

Individual flowering time and maternal fecundity in a summer-flowering mediterranean shrub: making the right prediction for the wrong reason

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Abstract

The study of the reproductive biology of those few Mediterranean perennials that flower during the summer drought period may provide an indirect test of the adaptive value of prevailing off-summer flowering in Mediterranean-climate plant communities. This paper presents a study of the correlates, in terms of female fecundity, of individual variation in flowering time in *Lavandula latifolia* Med. (Labiatae), a summer-flowering shrub, at a southeastern Spanish locality. The following questions are addressed: (1) Are individual differences in timing of flowering correlated with variation in total seed production on a per plant basis?; and (2) If they are, which of the maternal fecundity components determining total seed production are phenology-dependent? Total seed production of individual plants was significantly related to flowering time, early-flowering shrubs being more fecund than later-flowering ones. This was due to earlier-flowering plants producing fruits with a greater number of seeds, on average, than later-flowering ones. Results fully support the prediction, based on the assumption of increasing environmental severity as the dry season proceeds, that comparatively earlier-flowering individuals should gain some reproductive advantage over later-flowering conspecifics. Nevertheless, previous experimental studies on *L. latifolia* have shown that number of seeds per fruit, the single fecundity component responsible for the influence of flowering phenology on seed production, is not altered by experimental increases in pollination intensity and water availability, thus negating the premises underlying the prediction. Alternative explanations for observed patterns are tentatively suggested.

Keywords: Flowering phenology, Labiatae, maternal fecundity, Mediterranean plants, seed production, water stress.

Résumé

L'étude de la biologie de la reproduction de quelques pérennes méditerranéennes qui fleurissent à la période sèche de l'été peut apporter la preuve indirecte de la valeur adaptative d'une floraison qui, chez les peuplements végétaux méditerranéens, s'effectue majoritairement hors période estivale. Cet article étudie les corrélations, en termes de fécondité des femelles, de la variation individuelle du moment de la floraison chez *Lavandula latifolia* Med. (Labiatae), arbuste à floraison estivale du sud-est de l'Espagne. Les questions suivantes se posent : (1) les différences individuelles de la phénologie de la floraison sont-elles liées à la variation de la production totale de graines par plante? et (2) si tel est le cas, quels composants de la fécondité maternelle déterminant la production totale de graines sont phénologie-dépendants? La production de graines par individu est significativement corrélée au moment de la floraison, les arbustes à floraison précoce étant plus féconds que ceux à floraison tardive. En effet, les plantes à floraison précoce produisent des fruits dont le nombre de graines est, en moyenne, supérieur à celui des plantes tardives. Ces résultats corroborent totalement l'hypothèse selon laquelle la rigueur de

l'environnement croît au fur et à mesure qu'on avance dans la saison sèche, les individus comparativement précoces ayant alors un avantage reproducteur sur leurs «confrères» tardifs. Néanmoins, des études expérimentales préalables sur *L. latifolia* ont montré que le nombre des graines par fruit — seule composante de la fécondité responsable de l'influence de la phénologie de la floraison sur la production de graines — ne se modifie pas si l'on accroît expérimentalement l'intensité pollinisatrice et la disponibilité en eau, réfutant par là-même les bases de cette hypothèse. On tente de proposer d'autres explications répondant aux « patrons » observés.

INTRODUCTION

The Mediterranean-type climate is characterized by the predictable occurrence of a severe summer drought lasting for several months. Relatively few perennial species flower during that period in Mediterranean-climate plant communities (KUMMEROW, 1983; READER, 1984; C. M. HERRERA, 1984; J. HERRERA, 1986; ARROYO, 1988, 1990), a phenological pattern which was noted more than a century ago by COLMEIRO (1851) in his pioneering phenological studies on southern Spanish plants. The trend exhibited by Mediterranean perennials of "avoiding" summer as a flowering time may be interpreted as an evolved response to predictably unfavourable environmental conditions, either biotic or abiotic, prevailing during that period. On the abiotic side, summer drought generally imposes serious limitations on the photosynthetic activity of plants (LANGE *et al.*, 1982; TENHUNEN *et al.*, 1982, 1985, 1990). Among woody perennials, summer often marks the yearly minima for xylem water potential, cambial activity, and/or growth rate (*e.g.*, MERINO *et al.*, 1976; MOONEY *et al.*, 1977; MARGARIS & PAPADOGLIANI, 1978; MOONEY, 1983; ARIANOUT-SOU-FARAGGITAKI *et al.*, 1984; PSARAS & KONSOLAKI, 1986). On the biotic side, abundance and/or activity of insects often become much reduced during the hot and dry summer, presumably as a consequence of environmental severity (C. M. HERRERA, 1980; FERNÁNDEZ HAEGER & JORDANO BARBUDO, 1982; JORDANO, 1984; BAZ RAMOS, 1986). This may lead to reduced availability of potential pollinators during that period.

Studies on the reproductive biology of those few species which do flower in summer might provide an indirect test of the adaptive explanation outlined above. Supporting evidence for the adaptive value of off-summer flowering will be found if, among summer-flowering species, (1) water availability actually limits reproductive output; and (2) directional phenotypic selection (*sensu* LANDE & ARNOLD, 1983) on flowering time in the off-summer direction is detected. This paper presents a study of the correlates, in terms of female fecundity (seed production), of individual variation in flowering time in *Lavandula latifolia* Med. (Labiatae), a summer-flowering shrub, at a Mediterranean-climate locality of southeastern Spain. Previous investigations have demonstrated that water availability effectively limits seed production in this species (Condition 1 above) (C. M. HERRERA, 1991). The following questions, related to Condition 2 above, are addressed here: (1) Are individual differences in flowering time correlated with variation in total seed production on a per plant basis?; and (2) If they are, which of the maternal fecundity components determining total seed production are phenology-dependent? Results will be interpreted in the context of previous studies which have examined experimentally the

influence of biotic (pollination) and abiotic (water stress) factors on fecundity components in this species (C. M. HERRERA, 1990 *b*, 1991).

PLANT NATURAL HISTORY

L. latifolia is a low evergreen shrub (up to 35 cm high) producing long-stalked (up to 1.25 m) inflorescences in early summer. It is a common species in the well-insolated undergrowth of mixed woodlands at middle elevations in the eastern and southeastern Iberian Peninsula. The composition of the pollinator assemblage, the relation of the plant with pollinators, and aspects of its floral biology, have been described elsewhere (C. M. HERRERA, 1987 *a, b*, 1988, 1989, 1990 *a*). Flowers are hermaphroditic, have pale-blue tubular corollas (tube length 7-8 mm), and are produced over a short (3-6 cm) terminal portion of the stalks in a dichasium-like arrangement. Flowers are self-compatible, but spontaneous autogamy occurs very infrequently and seed set in the absence of pollinators is negligible. Flowers have four ovules, each potentially producing an independent nutlet. Developing nutlets (achenes) remain enclosed by the persistent calyx until maturation. For convenience, the unit formed by the persistent calyx plus the enclosed developing or ripe nutlet(s) will be termed here a "fruit". Nutlets develop synchronously within fruits, but fruit development is very asynchronous within plants and inflorescences, owing to the extended flowering period and slow rate of flower opening within single inflorescences. Fruit maturation takes nearly 5 weeks after anthesis, and flowers and ripe seeds are simultaneously produced on single inflorescences over nearly two-thirds of the flowering period. Investigations on the factors influencing individual variation in maternal fecundity in this species have been presented by C. M. HERRERA (1990 *b*, 1991), and the reader is referred to these publications for detailed treatments of this aspect of *L. latifolia* reproductive biology.

METHODS

This investigation was carried out during July-November of 1984 and 1986 on a population of *L. latifolia* growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz, at 1160 m elevation, in the Sierra de Cazorla (Jaén province, southeastern Spain). This is the 'Aguaderillos-I' site of C. M. HERRERA (1988), where further details may be found. *L. latifolia* plants grow there in a mixed woodland dominated by *Pinus nigra* and *Quercus rotundifolia*. A description of the vegetation of the area may be found in J. HERRERA (1984). The climate is of a Mediterranean type, with rainfall concentrated in autumn-winter (on average, only about 5% of total annual precipitation falls during July-September). At the nearest meteorological station (4.5 km away, similar elevation), mean monthly precipitation for July, August, and September, are 8.1 mm, 8.7 mm, and 37.6 mm, respectively ($N=29$ years).

This study was conducted on 15 shrubs that were individually marked in early July 1984. Shortly after the start of the 1984 flowering season, harvester ants (*Messor capitatus*) removed most flower buds and open flowers from one of the study plants, and it was excluded from the data set for that year. Two plants died between 1984 and 1986, hence only 13 plants were available for study in 1986. Shortly after the start of the 1984 and 1986 flowering seasons, 10 inflorescences were selected at random on each marked plant, and individually marked with numbered tags. Data from these inflorescences were used to assess individual variation in both flowering phenology and maternal fecundity.

Variation in flowering phenology was assessed using both "flowering curves" (describing temporal variation in the number of open flowers) and "cumulative flower production curves" (describing temporal variation in the number of flowers produced up to a given date, expressed as a proportion of the total eventually produced by the end of the flowering season). Both types of curve were obtained

for each plant (combining data from all marked inflorescences) and for the marked population as a whole (combining data from all marked plants). For the reasons outlined in Results, however, most analyses will be based on information from cumulative flower production curves. Flowering curves were constructed using data from periodic (every 3-6 days) counts of the number of open flowers on marked inflorescences. Cumulative flower production curves were obtained from weekly counts of flower production, based on marking of individual flowers (C. M. HERRERA, 1991).

The total number of flowers, fruits, and seeds produced over the whole flowering season by each marked inflorescence, as well as the total number of inflorescences produced, were determined for every individual shrub (see C. M. HERRERA, 1991, for details on methods). These data served to obtain estimates of total seed production on a per plant basis, and to dissect maternal fecundity into its partial components: number of inflorescences, average flower production per inflorescence, mean proportion of flowers setting fruit, and mean number of seeds per fruit.

All analyses of variance and covariance reported below were performed with the procedure GLM in SAS, using Type III sum of squares due to the unbalanced nature of the data (SAS Institute, 1988).

RESULTS

Flowering phenology

At the study population, the flowering season of *L. latifolia* spanned nearly 2.5 months. In both study years, flowering extended from mid-July through early October, thus encompassing the whole dry season (fig. 1). The timing of flowering for the population (as assessed from all study plants combined) differed somewhat between years. In 1984, the number of open flowers peaked in early September, while in 1986 it did in mid-August. This annual variation is also apparent in the curves of cumulative flower production. Regardless of differences in timing of flowering, however, the shape of population curves was remarkably similar in both seasons.

Extended flowering at the population level was mainly due to the long flowering periods of individual plants, and only secondarily to staggering of individual flowering times (fig. 2). The majority of plants were in flower for most of the population flowering season. There were, however, individual differences in timing of flowering (fig. 2). The flowering period of each individual plant in a given year was characterized by its curve of cumulative flower production. Flower production curves were selected because, given the relatively slow rate of flower production in this species, they reflect the phenological pattern intrinsic to each plant more accurately than the more usual curves describing the number of open flowers at a given date (PRIMACK, 1985). Furthermore, the number of flowers that are open at a given time depends on both flower production and flower disappearance rate, and the latter may reflect aspects extrinsic to the plants (e.g., frequency of pollination) to an unknown degree (C. M. HERRERA, unpubl.). For each plant and season, I obtained the dates corresponding to the 25% (PCT25), 50% (PCT50) and 75% (PCT75) percentiles of the cumulative flower production curve. In the terminology of PRIMACK (1985), PCT50 represents the "modal flowering date" (though it should more properly be termed "median" date).

The timing of flowering of individual plants remained consistent between years for the 12 plants with data for both study seasons. Consistency was most marked with respect to the date of initiation of flowering. The correlation between years of PCT25 dates for individual plants was statistically significant ($r=0.663$, $P=0.027$), that for PCT50 dates was only marginally significant ($r=0.565$,

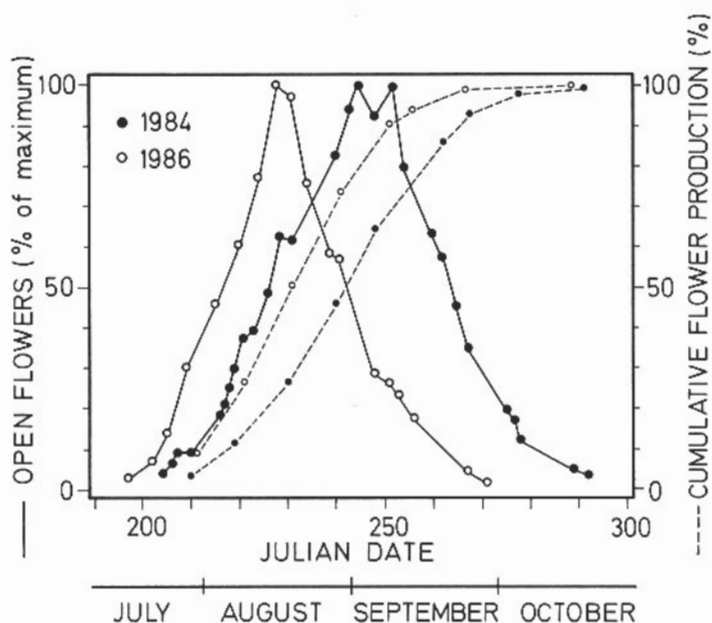


FIG. 1. — Flowering phenology of the marked *Lavandula latifolia* population in the two study seasons. Shown are the "flowering curves" (continuous line; number of open flowers on a given date, expressed as percent of the season's peak) and the "cumulative flower production curves" (dashed line; number of flowers produced up to a given date, expressed as percent of total produced by the end of the season) for all marked plants combined.

$P=0.055$), and that for PCT75 dates barely approached significance ($r=0.500$, $P=0.097$). In all subsequent analyses the phenology of individual plants will therefore be described by means of their PCT25 dates alone.

Phenology and maternal fecundity

Individual variation in maternal fecundity was assessed using estimates of total seed production (on a per plant basis) over the whole reproductive season (TNSEED). TNSEED ranges were 2004-10960 seeds (Mean \pm SD = 5728 ± 3018 seeds, $N=14$ plants) and 673-11162 seeds (5057 ± 3182 seeds, $N=13$ plants) in 1984 and 1986, respectively. Analysis of covariance (ANCOVA) was used to determine whether individual variation in fecundity was related to differences in flowering time. TNSEED was used as the dependent variable, PCT25 was the independent variable, and the study year (1984 or 1986) was included as a covariate. Prior to the analysis, and to render data from the two years comparable (given the annual differences in absolute timing of flowering), PCT25 values for each year were standardized to mean zero and standard deviation unity.

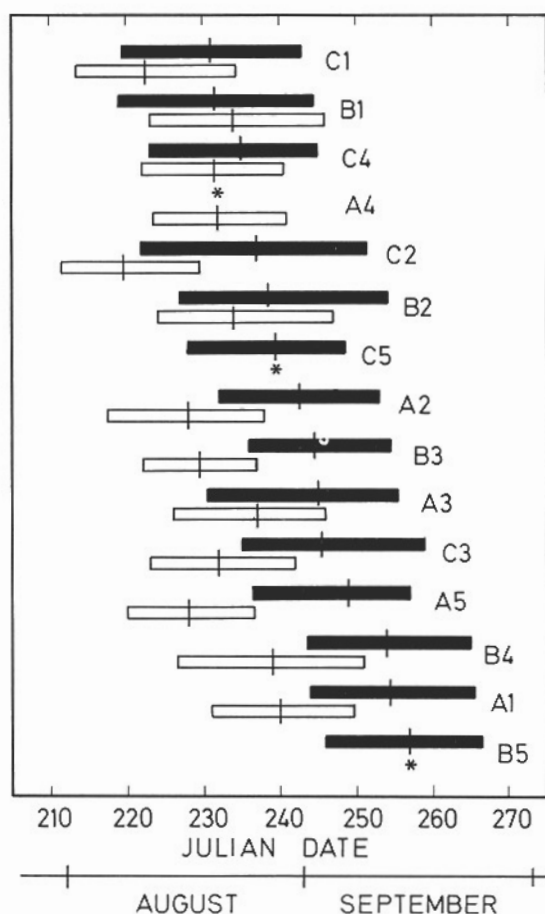


FIG. 2. — Flowering phenology of individual *Lavandula latifolia* shrubs in the two study seasons (filled bars, 1984; open bars, 1986). Bar extremes show the dates corresponding to the 25% (left) and 75% (right) percentiles of the cumulative flower production curve for a given plant and year. Vertical segments mark the position of the median (50% percentile) of the cumulative distribution. Asterisks indicate that data for a given plant and season were not available (see text).

There was a significant effect of flowering time on TNSEED, and this effect was similar in both years (the interaction term was not significant) (table 1 A). The relationship between TNSEED and standardized PCT25 values was a negative one, later-flowering plants tending to produce significantly fewer seeds than earlier-flowering ones (fig. 3). Combining the data for the two years into a single sample

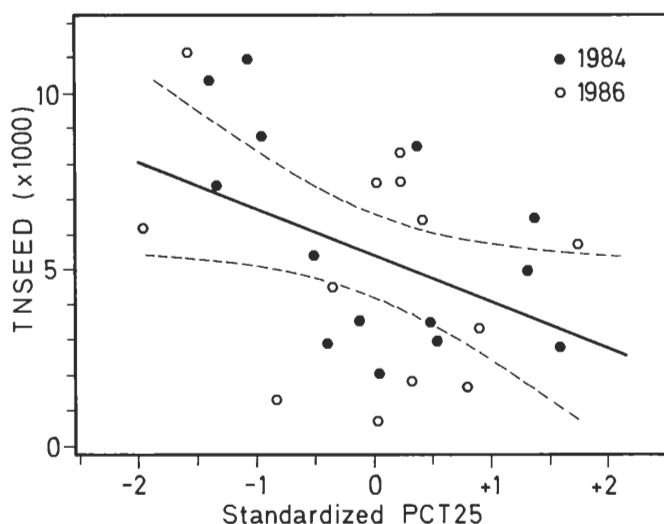


FIG. 3. — Variation of maternal fecundity (TNSEED, total number of seeds produced by a plant over the whole reproductive season) with flowering phenology in *Lavandula latifolia* plants. Phenology of individual plants is described by the standardized (mean zero, standard deviation unity) 25% percentile (PCT25) of its cumulative flower production curve. Shown is also the least-squares fitted regression line (see text for equation) and the 95% confidence limits of mean predicted values. Results of an analysis of covariance for these data are shown in table 1A.

(as no significant effect of year on TNSEED was found, table 1A), the least-squares fitted linear regression of TNSEED on standardized PCT25 was: $TNSEED = 5404 - 1324PCT25$ ($F = 5.50$, $df = 1, 25$, $P = 0.027$; $R^2 = 0.180$). Variation in flowering time of individual plants of one standard deviation respect to the population mean thus leads to a predicted variation in seed production of nearly 1300 seeds.

Phenology and fecundity components

For each year, the total number of seeds produced by a plant over the whole reproductive season was estimated as the product (number of inflorescences produced, NI) \times (mean number of flowers produced per inflorescence, NFPI) \times (mean proportion of flowers setting fruit per inflorescence, FS) \times (mean number of seeds per fruit, NS) (C. M. HERRERA, 1991). The significant negative relationship between PCT25 and TNSEED documented above must thus necessarily be due to the influence of flowering time on one or more of these four partial components of maternal fecundity. To determine which fecundity components were affected by flowering time, multivariate analysis of covariance (MANCOVA) was used. Fecundity components (NI, NFPI, FS, and NS) were used as dependent variables,

TABLE 1. — ANOVA tables for the effects of study year and flowering phenology on individual variation in total seed production over the entire reproductive season (A), and mean number of seeds per fruit (B). PCT25 = date corresponding to the 25% percentile of the cumulative flower production curve for each plant, standardized in each study season to mean zero and standard deviation unity (see text for further details).

Source of variation	df	Mean square	F	P
(A) Total seed production				
PCT25.....	1	42744319.7	5.11	0.033
Year.....	1	3042689.5	0.36	0.555
PCT25*Year.....	1	3720166.5	0.44	0.511
Error.....	23	8363934.4		
(B) Number of seeds per fruit				
PCT25.....	1	0.394181	9.33	0.006
Year.....	1	0.001007	0.02	0.879
PCT25*Year.....	1	0.000059	0.00	0.970
Error.....	23	0.042253		

standardized PCT25 was the independent one, and year of study was entered as a covariate. There was an overall effect of phenology (standardized PCT25) on fecundity components (Wilk's Lambda = 0.581, $df=4,20$, $P=0.022$). This overall effect was consistent among years, as neither the year (Wilk's Lambda = 0.794, $df=4,20$, $P=0.306$) nor the year \times PCT25 (Wilk's Lambda = 0.919, $df=4,20$, $P=0.778$) overall effects on partial fecundity components were significant.

Separate univariate ANCOVA's for each fecundity component revealed that the overall influence of phenology on fecundity was due exclusively to its influence on mean number of seeds per fruit (NS) (table 1 B). No significant effect of phenology on any of the other three partial components examined (NFPI, NI, FS) was found, and results of these analyses have been omitted. For the two years combined, the regression equation relating mean number of seeds per fruit (NS) of individual plants to their standardized PCT25 values was: $NS = 1.46 - 0.13 \text{ PCT25}$ ($F=10.13$, $df=1,25$, $P=0.004$; $R^2=0.288$). The decrease in total female fecundity associated with delayed flowering (*i.e.*, larger PCT25 values) was thus attributable to a reduction in the mean number of seeds per fruit among comparatively later-flowering plants.

DISCUSSION

In the study region, the flowering period of *L. latifolia* virtually encompasses the summer dry season. Seed growth and maturation also take place, for the most part, during that adverse period. Not unexpectedly, water availability actually limits seed production in this species at the study site, via limitations on flower production and fruit set (C. M. HERRERA, 1991). Furthermore, as environmental harshness to plants (biotic, abiotic, or both) presumably increases as the dry season proceeds, comparatively earlier-flowering individuals are expected to produce more seeds than later-flowering conspecifics. This would involve directional phenotypic selection (*sensu* LANDE & ARNOLD, 1983) on flowering phenology in the sense of favouring early flowering individuals, as noted in the Introduction. Results of this study fully support this prediction. Total seed production on a per plant basis was

significantly related to flowering time, with early-flowering shrubs being more fecund than late-flowering ones, and this relationship remained consistent between years.

Total maternal fecundity over a single reproductive episode may be partitioned into four non-overlapping, sequential components, as done here (see also C. M. HERRERA, 1991): inflorescence production, flower production per inflorescence, percent fruit set (proportion of flowers setting fruit), and average number of seeds per fruit. Total seed production on a per plant basis results from combining multiplicatively these four magnitudes. Phenology-dependence of one or more of these fecundity components will thus lead to differential seed production being related to variation in flowering time. Previous studies on other species have often documented the influence of flowering time on one or more of the fecundity components considered here, including flower production (ZIMMERMAN & GROSS, 1984; DIERINGER, 1991), fruit set (PRIMACK, 1980; C. M. HERRERA, 1985; THOMSON, 1985; KEPHART, 1987; MELAMPY, 1987; MULLINS & MARKS, 1987), and number of seeds per fruit (GROSS & WERNER, 1983; DELPH, 1986; LUBBERS & CHRISTENSEN, 1986; PELLMYR, 1987; JENNERSTEN *et al.*, 1988). In the case of *L. latifolia*, the influence of flowering time on individual variation in seed production was due exclusively to its effect on a single fecundity component (number of seeds per fruit). Earlier-flowering plants were characterized by fruits having, on average, more seeds than those from later-flowering ones, and this pattern remained consistent between years. No significant effect of flowering time on the remaining fecundity components was found.

L. latifolia has a fixed number of four ovules per flower, as is characteristic of species in the family Labiatae. Variation in seed number per fruit cannot thus be due to intraseasonal variation in the ovule complement of individual flowers, as found in some species with an indeterminate number of ovules per flower (THOMSON, 1985; PELLMYR, 1987). At the study population, overall abundance of *L. latifolia* pollinators tends to decrease over the flowering season (C. M. HERRERA, 1988). In addition, water stress presumably increases in the course of summer, as evidenced for plants from other Mediterranean-climate regions (POOLE & MILLER, 1981). The negative effects of drought on components of reproduction in plants are well known (KRAMER, 1983; DELPH, 1986; SMITH-HUERTA & VASEK, 1987; and references therein). The two most intuitively obvious explanations for the observed phenological pattern of variation in mean number of seeds per fruit (NS) are, therefore, intraseasonal variation in pollination and/or water stress levels. Previous experimental studies on *L. latifolia* at the study site, however, unequivocally negate both explanations.

Despite the intraseasonal variation in pollinator abundance noted above, prior investigations have revealed no evidence for pollination limitation of seed production in *L. latifolia* at the study population. Additional pollinations over the whole flowering period did not produce any significant increase in either the proportion of flowers setting fruit or the mean number of seeds per fruit at any time during the flowering season (C. M. HERRERA, 1990b, 1991, and unpublished). Experimental irrigation of *L. latifolia* plants at the study site over the whole flowering period did significantly increase total flower production per inflorescence and the proportion of flowers setting fruit, but the number of seeds per fruit remained unchanged (C. M. HERRERA, 1990b, 1991). These findings demonstrate that even though water stress

effectively limits seed production, fruit seediness, the single fecundity component responsible for the influence of flowering phenology on seed production, is unaffected by increased water availability. The relationship found between flowering time and fecundity, therefore, although formally supporting the prediction based on the hypothesis of environmental adversity during the summer drought, was not actually mediated by increasing pollination or water limitation as the drought season proceeded. In other words, the prediction of the relationship between flowering time and fecundity was a right one, but it was actually based on wrong premises.

The average number of seeds per fruit of individual *L. latifolia* plants not only was unaltered by experimental increases in pollination and water resources, but also was insensitive to increments in the amount of resources specific for seed production (C. M. HERRERA, 1990b). Furthermore, this magnitude is, among all fecundity components considered, the one exhibiting, by far, the greatest interannual constancy for individual plants (C. M. HERRERA, 1991). These observations suggest that mean fruit seediness probably is an inherent, characteristic feature of individual plants, and that the relationship with flowering time reported here is of an indirect, not causal nature. Such a relationship might simply be the consequence of both fruit seediness and flowering time being traits correlated with a third variable not accounted for here. Variation among *L. latifolia* plants in the time of flowering depends on individual differences in the rates of inflorescence initiation and development, which in turn depend closely on the rate and timing of production of new leaves (which later subtend inflorescences). If phenotypes characterized by an ability to produce new leaves and inflorescences at a high rate (and, thus, start flowering earlier) are, for whatever reasons, simultaneously characterized by producing fruits with a higher than average number of seeds, this circumstance would explain the phenological patterns documented here. A test of this hypothesis is not possible with the data available, and it must await future investigations.

The results of the present investigation are inconclusive in relation to the original hypothesis under consideration. Nevertheless, they are at least worth a reflection on the risks of uncritically accepting causation from correlation in phenological studies, and of making right predictions for erroneous, no matter how intuitively and ecologically appealing, reasons.

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