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Source: *Botanical Gazette*, Sep., 1984, Vol. 145, No. 3 (Sep., 1984), pp. 323-328

Published by: The University of Chicago Press

Stable URL: <https://www.jstor.org/stable/2474725>

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FACTORS THAT INFLUENCE THE DURATION OF THE STAMINATE AND PISTILLATE PHASES OF *LOBELIA CARDINALIS* FLOWERS

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Staminate duration in *Lobelia cardinalis* is significantly affected by the amount and frequency of pollen removal from the anther tube. Repeated pollen removal shortens the staminate phase, while limited or no pollen removal greatly increases this phase. Pistillate duration is decreased significantly by both pollination and an increase in the duration of the staminate phase. Both staminate duration and pistillate duration increase with flower position on inflorescences with no developing fruit but show no change in duration with position when developing fruits are present. Because the duration of both the staminate and pistillate phases in natural populations falls between the minimum and maximum duration in experimental plants, we conclude that the actual duration of the respective phases in natural populations is controlled by pollinator activity.

Introduction

Dichogamy, the temporal separation of pollen maturation and stigmatic receptivity within a flower, has been viewed as a mechanism that decreases the probability of self-pollination (DARWIN 1876). Recent research with dichogamous species has explored the length of each sexual phase, the amount of nectar produced during each sexual phase, and the timing of the sex change relative to other flowers on the inflorescence. These studies reveal that differences in the duration and nectar production of the sexual phases are common (PYKE 1978a, 1978b; SCHEMSKE 1978; BEST and BIERZYCHUDEK 1982; LLOYD and YATES 1982; DEVLIN and STEPHENSON, unpublished data); that sex differential differences in nectar production can influence the pattern of pollinator foraging (PYKE 1978a, 1978b; BEST and BIERZYCHUDEK 1982; DEVLIN and STEPHENSON, unpublished data); that the duration of the sexual phase may influence the number of pollinator visits (LLOYD and YATES 1982); and that the timing of the sex change relative to the other flowers on a plant can affect the probability of geitonogamy (PONOMAREV 1960; BELL 1971; CRUDEN and HERMANN-PARKER 1977; THOMSON and BARRETT 1981). These detailed studies imply that dichogamy can differentially emphasize the two sexual functions, influence the amount of pollen that is disseminated, and determine the proportion of outcrossing, in addition to hindering pollen transfer within the flower.

In field populations of *Lobelia cardinalis* L. (Lobeliaceae), the staminate phase of the flowers lasts significantly longer and produces more nectar (total sugar) per day than the pistillate phase; pollen

is presented over several days in each flower; the foraging pattern of the pollinator, the ruby-throated hummingbird, tends to promote outcrossing; and staminate phase flowers are visited more often than pistillate phase flowers (DEVLIN and STEPHENSON, unpublished data). In the present study, we explore the interrelationships between the two sexual functions. We address three questions: (1) Does pollen removal affect the length of the staminate phase? (2) Is the duration of the pistillate phase affected by either pollination or the duration of the staminate phase? (3) Does fruit production on the first flowers to open affect the duration of the sexual phases on the flowers produced later in the season?

Description

Lobelia cardinalis is an herbaceous perennial that grows in shaded to open, wet sites throughout much of eastern North America (GLEASON and CRONQUIST 1963). The large, red, zygomorphic flowers are self-compatible (unpublished data) and pollinated by hummingbirds (BAKER 1975; BERTIN 1982; DEVLIN and STEPHENSON, personal observation).

In the autumn, each plant produces one or more basal offshoots (rosettes) and overwinters in this state. During the spring and summer the rosettes elongate and eventually produce a single terminal racemose inflorescence of two to more than 50 flowers. In central Pennsylvania, flowering commences in early August and terminates in mid-September. The inflorescence develops acropetally, and the flowers are protandrous. Consequently, in mid-season, a typical raceme will have developing fruits, open flowers, and flower buds.

The style is enclosed in a tube formed by the fusion of the five filaments and anthers (anther tube). The anthers shed pollen internally into the distal portion of the tube, and pollen is liberated through a ventral valve. A cluster of brushlike hairs is found directly behind the valve, and, when these hairs are pushed back, the valve opens and pollen is re-

Manuscript received December 1983; revised manuscript received March 1984.

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leased. At the end of the staminate phase, the style lengthens until it is exerted from the anther tube. After full extension, the two stigmatic lobes reflex and are then receptive to pollen.

Material and methods

In each experiment, the mature staminate phase is defined as the time when pollen is present in the anther tube before the style elongates through the anther tube. The mature pistillate phase is defined as the time when the stigmatic lobes are reflexed prior to the wilting of the flower.

EFFECTS OF POLLEN REMOVAL ON THE DURATION OF THE STAMINATE PHASE

One greenhouse and two field experiments were performed to determine the effects of pollen removal on the length of the staminate phase. In early May 1982, 12 rosettes from a field site were transplanted into pots and placed in a greenhouse. Just prior to anthesis (early August), the plants were randomly assigned to two treatments (six per treatment). In treatment 1, all of the flowers had a portion of their pollen removed by a thumb stroke against the hairs of the anther tube. The hairs were stroked three times on each day that the flowers remained in the mature staminate phase (3-stroke treatment). In treatment 2, the hairs were never disturbed (0-stroke treatment). Thus, pollen was present in the anther tube until it was forced out by the elongation of the style.

At the field site in 1982, we randomly selected one flower on each of 15 plants. Each day that the flowers remained in the staminate phase, we repeatedly brushed the hairs of the anther tube against the inside of a glass vial, until the pollen was completely evacuated from the anther tube. On one flower on each of eight plants, pollen was totally removed every other day throughout their staminate phase, using the same technique as above. Pollinators were excluded from the flowers by placing cheesecloth bags over the inflorescences for the duration of the experiment.

In 1983, we removed the pollen from every other flower on 100 inflorescences on each day that these flowers remained in the staminate phase, as above. The other flowers on these inflorescences had a portion of their pollen removed each day by the hairs of the anther tube being stroked four times. Again, inflorescences were screened to prevent pollinator visitation.

EFFECTS OF POLLINATION ON THE DURATION OF THE PISTILLATE PHASE

To determine the effects of pollination on the duration of the pistillate phase, six rosettes from the field site were transplanted into pots and placed in a greenhouse in May 1982. A portion of the pollen

from all of the flowers was removed by stroking a thumb against the hairs of the anther tube. The hairs were stroked three times on each day that the flowers remained in the staminate phase. When flowers on each plant entered the pistillate phase, they received one of three treatments: (1) Every third flower on each plant was outcrossed; (2) one-third of the flowers on each plant were self-pollinated, using pollen from another flower on the inflorescence; and (3) one-third of the flowers were not pollinated (two-thirds pollination treatment). All pollinations were performed on the first day of the mature pistillate phase.

EFFECTS OF STAMINATE DURATION ON PISTILLATE DURATION AND THE EFFECTS OF FRUIT SET ON STAMINATE AND PISTILLATE DURATION

The position of each flower within the inflorescence and the length of the staminate and pistillate phases were recorded for all flowers on the 1982 greenhouse plants (0-stroke, 3-stroke, and two-thirds pollination treatment). These data were then analyzed by multiple regression to determine whether (1) there was a relationship between staminate and pistillate duration and (2) the duration of the staminate or pistillate phases within the inflorescence changes over time. Because the flowers on the inflorescence mature acropetally, floral position reflects the aging of the inflorescence. The data were separated into two groups: (1) plants with no developing fruits (0-stroke and 3-stroke treatments) and (2) plants with developing fruits (two-thirds pollination treatment). This dichotomy is important because fruit development would affect resource levels within the plant and, therefore, might affect floral duration.

The following were used in the analysis of pistillate duration (the dependent variable): (1) staminate duration (SD), (2) position (PO, the lowest flower on the inflorescence is no. 1, the next is no. 2, etc.), (3) the number of flowers each plant produced (NF, range = 5–34 flowers), (4) flower-pollinated or unpollinated (FP, appropriate for two-thirds pollination treatment). NF was included because the duration of the pistillate phase may change with inflorescence size. Variables in the analysis of staminate duration (the dependent variable) were (1) the number of strokes (NS, appropriate only for plants without developing fruits), (2) PO, and (3) NF. Staminate and pistillate durations of the plants without developing fruits were normalized by log-transformation.

The four models are: without developing fruits: pistillate duration = SD NF PO, and staminate duration = NS NF PO; with developing fruits: pistillate duration = FP SD NF PO, and staminate duration = NF PO.

To determine the relative contribution of each independent variable, we report the coefficients of

partial determination. The coefficient of partial determination (r^2) measures the marginal contribution of an X variable, when all other variables are already included in the model (NETER and WASSERMAN 1974, pp. 265–266).

Results

In the 1982 greenhouse experiment, the staminate phase of the flowers lasted significantly longer (Mann-Whitney U -test, $P < .0001$) in the 0-stroke treatment (9.6 ± 4.1 days; mean \pm SD; no. = 111) than in the 3-stroke treatment (6.1 ± 1.8 days; no. = 82). In the 1982 field experiment, in which all of the pollen was either removed from the flowers daily (no. = 15) or every other day (no. = 8), the mature staminate phase was significantly longer (Mann-Whitney U -test, $P < .0001$) when the pollen was removed every other day (7.5 ± 1.2 days) than when the pollen was removed daily ($3.4 \pm .5$ days). In the 1983 field experiment, in which pollen was completely removed each day from every other flower on 100 inflorescences and partially removed from the remaining flowers, the mature staminate phase lasted significantly longer ($t = 18.57$, $P > .0001$; $df = 2,168$) when the pollen was partially removed (5.0 ± 1.5 days) than when the pollen was completely removed each day (3.7 ± 1.9 days). These three experiments demonstrate that the amount and frequency of pollen removal exert a significant effect on the duration of the staminate phase of the flowers of *Lobelia cardinalis*.

In the experiment designed to determine the effects of pollination on the duration of the pistillate phase, 48 flowers on six plants were hand pollinated on the first day of the pistillate phase. The pistillate phase of these flowers lasted for 1.9 ± 1 days, while the pistillate phase of the 23 unpollinated flowers on the same six plants was 2.7 ± 1.5 days. These differences are significant (Mann-Whitney U -test, $P < .01$). Thus, pollination significantly decreases the duration of the pistillate phase.

The results of the regression analyses can be summarized as follows. When there are no developing fruits on an inflorescence, the variances of both pistillate and staminate duration were significantly decreased by the independent variables in the model (staminate duration: $R^2 = .34$, $P < .0001$, no. = 196; pistillate duration: $R^2 = .62$, $P < .0001$, no. = 196).

The analysis of pistillate duration reveals that (1) pistillate duration decreases significantly with an increase in the duration of the staminate phase, (2) pistillate duration decreases significantly as the number of flowers increases, and (3) pistillate duration increases significantly with flower position (table 1).

The analysis of staminate duration reveals that

(1) the number of strokes significantly affects staminate duration (pollen removal shortens the staminate phase), (2) staminate duration does not change with the number of flowers on the plant, and (3) staminate duration significantly increases with position (table 1).

In contrast, when developing fruit are present on an inflorescence, the variance of the pistillate duration was significantly decreased by the model ($R^2 = 0.36$, $P < .0001$, no. = 71) but only with respect to the effects of staminate duration and pollination. The analysis reveals that pistillate duration is inversely related to staminate duration and that pollination shortens the length of the pistillate phase (table 1). The variance in staminate duration on plants with developing fruits is not significantly decreased by either position or flower number ($R^2 = .03$, $P < .33$, no. = 71).

These models show that, within a flower, an increase in the staminate duration tends to decrease the length of the pistillate phase. Also, these analyses suggest that, when no fruit are developing on an inflorescence, the duration of both sexual phases progressively increases toward the terminal portion of the inflorescence. However, when developing fruits are present, this pattern disappears.

Discussion

In perfect-flowered plants where both sexes are simultaneously present in the same flower, it is difficult to determine whether the roles of pollen dissemination and reception are continuous throughout the lifetime of the flower or whether one role occupies a greater proportion of time. In dichogamous species, however, it is relatively simple to assign the proportion of time devoted to each sexual function. Data, collected in 1980, revealed that the staminate duration in field populations of *Lobelia cardinalis* was approximately twice that of the pistillate duration. These data prompted us to examine the factors that control staminate and pistillate duration and, ultimately, to determine whether this difference in duration is an inherent feature of the species.

The data from this study show that the duration of the staminate phase is significantly affected by the amount and frequency of pollen removal. When the anther tube of *L. cardinalis* is completely drained of its pollen on a daily basis, mature pollen can be removed from the anther tube for 3–4 days. This finding implies either that pollen is being matured over several days or that previously matured pollen is being released into the anther tube over a 3–4 day period. Thus, 3–4 days can be considered as the minimum duration of the staminate phase. If pollen is not removed from the anther tube, the average length of the staminate phase increases to 9.6 days. Thus, 9–10 days can be considered as the maximum duration of the staminate phase. An in-

TABLE 1
FACTORS THAT INFLUENCE STAMINATE AND PISTILLATE DURATIONS: MULTIPLE REGRESSION RESULTS
A. PISTILLATE DURATION

	Flowers pollinated/ unpollinated (FP)	Staminate duration (SD)	No. flowers (NF)	Position on inflorescence (PO)
Without A ^a developing fruit:				
Slope	-.17	-.04	.06
r ²56	.24	.29
P > F0001	.0001	.0001
With developing fruit:				
Slope	Pollinated = 4.2 ^b Unpollinated = 4.8 ^b	-.42	.004	.004
r ²06	.27	.0009	.0005
P > F03	.0001	.81	.85

B. STAMINATE DURATION				
		No. strokes (NS)	No. flowers (NF)	Position on inflorescence (PO)
Without ^a developing fruit:				
Slope	0-stroke = 1.9 ^b 3-stroke = 1.49 ^b		.005	.02
r ²24	.009	.08
P > F0001	.18	.0001
With B ^a developing fruit:				
Slope			-.001	.04
r ²005	.001
P > F96	.24

^a Staminate and pistillate durations of plants without developing fruits were log-trans-
formed. Overall intercept: A = 2.6, B = 5.4.
^b Because FP and NS are classification variables, the values represent the intercept for
a given treatment.

termediate level of pollen removal such as that found in the 3-stroke treatment resulted in an intermediate duration for the staminate phase. In naturally pollinated plants at the field site in 1980 and 1982 (DEVLIN and STEPHENSON, unpublished data), the duration of the staminate phase also fell between the minimum and maximum reported in this study.

The factors that influence pistillate duration include pollen deposition and staminate duration. When flowers are pollinated on the first day of the pistillate phase, the duration of the pistillate phase is, on average, less than 2 days. If flowers are never pollinated (3-stroke treatment), the duration increases to 2.4–3.4 days, depending on the presence of developing fruit and the length of the staminate phase. These values can be viewed as the minimum and maximum durations of the pistillate phase. At the field site in 1980 and 1982, naturally pollinated flowers produced intermediate values for pistillate duration (DEVLIN and STEPHENSON, unpublished data).

It is of interest that the minimum duration of the staminate phase is approximately equal to the maximum duration of the pistillate phase (with no de-

veloping fruit on the inflorescence and all pollen removed daily from the staminate phase of the flowers). This, however, could occur on natural field populations only if the hummingbirds regularly visited the staminate phase flowers but completely neglected the pistillate phase flowers. This is unlikely. Rather, we found consistent differences in duration of the sexual phases under both field and greenhouse conditions over three seasons of study. Consequently, we conclude that the differences in the length of the sexual phases are an inherent feature of *L. cardinalis*.

Another factor that appears to influence the duration of the staminate and pistillate phases is the presence or absence of developing fruit. Regression analyses reveal that both staminate and pistillate durations increase significantly with floral position on the inflorescence if there are no developing fruits on the inflorescence (0-stroke and 3-stroke treatments), but the durations of the two phases do not change with floral position if developing fruits are present (two-thirds pollination treatment).

Apparently, there is something about the lack of developing fruit that progressively increases the

duration of those flowers produced later (higher) on the inflorescence. We speculate that the resources that would have been allocated to fruit developing on the lower portion of an inflorescence are reallocated, at least in part, to the flowers on the upper portions. This explanation assumes that prolonging the duration of both sexual phases of a flower requires additional resources. There should be an increase in the metabolic costs associated with maintaining a flower for a longer period of time, but it would also be interesting to know whether the apical flowers on unpollinated inflorescences also produce more nectar, pollen, and ovules than the apical flowers on pollinated inflorescences.

Our interpretation of the position effect is analogous to the interpretation of the pattern of fruit maturation in herbaceous species with protracted flowering periods. In these species, the first flowers to open usually have a very high probability of maturing a fruit, but the last flowers almost never set fruit (STEPHENSON 1981). Temporal decline in fruit set can be averted if the early-blooming flowers are thinned before or after pollination. Under these conditions, fruit set on the remaining flowers approaches the proportion expected from the earlier flowers (MANN and ROBINSON 1950; VAN STEVENICK 1957). These studies show that flowers are inhibited from setting fruit if other pollinated flowers and juvenile fruit are developing. This suggests that flowers and young fruit compete for limited resources and that the pattern of resource allocation can be altered within a plant during the growing season.

The data on the duration of the sexual phases of *L. cardinalis* can also be used to evaluate LLOYD and YATES'S (1982) conclusions on the evolution of dichogamy. They predicted that, when fruit and seed production is limited by resources, the duration of the staminate phase should be prolonged (emphasized) with respect to the duration of the pistillate phase, thereby increasing the opportunities for pollen donation. In addition, they predicted that the staminate phase should be retained until all pollen is removed. Our data support these predictions. In all field and experimental situations, the staminate phase of *L. cardinalis* flowers is longer than the pistillate phase. Furthermore, because there is a negative relationship between pollen removal

and the length of the staminate phase and because the length of the staminate phase in natural populations falls below the maximum staminate duration, it is reasonable to conclude that, in most instances, the staminate phase lasts until the pollen is removed.

LLOYD and YATES (1982) also postulated that the temporal divergence of the male and female sex organs within the flower is a mechanism that prevents each type of organ from interfering with the performance of the other. Our data suggest that the duration of the pistillate phase in *L. cardinalis* is inversely related to the staminate phase. Consequently, even though the phases are temporally separated, interference can occur. This interference, however, is likely to occur only in plants that are infrequently visited by hummingbirds. Thus, the importance of this phenomenon in natural populations is unclear.

Finally, it is clear from our data that the length of both the staminate and pistillate phases of *L. cardinalis* is the result of a complex interaction of many factors. Because the duration of both the staminate and pistillate phases in natural populations of *L. cardinalis* falls between the minimum and maximum length, it is reasonable to conclude that the duration of the respective phases in natural populations is controlled by pollinator activity. Pollinator activity may influence the relative success of plants as pollen donors and seed producers (MÜLLER 1873; HENSLow 1888; WILLSON and PRICE 1977; BAWA 1980; BEACH 1981). However, in *L. cardinalis*, pollinator activity (or the lack of it) can influence the number of staminate and pistillate phase flowers that are open on an inflorescence at any given time and thereby influence the ratio of staminate to pistillate flowers in the population as a whole.

Acknowledgments

We thank LLOYD DRIVER for the use of the greenhouse facilities and the general care of the greenhouse plants, G. TUCKER and S. T. STEPHENSON for assisting with the greenhouse experiments, and J. B. HORTON and L. R. STARK for constructive comments on a previous version of this manuscript.

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