

Rainfall and flowering synchrony in a tropical shrub: variable selection on the flowering time of *Erythroxylum havanense*

CÉSAR A. DOMÍNGUEZ and RODOLFO DIRZO

Centro de Ecología, Dept. Ecología Evolutiva, Universidad Nacional Autónoma de México, AP 70–275, México DF 04510, México

Summary

We tested the adaptive significance of flowering synchrony by means of a quantitative analysis of selection and by flowering induction experiments with the deciduous shrub *Erythroxylum havanense*. Temporal schedules of flower and fruit production were determined for a local population (in three sites) in a Mexican seasonal forest for 2 years (1987–1988). The consequences of natural variation in flowering time (flowering initiation day) on maternal reproductive success (fecundity) were evaluated. We observed high levels of inter- and intraindividual flowering synchrony in 1987, but not in 1988 and this contrast was related to differences in rainfall patterns between the two years. A significant proportion (15.4%) of the phenotypic variation in flowering initiation day was accounted for by environmental variance. The expression of phenotypic variance of flowering time and, consequently, the opportunity for selection to act, are controlled by annual variation in rainfall. Despite the between-year difference in flowering synchrony, we detected a relatively intense directional selection on flowering initiation day in both years, but selection coefficients were of opposite sign (standardized directional gradients were -0.326 and 0.333 for 1987 and 1988, respectively). For both years there was a significant relationship between individual relative fitness and the number of neighbouring flowering plants in a given day, suggesting positive frequency-dependent selection.

Keywords: *Erythroxylum havanense*; fitness; flowering synchrony; flowering phenology; phenotypic natural selection; temporal variation in selection; frequency-dependent selection; tropical dry forest; watering experiments; flowering induction

Introduction

Flowering phenology is a critical reproductive trait of plants, since it determines the number of potential mates and, thus, successful reproduction for outcrossing species (Rathcke, 1983; Rathcke and Lacey, 1985; Bronstein *et al.*, 1990). Of the known patterns of flowering phenology, mass-flowering (big-bang flowering *sensu* Gentry, 1974) provides, perhaps, the most extreme example of flowering synchrony at both the population and individual levels (Frankie *et al.*, 1974). Current explanations for the evolution of mass-flowering emphasize the role of stabilizing selection on flowering time (Janzen, 1969, 1976; Beattie, 1971; Mosquin, 1971; Beattie *et al.*, 1974; Gentry, 1974; Opler *et al.*, 1976; Augspurger, 1980, 1981; Mori and Pipoly, 1984). It is expected that synchronous individuals within the population should have a higher fitness than plants flowering out of synchrony, because of an increase in the number of visits by pollinators, higher rates of pollen donation–deposition, greater opportunities to find mates, a higher potential for outcrossing, and/or larger number of seeds that escape predation. So far, however, relatively few studies have examined quantitatively the selective consequences of flowering synchrony in natural populations (Augspurger, 1980, 1981; Gross and Werner, 1983; Dieringer, 1991; Gómez, 1993).

Although flowering synchrony can be viewed as an emergent trait of a population, it could arise and/or be maintained by natural selection if individual reproductive success increases as a function of the number of individuals flowering simultaneously. If so, it could be expected that those plants with the same requirements (threshold) to initiate flowering would be favoured. Natural selection reduces the amount of additive genetic variance in those attributes highly related to fitness (Fisher, 1958). In this context, the reduced phenotypic variance in flowering time of mass-flowering species could be envisioned as the evolutionary result of natural selection.

In this paper we document temporal patterns of natural selection on flowering time (more specifically, flowering initiation day) in a natural population of a distylous mass-flowering shrub, *Erythroxyllum havanense* Jacq. (Erythroxyllaceae), over a 2 year period. The specific aims of this research were (1) to quantify the amount of interindividual variation in flowering initiation day, (2) to determine the proximal cause(s) of such variation, (3) to evaluate the fitness consequences of such variation and (4) to determine the annual variation of selection regimes on flowering initiation day in a natural population. We predicted that those individuals flowering in synchrony with the population would have a higher fitness than those flowering asynchronously.

Methods

Study system

The study took place at the Chamela Biological Station (19° 30' N, 105° 03' W), near the Pacific coast of Mexico. The mean annual rainfall (1977–1987) is 699 mm and 80% of the total rain falls between the months of July and October (Bullock and Solís-Magallanes, 1990). Detailed climate features of the Chamela region are described by Bullock (1986a). The elevation of this 1600 ha preserve ranges between 50 and 150 m and is dominated by tropical deciduous forest in the uplands and tropical semi-deciduous forest on arroyo sites. A description of the flora and vegetation structure of upland and arroyo forests can be found in Lott *et al.* (1987).

Erythroxyllum havanense is a common understory shrub in tropical deciduous forests of the Pacific coast of Mexico. It is a long-lived distylous species, with a diallelic incompatibility system that prevents fruit production among monomorphic pollinations (Domínguez, 1990). Thus, pollinator visitation is required in order to produce fruits. The principal flower visitors are hymenopterans, accounting for 94% of the total visits recorded ($n = 8745$) during 84 h of direct observation (Domínguez, 1990). Social bees in the genus *Trigona* were the most frequent flower visitors and one single species, *Trigona hellwegeri*, accounted for 55% of the total number of visits (Domínguez, 1990). Butterflies and dipterans also visited the flowers.

Mass-flowering of *E. havanense* occurs soon after the first heavy rains following the dry season (Bullock, 1986b; Domínguez, 1990). Such rains can occur any time from May to July (Domínguez, 1990). Previous experiments with this species have shown that flowering is triggered by the increase in soil humidity brought about by the rains (Bullock, 1986b; Domínguez, 1990). Flowering is highly synchronous within and among individuals. Each individual plant flowers once a year for a mean of 3 days ($SE = 0.1$, $n = 120$, range 2–5). Each individual flower lasts only 1 day and a shrub produces, on average, 71% ($SE = 1.9$, $n = 120$) of its flowers on one peak day. The population flowering period lasts 1 week and up to 62% of the annual flower production can be produced during one peak day. Nevertheless, both interindividual and yearly variation in flowering time occur.

Natural variation in flowering time

Flowering and fruiting phenology and natural variation in flowering initiation day were determined in three sites (Tejón, Camino Antiguo Sur and Eje Central) of the local *E. havanense*

population during the natural flowering seasons of 1987 and 1988. At each site we measured the size of all reproductive individuals of *E. havanense*. Because of the high occurrence of dead branches, size was estimated as the sum of the basal area of all living branches. Twenty study plants were randomly selected within each of the three sites ($n = 60$). After the first rains of 1987 and 1988 (16 July and 26 June, respectively), for all 60 plants, the numbers of flowers and immature and mature fruits were counted daily throughout the entire reproductive season. For each plant the census was initiated at its first day of flowering (flowering initiation day) and continued until fruit ripening finished.

Due to the difficulty of measuring directly the heritability of characters in this long-lived plant, an estimate of the upper limit of the heritability of flowering initiation day of *E. havanense*, the repeatability index, t (interclass correlation), was calculated. This index measures the proportion of the phenotypic variance in a trait due to permanent differences between individuals (Falconer, 1981). This index is only an estimate of the upper limit of heritability, since permanent differences can be attributed both to genetic variance and to the local environment. Repeatability was calculated by means of a correlation analysis between the individual flowering initiation days of 1987 and 1988 (Turner and Young, 1987). The standard error of t was estimated as $\sigma_t = 1 - t^2/\sqrt{n} - 1$ (Turner and Young, 1987).

Since flowering of *E. havanense* is triggered by the first rains of the season (see Bullock, 1986b; Domínguez, 1990), individual variation in flowering initiation day could be due to local heterogeneity in water availability to plants. In order to evaluate such heterogeneity, three variables were considered. First, we defined three zones that presumably vary in water availability to plants: plateaus, slopes and gullies. The position of each marked plant within such zones was noted. Secondly, slope and slope orientation (aspect) were determined with a field compass (Brunton Co.). Aspect then was broken down into its east–west and north–south components by calculating the sine and cosine functions of the measured angles. The north–south influence on individual flowering time is measured by the magnitude of the cosine effect, while the sine effect assesses the east–west component. This method enabled us to use conventional statistics with these circular variables. Slope measures were arcsine transformed (Snedecor and Cochran, 1978) for statistical analysis regarding their differences among zones and their effect on flowering. Finally, the water infiltration rate below each plant was measured. Before the onset of the 1990 rainy season, the water infiltration rate was measured by burying a pipe (0.5 m long and 0.1 m in diameter) at a distance of 1.0 m from the trunk of each marked plant. We then poured 3 l of water into the pipe and the time required for total infiltration was measured with a chronometer. This method gives a reliable assessment of soil attributes, since the infiltration rate depends on texture, organic matter content, etc. (J. M. Maass, personal communication).

The effects on such qualitative (topographic zone) and quantitative (slope, aspect and infiltration) variables on flowering time were tested using GLM and REG procedures of the SAS Institute (1987). These analyses were carried out only with the 1988 data set, since only in that year was individual variation in flowering time evident (see below).

Experimental evaluation of flowering time

Additional plants of *E. havanense* were randomly selected for a series of experiments of flowering induction by means of watering. These experiments were designed to assess the proximal cause of flowering variation and the environmental correlates of the cause. Flowering was induced by watering the soil within a 30 cm radius around each plant. There were two experimental designs, each intended to stimulate either an extremely high or low amount of rainfall. The first design mimicked an intense storm that would bring about a sudden increase in soil humidity and, therefore, an unambiguous cue to trigger flowering. The treatment consisted

of an initial input of 20 l of water and 10 l every other day until the plant flowered ($n = 30$ and $n = 34$ plants for 1987 and 1988 experiments, respectively). In the second design, the initial input was only 5 l of water followed by 3 l every other day (1990 experiment, $n = 120$), simulating a light rainfall in which soil humidity rises gradually. We expected from this design that individual variations in the threshold required to initiate flowering would be expressed. From the first design, in contrast, we expected that the threshold of all plants would be surmounted.

All the experiments were carried out approximately 1 month before the onset of the rainy season. The time which elapsed between the first irrigation and the first day of flowering for each plant was used as the response variable in these experiments.

Analysis of selection

The magnitude of selection acting on flowering time was evaluated by a regression analysis of the relationship between maternal reproductive success (fruit production) and individual variation in flowering time (see Lande and Arnold, 1983; Arnold and Wade, 1984a,b; Schluter *et al.*, 1985; Endler, 1986). This analysis used the data collected as described in the section on natural variation in flowering time. We used the number of mature fruits per individual as an estimate of absolute fitness. Since fruits of *E. havanense* produce only one seed, fruit production is a reliable estimation of maternal fitness. Individual values of absolute fitness were transformed to relative fitness (mean=1) prior to the regression analysis (Lande and Arnold, 1983). Individual flowering time was defined as the number of days which elapsed between the flowering initiation day of the first plant in the population and that of the individuals being studied. This measure was envisioned as an indirect estimate of flowering threshold variation among individuals and, therefore, as the attribute under selection. Prior to the estimation of selection gradients, phenotypic values (flowering initiation day) were standardized to mean = 0 and variance = 1. Therefore, the selection coefficients reported here are the standardized partial regression coefficients (Sokal and Rohlf, 1981; Lande and Arnold, 1983). For each year, selection gradients were estimated separately for directional selection and for stabilizing/disruptive selection (Lande and Arnold, 1983; Endler, 1986). Because of the normal distribution of errors from regression (Lande and Arnold, 1983), the significance of the directional and stabilizing/disruptive selection gradients was tested using the REG procedure of the SAS Institute (1987).

Fitness surfaces were estimated by quadratic regression (Lande and Arnold, 1983) and results were corroborated by non-parametric estimations (generalized cross-validation; Schluter, 1988). This method does not depend on *a priori* assumptions about the parametric form of the fitness function and, thus, it provides a more reliable assessment of the fitness surface shape than least squares-based curve fitting. The accuracy of the estimates was judged by bootstrapping, where fitness surfaces are repeatedly estimated on data resampled from the original data set. We estimated the coefficients of selection intensity, V , as the squared coefficient of variation among individuals in the predicted values of fitness (Schluter, 1988). This measure reflects selection in all the moments of the phenotypic distribution.

Results

Natural variation in flowering time

There were marked differences in flowering phenology between the two years (Fig. 1). During 1987, plants showed a striking interindividual synchrony as indicated by the unimodal distribution of the flowering initiation day (Fig. 1A). Most plants (91.7%) began flowering in the first 2 days of that year's rainy season and there were only six asynchronous plants. If the first day of flowering of the season is designated as 'day 1', then the mean flowering initiation day was 1.6 and

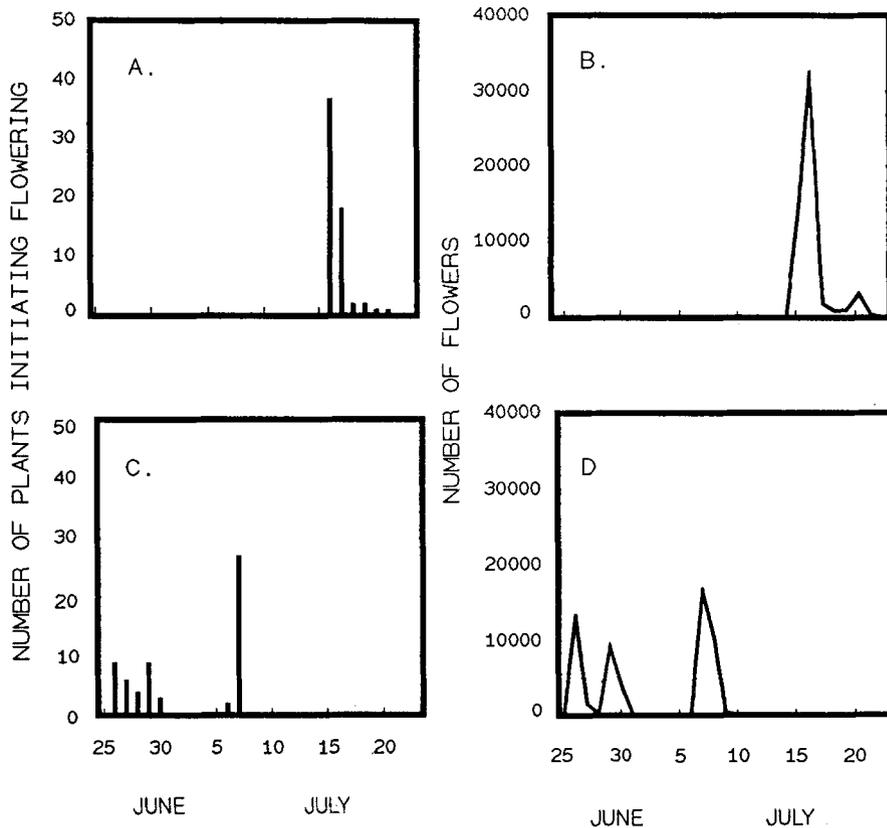


Figure 1. Natural flowering phenology of *E. havanense* during 1987 (A) and (B) and 1988 (C) and (D): (A) and (C) distribution of flowering initiation day and (B) and (D) daily flower production of the population.

the variation around this mean was small (± 0.13). (All means are reported ± 1 SE.) In contrast, 1988 was characterized by low flowering synchrony and the individual flowering initiation day had a more even distribution (Fig. 1C) with a mean of 8.3 (± 0.7) days. The flowering initiation day was significantly different between the years (Mann – Whitney $U_{(61)} = 6.43$, $p < 0.0001$).

The difference in time between the first and the last plant initiating flowering was 11 days in 1988 and only 5 days in 1987. In 1987, the year with greater synchrony, flower production by the population was concentrated in the first 2 days (84%) and only a small fraction (13.6%) was distributed among the next 5 days of flowering (Fig. 1B). During 1988, the peak flowering day for the population (7 July) accounted for only 30.0% of the total flower production and there were two other peaks with productions of 23.3 and 16.9% (26 June and 29 June, respectively; Fig. 1D).

We investigated whether or not annual variation in rainfall patterns could be the proximal cause of the differences in flowering synchrony between the years. Previous experimental evidence had shown that plants flowered 7–9 days after they had been heavily watered (6.5 days for 1987 and 9.3 days for 1988) (Domínguez, 1990; see below). Thus, it is possible to determine which was the most likely ‘triggering’ rain (i.e. that rainfall level that raises soil humidity to the lowest individual flowering threshold). Such triggering rains occurred on 10 July in 1987, and on 18 June in 1988 (see arrows in Fig. 2). In 1987 a rain of only 12.7 mm was sufficient to cause mass flowering, while a rainfall level of 15.75 mm produced quite a distinct pattern in 1988 (cf. Fig. 1). Thus, two contrasting flowering patterns were produced with relatively similar quantities of

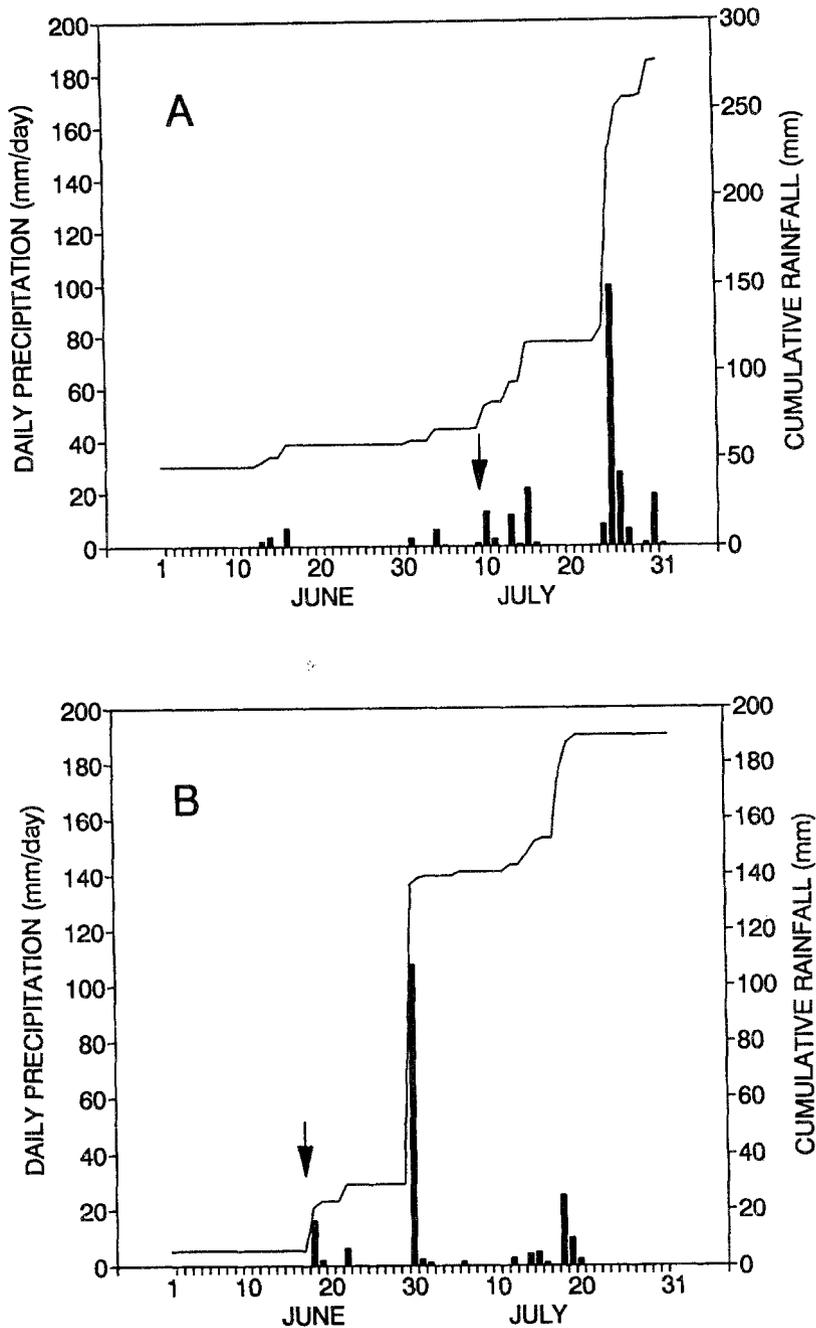


Figure 2. Daily precipitation (bars) and cumulative rainfall (-) for (A) 1987 and (B) 1988. Arrows indicate the likely triggering rains of both years. Please note that the scales for the cumulative rainfall are different.

rainfall. However, when cumulative rainfall is considered this apparent contradiction disappears. The cumulative rainfall at the moment of the triggering rain was higher during 1987 as a consequence of the early rains of that year (Fig. 2A). This result suggests that soil humidity was

Table 1. Mean values (± 1 SE) of physical characteristics for the three zones and results of univariate comparisons among zones

Zone	Infiltration (s)	Slope ($^{\circ}$)	Sine (east–west)	Cosine (north–south)
Plateaus	11.4 (0.9)	9.1 (0.7)	–0.32 (0.10)	0.07 (0.12)
Slopes	17.8 (5.4)	21.4 (2.9)	0.59 (0.12)	0.34 (0.13)
Gullies	22.7 (4.7)	14.7 (1.3)	–0.20 (0.19)	–0.06 (0.35)
<i>F</i>	5.193	41.153	6.042	0.045
<i>p</i>	0.026	<0.0001	0.017	n.s.

Sine refers to the east–west component and cosine refers to the north–south component of aspect. (See text for further details.)

Table 2. Partial regression coefficients (± 1 SE) for the effect of five physical variables on the flowering initiation day of *E. havanense* in 1988

Variable	Coefficient	<i>t</i>	<i>p</i>
Constant	7.293 (1.356)	5.380	0.0001
Sine (east–west)	1.670 (0.925)	1.806	0.0760
Cosine (north–south)	0.506 (0.913)	0.554	0.5820
Infiltration	–0.010 (0.044)	–0.218	0.8290
Slope	0.082 (0.098)	0.841	0.4040

near the flowering threshold of most plants when the triggering rain arrived and mass flowering was readily produced with only a small amount of water. Conversely, the triggering rain in 1988 (Fig. 2B) was almost the first rain of that year and cumulative rainfall was negligible at that moment. Hence, it seems that the increase in soil humidity brought about by such rain only triggered the plants with a low flowering threshold (see arrow in Fig. 2B), while the remaining plants (those with a presumably higher threshold) flowered synchronously as a consequence of the heavy precipitation of 30 June (Fig. 2B).

We further considered the idea that individual variation in flowering time within years could be due to microenvironmental heterogeneity of water availability to plants. In 1988, significant differences in the flowering initiation day among zones ($F_{(2,57)} = 5.21$, $p = 0.0084$) accounted for 15.4% of the total variance in flowering time. The mean values of the flowering initiation day were $7.0 (\pm 0.8)$ for plateaus, $11.0 (\pm 0.9)$ for slopes and $6.0 (\pm 2.0)$ for gullies. There was a significant delay in the flowering initiation day for those plants located on slopes relative to those on the other two zones ($p < 0.05$; plateaus and gullies did not differ significantly, $p > 0.1$; Scheffé's test). Overall differences between plateaus, slopes and gullies in the mean values of the physical characters (slope, slope orientation and water infiltration rate) were tested with a multivariate analysis of variance. There were significant differences among zones in the overall physical environment (Wilks' lambda = 0.484, $F_{(4, 55)} = 14.679$, $p < 0.0001$). Separate univariate tests of differences in slope, slope orientation (sine effect) and infiltration rate also yielded significant results (Table 1).

A multiple regression testing simultaneously for the effect of the physical variables on the individual flowering initiation days revealed that none of the considered physical variables had a significant influence ($F_{(4, 55)} = 1.381$, $p > 0.2$; Table 2). Thus, although the flowering initiation day differed among the three zones, we failed to detect the proximal causal environmental mechanism(s).

The above evidence indicates that the phenotypic variation in the flowering initiation day within a year depends at least partially (ca. 15% of explained variance) on environmental heterogeneity. However, the possibility of genetically based variation is not ruled out by such results. In fact, the estimated repeatability of the flowering initiation day for *E. havanense* was 0.319, which significantly differs from zero ($p < 0.01$).

Experimental evaluation of flowering time

There was high synchrony when flowering was induced by a large (20 l) input of water (1987 and 1988 experiments; Figs. 3A and B). Plants flowered on average 7.9 (± 0.2) days after the first watering and there was a 2 day difference between the first and the last plant initiating flowering ($n = 62$, pooled data from 1987 and 1988; two plants defoliated by leaf-cutting ants (*Atta* sp.) were excluded from the analysis). During 1987, flowering began on average 6.5 (± 0.1) days after the initial irrigation, whereas in 1988 that value was 9.3 (± 0.1) days ($t_{60} = 47.27$, $p < 0.0001$). This result is probably due to the differences in cumulative rain between 1987 and 1988 (Fig. 2).

Flowering induced by low watering (5 l, 1990 experiment) was quite different from that observed in 1987 and 1988 (Fig. 3C). During this experiment there were two events of flowering: the first 7–10 days and the second 21–22 days after the initial irrigation. The mean flowering initiation day was 10.4 (± 0.5 ; $n = 105$; 15 plants defoliated by leaf-cutting ants were excluded from the analysis), which is significantly different from those values obtained in 1987 and 1988

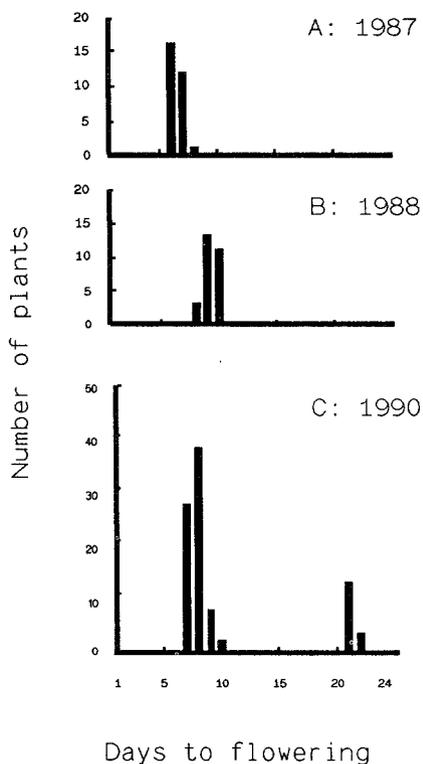


Figure 3. Distributions of flowering initiation day for the plants of the watering experiments simulating an intense storm (A) and (B) and a light rainfall (C) in which soil humidity rises gradually.

Table 3. Standardized directional and stabilizing/disruptive selection gradients (± 1 SE) associated with variation in flowering initiation day in *E. havanense*

Standardized selection gradients	1987	1988
Directional	-0.326 (0.125) $p < 0.0001$	0.333 (0.084) $p < 0.0003$
Stabilizing/disruptive	0.111 (0.071) $p > 0.131$	0.009 (0.219) $p > 0.90$

(Kruskal–Wallis' $H_{(30,32,105)} = 69.1, p < 0.0001$). The period between the first and the last plant initiating flowering was 15 days, which contrasts with the period of only 2 days found in the intense watering experiments. These results suggest that there is considerable individual variation in the threshold to initiate flowering.

Analysis of selection

Regression analyses indicate that natural selection did act on the flowering initiation day during the reproductive seasons of both years ($F_{(1,28)} = 6.778, p = 0.015$ and $F_{(1,42)} = 15.548, p = 0.0003$ for 1987 and 1988, respectively). Directional, but not stabilizing/disruptive selection, was found in both years, as shown by the standardized selection gradients (Table 3). Quite unexpectedly, the selection gradients for 1987 and 1988 were opposite in sign, indicating that the natural selection regime varied between years. For 1987 the relative fitness of the early flowering individuals was higher than that of the late flowering ones. In contrast, in 1988 the reverse was true. The natural selection on the flowering initiation day was relatively intense. In both years the

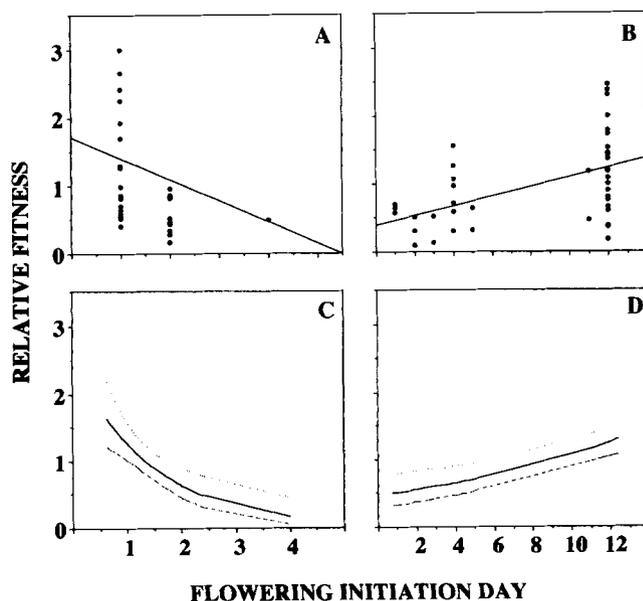


Figure 4. Variation in relative fitness (fecundity) as a function of flowering initiation day in 1987 (A) and (C) and 1988 (B) and (D): (A) and (B) observed values and least squares-fitted regression line; and (C) and (D) non-parametric regression line (± 1 SE) using a generalized cross-validation method. (See text for details.)

standardized directional selection gradients indicate that a shift of 1 SD of flowering initiation day produces a change in fitness of approximately 33% (see Table 3).

Fitness surfaces for 1987 and 1988 are shown in Fig. 4. The presence of directional selection was evident in both years, but it was of opposite sign (Fig. 4A and B). The adjusted fitness surfaces and the standard errors resulting from 250 bootstraps (Fig. 4C and D), agree with the former analyses and confirm the presence of directional selection (though of opposite trend) on flowering time during 1987 and 1988. The estimated selection intensity coefficients for flowering time of *E. havanense* were $V_{1987} = 0.1265$ and $V_{1988} = 0.1057$.

The observed fitness surfaces suggest that the highest values of relative fitness correspond to those days when most individuals flowered (see Fig. 4). Spearman rank correlation coefficients ($r_s = 0.5841$, $p = 0.0017$ and $r_s = 0.5612$, $p = 0.0002$, for 1987 and 1988, respectively), indicated that individual relative fitness increased significantly with the number of flowering plants in a given day in both years of the study. This suggests that the opposite directions of selection of the 2 years could be due to positive frequency-dependent selection.

Discussion

In this paper we have shown that despite its high degree of synchrony, the flowering initiation day in *E. havanense*, an attribute with a presumed adaptive value (see Janzen, 1969, 1976; Beattie, 1971; Gentry, 1974; Opler *et al.*, 1976; Augspurger, 1980, 1981; Mori and Pipoly, 1984), has enough phenotypic variation for natural selection to act. This was indicated both by the observation of natural flowering plants and by the experimental induction of flowering. We further demonstrated that phenotypic variation in flowering time had marked consequences on individual reproductive success. Although differences in the amount of phenotypic variation in flowering time between years were evident, it was possible to detect the presence of selection in both years. In spite of the reduced variation in flowering time among individuals in 1987, the intensity of selection was comparable to that of 1988. Moreover, fecundity in *E. havanense* has a marked dependence on flowering initiation day. Selection analyses showed that flowering time explained between 20 and 27% (1987 and 1988, respectively) of the variation in fecundity, indicating that this attribute strongly affects fitness. Moreover, the estimated selection intensities for flowering time of *E. havanense* rank between those considered as relatively intense by Schluter (1988; e.g. $V = 0.453$ for survival in Galapagos finches and $V = 0.114$ for reproduction in female song sparrows).

It is noteworthy that selection on the flowering initiation day operated in opposite directions between the 2 years. This fact could be explained if frequency-dependent selection is acting on the flowering phenology of *E. havanense*. Frequency-dependent selection operates when the fitness of a particular strategy depends on the types and frequencies of other strategies in the population (Parker, 1984; Williams, 1992). In this context, the variation in the flowering initiation day of *E. havanense* could be envisioned as a set of flowering strategies. This study demonstrates that the individual relative fitness depends on the number of simultaneously flowering plants (see also Copland and Whelan, 1989). However, the number of flowering plants in a given day is a function of the variation in the flowering response thresholds among individuals. Those plants with similar water requirements to initiate flowering (the same strategy) would tend to flower synchronously. Hence, natural selection will favour the most frequent phenotype in the population, i.e. those plants with similar flowering thresholds that altogether produce the most synchronous flowering day. Therefore, our results could be explained as the effect of frequency-dependent selection acting on the temporal variation of the expression of phenotypic variance in the flowering initiation day of *E. havanense*.

Information on the compatibility system of *E. havanense* and on the behaviour of its pollinators, suggests that frequency-dependent selection acted through pollination success. The main pollinators of this species are social bees that forage in a density-dependent manner (Domínguez, 1990; see also Johnson and Hubbell, 1975; Johnson, 1982; Bullock *et al.*, 1989). Moreover, crosses between flowers of the same individual and between individuals of the same floral morph do not produce seeds (Domínguez, 1990). Thus, the number of potential consorts and available pollinators are enhanced when mass flowering occurs. In accordance, the ecological conditions that maximize pollination success in *E. havanense* are achieved when most plants flower simultaneously, which in turn depends (1) phenotypically on the individual variation in flowering threshold and (2) environmentally on annual differences in rainfall patterns.

Our results demonstrate that temporal variation in the expression of phenotypic variance had marked consequences on the dynamics of natural selection. We also demonstrate that the expression of phenotypic variance in the flowering time of *E. havanense* depends, in turn, on the annual variation in rainfall patterns. We suggest that these features could have important consequences for the evolutionary dynamics of the flowering time of this species. Theoretically, the recurrent action of natural selection reduces the amount of additive genetic variance in those attributes highly related to fitness (Fisher, 1958; Falconer, 1981). Thus, the end result is for selection to reduce the genetic variability to zero. We argue that the shifting regime of expression of phenotypic variance in the flowering time of *E. havanense* could act as a mechanism maintaining the additive genetic variance of this attribute. Although intense natural selection on flowering time was detected in both years, the best phenotype changed through time. Thus, genetic variation for flowering time could persist because selection never favours one phenotype (genotype) for long enough to fix it in the population. This argument is consistent with the proposal that genetic variance could be maintained in natural populations by temporal changes in selective pressures (Turelli, 1988; Barton and Turelli, 1989; Bulmer, 1989). In the particular case of *E. havanense*, frequency-dependent selection could explain the observed changes in the favoured phenotypes. This process depends, in turn, on an unpredictable phenomenon such as the annual variation in rainfall patterns.

From an evolutionary viewpoint, the reduced phenotypic variance in the flowering time of *E. havanense* could be the result of natural selection. Nevertheless, it would appear that the eroding effect of natural selection has a limit imposed by the expression of flowering time as determined by environmental heterogeneity.

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