of flower visitation*

The mean observed number of total and legitimate visits per flower per minute were almost 5-fold higher in 1991 than in 1992 (Table 4). There were

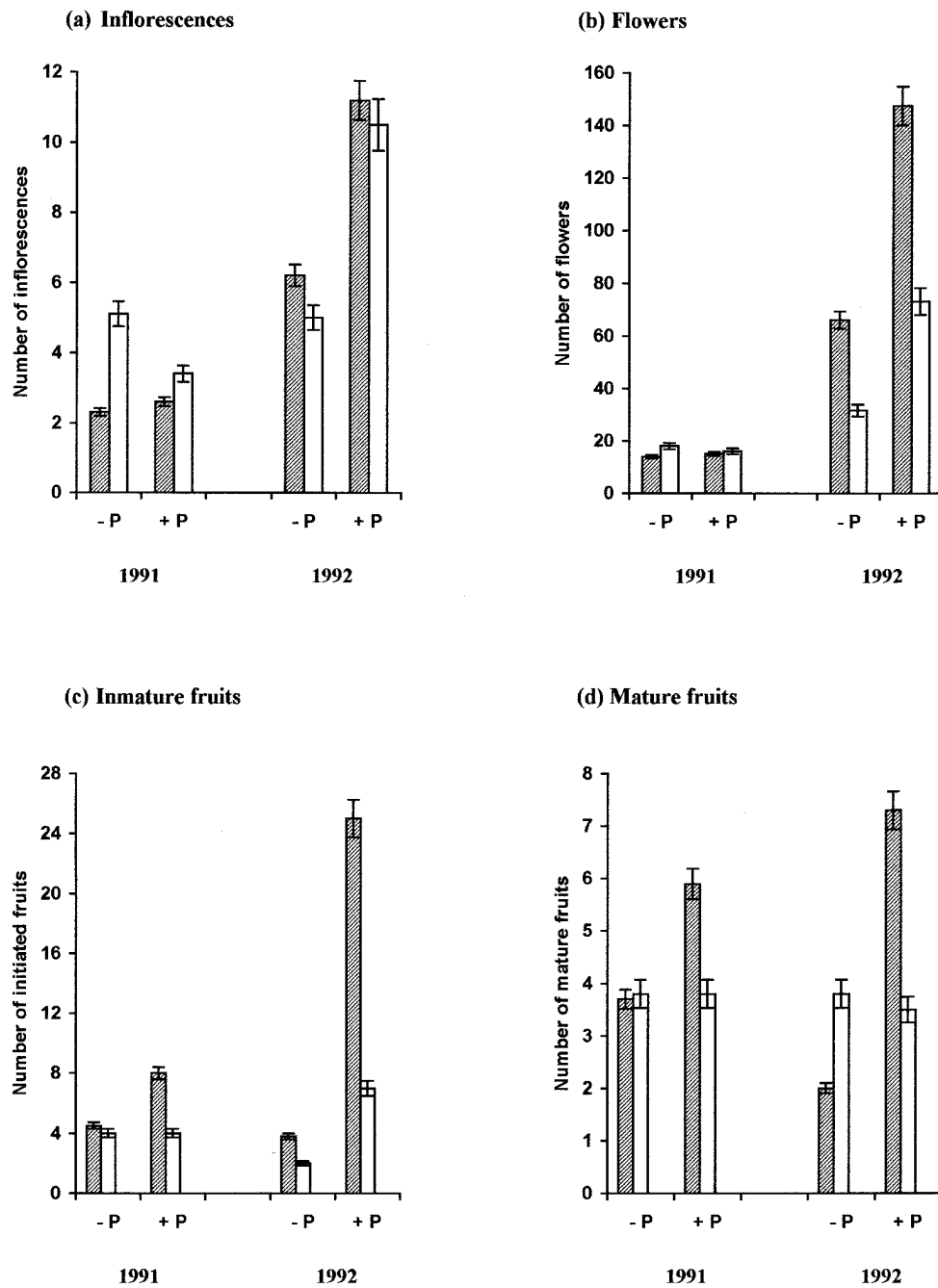


Figure 2. Variation in (a) total number of inflorescences, (b) total number of flowers, (c) total number of initiated fruits and (d) total number of mature fruits, for *Ipomoea wolcottiana* trees in a tropical dry forest of Chamela, western México, with addition of phosphorus and control of leaf herbivory with insecticide in a tropical dry forest of Chamela, western México. Means  $\pm$  SE are presented for 1991 and 1992. Open bars, no insecticide; hatched bars, treatment with insecticide. (See Table 2 for statistics.)

Table 3. Percentage of *Ipomoea wolcottiana* flowers producing mature fruits by open pollination and by manual cross-pollination (mean  $\pm$  SE) in a tropical dry forest of Chamela, western México. Statistics were made on arcsine-transformed data with the Freeman-Tukey modification (Zar 1984).

	Year			
	n	1991	n	1992
Open pollination	50	16.0 $\pm$ 1.42	50	6.0 $\pm$ 1.13
Manual pollination	50	38.0 $\pm$ 1.13	50	24.0 $\pm$ 1.42
Paired-t		2.77*		3.05*

\*P < 0.05.

Table 4. Mean ( $\pm$  SE) of the total number of visits and number of legitimate visits per minute to flowers of *Ipomoea wolcottiana* in a tropical dry forest of Chamela, western México.

	Year				t-test
	1991	n	1992	n	
Total visits	1.52 $\pm$ 0.43	10	0.308 $\pm$ 0.51	10	8.24**
Legitimate visits	0.012 $\pm$ 0.005	10	0.0021 $\pm$ 0.0004	10	2.02*

\*P < 0.05, \*\*P < 0.01.

no notable differences in species of visitors: the most common and legitimate visitors in both years were *Xylocopa mexicanorum* and *X. tabaniformis* (Anthophoridae), while the frequent but not legitimate ones were *Melissodes tepaneca* (Anthophoridae) and *Partamona bilineata* (Apidae). The proportion of legitimate visits was very low in 1991 (0.78%) and 1992 (0.68%) although such values represented averages of 5.04 and 0.882 legitimate visits per flower per day, respectively (Table 4).

#### *Parasitism of flower buds*

Flower buds were parasitized by larvae of *Phytodectoidea quaturdecimpunctata* (Coleoptera: Chrysomelidae). A significant 2-fold difference between the relatively high percentages of parasitized buds of 1991 (18%  $\pm$  3.3 SE) and 1992 (33.5%  $\pm$  4.3  $\pm$  SE) was found ( $t = 2.161$ ,  $df = 18$ ,  $P < 0.05$ ; arcsine-transformed data).

## DISCUSSION

#### *Resource limitation*

Through experiments with addition of phosphorus and control of foliar herbivory, this study has shown that resource limitation is important in the production of reproductive structures in *Ipomoea wolcottiana*. Overall, the results suggest that phosphorus may be the more important factor limiting reproduction in this population, but the differences between years indicate that other factors may be involved. Foliar herbivory plays a lesser but nevertheless significant role.

The difference in response between the two years is notable. Trees with



additional phosphorus did not respond in the first year with either an accumulation of biomass (DBH) or a greater number of reproductive structures. This is probably attributable to the trees allocating available phosphorus to other structures, such as leaves and roots, as has been observed in trees of *Clusia trochiformis* Vesque and *Weinmannia glabra* L. in similar experiments (Tanner *et al.* 1990). The notable gain in seed weight was significant (12% with phosphorus alone or 22% with phosphorus and insecticides combined) indicating that the trees were able to respond rapidly to added nutrition. There is evidence that seed weight in some species is very sensitive to defoliation or nutrient deficiency (Bentley *et al.* 1980, Willson & Price 1980). It has been reported that plants in nutrient-poor environments allocate proportionally more resources to seed weight (Fenner 1986), and that seed weight is important to success, being positively correlated with the probability of germination and establishment in many species (Jurado & Westoby 1992). In *Ipomoea wolcottiana* the quality of the seeds may be one of the most important factors in reproductive success, because it shows the most immediate response to increased resource availability (but see Westoby *et al.* 1992).

However, it is not clear why the trees did not respond in other components of reproduction in the first year but did so in the second. The latter shows the importance of other variables (e.g. water availability). Perhaps the extra resources were allocated to non-reproductive functions in the first year. In this regard, the physiological origin of the increase in seed weight is unknown. Other experiments with phosphorus fertilization at Chamela have demonstrated increased phosphorus concentration in leaves of various tree species (Jaramillo & Maass 1993). In that study and others (Tanner *et al.* 1990, Tanner *et al.* 1992) it has been suggested that response to phosphorus in leaf and stem growth can appear long after the application. In *Ipomoea wolcottiana*, the addition of phosphorus and the control of herbivores did not affect trunk growth in the 2 y studied, but further years of observation might show significant effects. In contrast, the response in various reproductive features was already apparent by the second year (see also McMaster *et al.* 1982, Vaughton 1991).

#### *Limitation by pollen compatibility*

Cross-pollination by hand significantly increased (by an average of 66%), the probability of fruit maturation in both years, suggesting that a lack of adequate compatible pollination is the major factor in reproductive success as measured by the numbers of mature fruits. Limitations by pollen compatibility is apparently a common cause of low fruit production in tropical trees with large floral displays and self-incompatibility, due to the majority of pollinator movements occurring between flowers of the same tree (Arroyo 1976, Bullock *et al.* 1989). However, it is evident that to fully test the idea of limited pollination in *Ipomoea wolcottiana*, it would be necessary to make other experiments with massive pollination by hand to avoid the possible effect of translocation of resources to

treated flowers (Bawa & Webb 1984), as well as to repeat experiments on the same individuals in successive years.

The flowers of *Ipomoea wolcottiana* are visited by at least 20 species of insects, mainly bees, and occasionally orioles and hummingbirds (Arizmendi & Ornelas 1990, Bullock *et al.* 1987). Only two of these species, *Xylocopa mexicanorum* and *X. tabaniformis* (Anthophoridae), are effective pollinators and move consistently between flowers of different trees. These two species were common in the study seasons, although in the second year there was a drastic decrease in visitation rate. This reduction was probably due to the unusual heavy rains in January 1992 which desynchronized flowering in *I. wolcottiana* and caused aseasonal flowering in many other species as a larger attraction for other floral resources and an increased competition for pollinators may have taken place. In fact, the decrease in visits per flower could have caused the lower fruit production in the second year (Table 3). In this regard, there is evidence from other studies that temporal changes in pollinator density can have a large effect on plant fecundity (Herrera 1988, Vaughton 1991). The results suggest that important limitations can exist in the supply of compatible pollen and in the frequency of pollinator visits for *I. wolcottiana*, although the extent of their consequences could vary in different years.

#### *Parasitism of floral buds*

Parasitism of floral buds was substantial in both years (18 and 33%). High levels of bud destruction have been reported for other tropical trees, e.g. in *Bauhinia unguolata* potential fruit production was reduced by 50% by the predation of flowers and fruits (Heithaus *et al.* 1982). The differences in level of parasitism among individuals of *Ipomoea wolcottiana* were great, but unfortunately it was not possible to obtain data from the same individuals in both years. The cost of lost buds and the possibility of their replacement also remain to be studied, but the data suggest that the parasitism of floral buds in this species could be very important.

#### *Evolutionary hypotheses*

The evidence on proximal factors reported here have notable implications for the evolutionary explanations of low fecundity in hermaphroditic plants.

The experimental data on phosphorus application and control of herbivory clearly show that reproduction in *Ipomoea wolcottiana* is resource-limited. According to Lloyd's (1980) serial adjustment hypothesis, when resource limitation exists, plants can adjust available resources during several stages of the reproductive process. This adjustment occurs through abortion of inflorescences and/or flowers, and the selective abortion of seeds and fruits (Lloyd 1980). In *I. wolcottiana*, resource levels do not affect the number of fruits but rather the number of inflorescences or flowers, suggesting that this is the level where adjustments to resource availability may regulate fruit number. Similar results have been observed in *Banksia ericifolia* Sm (Copland & Whelan 1989) and in

*B. spinulosa* R. Br. (Vaughton 1991), where increases in available nutrients also resulted in increased production of inflorescences without modifying the number of fruits per inflorescence.

Selective abortion of seeds and fruits occurs when these structures are in bad condition or are of low genetic quality (Lloyd 1980). However, in *Ipomoea wolcottiana* we did not observe resource limitation effects on the number of fruits produced. Thus it appears unlikely that selective abortion of seeds occurs in response to resource limitation in this species, although specific experiments with other resources are lacking. On the other hand, resource limitation can also foster sexual selection (Willson 1979). Thus, it is proposed that the over-production of flowers may have a function in increasing paternal fitness through a higher rate of pollen dispersal and fertilization of ovules, more than increasing maternal fitness through increased fruit production. In this sense, *I. wolcottiana* shows a negative relationship between the number of flowers produced and pistil biomass, but there is a positive relationship between pistil biomass and fruit production (Parra-Tabla 1995). These patterns suggest that the large floral display in this species probably responds to selective pressures on the male function. In the context of sexual selection, it is also important to evaluate the selective pressure on floral traits that affect plant-pollinator interactions. Some authors have proposed that in conditions of marginal activity or low density of pollinators, we should expect a strong selective pressure on male success through attractive structures (e.g. number of flowers) (Willson *et al.* 1994). In *I. wolcottiana*, in spite of the high number of floral visitors, only two species appear to be legitimate pollinators. Additionally, we observed an important between-year variation in rate of floral visitation; thus it is reasonable to consider that in this species the selective pressure on pollinator attraction is important.

The bet-hedging idea (Koslowski & Stearns 1989) states that plant reproductive strategies must maximize success in spite of temporal variation in any of a series of factors that can limit reproduction. Thus, a likely strategy would be the over-production of structures such that the plants can take advantage of occasions when limits are less severe. Even in bad years, some minimum number of descendants will be left. Non-equivalent limiting factors may be biotic, such as pollinators and herbivores, or abiotic, such as available nutrients and water. In *Ipomoea wolcottiana* we observed significant differences between years in the intensity of parasitism of flower buds, pollinator visitation rates, and natural fruit production. Inter-annual variation in the amount and seasonality of rainfall affects the reproductive system through variation in phenology, and possibly through changes in nutrient availability and capture (Mooney & Kummerow 1981). Such evidence may at least partially support the bet-hedging hypothesis as an explanation for the great losses of flowers and young fruits in *I. wolcottiana*. However, it is clear that multi-year data are needed.

Many authors have suggested that plant reproductive systems have been

molded by combinations of selective forces, leading to very diverse responses (Lloyd 1980, Stephenson 1981, Sutherland 1986). In this sense, the evolutionary hypotheses which attempt to explain high levels of abortion of reproductive structures, especially in a large number of hermaphroditic species, cannot be considered mutually exclusive. In fact, the combination of these hypotheses will surely give a better understanding. The results of this study support the idea of that complex interaction of selective forces affects patterns of reproduction in plants, and is particularly relevant to ideas of sexual selection and bet-hedging.

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