

FLORAL LONGEVITY AND REPRODUCTIVE ASSURANCE: SEASONAL PATTERNS AND AN EXPERIMENTAL TEST WITH *KALMIA LATIFOLIA* (ERICACEAE)¹

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Floral longevity is assumed to reflect a balance between the benefit of increased pollination success and the cost of flower maintenance. Flowers of *Kalmia latifolia* (Ericaceae), mountain laurel, have a long duration and can remain viable up to 21 d if unpollinated. I experimentally tested whether this long duration increases pollination success by clipping stigmas to reduce functional floral longevity to 3–4 d. Clipping stigmas decreased fruit set from 65% to only 10%. Flowers with natural life spans were not pollination-limited, demonstrating that long floral duration ensured female reproductive success. The long floral duration of *K. latifolia* was unique in this site (the Great Swamp, Rhode Island, USA). Coflowering shrubs in summer had a mean floral life span of 3.4 d. Spring-flowering species had significantly longer mean floral durations (7.2 d). These duration differences may reflect seasonal variation in pollinator availability. However, *K. latifolia* flowers in summer, when its bumble bee pollinators are abundant but it is a poor competitor for bees because its flowers produce little nectar. The long floral duration allows *K. latifolia* to outlast coflowering competitors and attract sufficient pollinators. I hypothesize that the long floral duration of *K. latifolia* functions as a mechanism for competitive avoidance and reproductive assurance.

Key words: competition for pollinators; competitive avoidance; Ericaceae; floral longevity; flowering phenology; fruit set; Great Swamp, Rhode Island; induced floral senescence; *Kalmia latifolia*; pollination limitation; reproductive assurance.

In pollination studies, much attention has focused upon floral traits that assure successful pollination by increasing the attraction or rewards for animal pollinators (e.g., Waser, 1983; Bell, 1985; Real and Rathcke, 1991; Caruso, 2000) or by increasing the effectiveness of pollen transfer (e.g., Campbell et al., 1996). More recently, it has been recognized that floral longevity (the length of time a flower remains open and functional) is a trait that could ensure successful pollination in habitats where pollinators are sparse or uncertain (Primack, 1985; Ashman and Schoen, 1994, 1996; Khadari et al., 1995). For example, plants growing in alpine habitats, which typically have few, unpredictable pollinators, have longer floral durations than plants at lower elevations with more abundant, predictable pollinators (Arroyo et al., 1981; Stratton, 1989; Bingham and Orthner, 1998; Blionis and Vokou, 2001; Blionis et al., 2001). Ashman and Schoen (1994, 1996) have proposed a mathematical model in which the duration of floral life is determined by a balance between female fitness accrual rates (pollen receipt), male fitness accrual rates (pollen dissemination), and the cost of flower maintenance (see also Charnov, 1996). By measuring pollen deposition and removal and estimating maintenance costs, Ashman and Schoen (1994) found a significant positive correlation between floral longevity observed in the field and predicted floral longevity for 11 plant species. However, they note that there was not a close quantitative fit and that environmental factors, including pollination, may influence floral longevity in the field. Also, they did not measure effects on fruit or seed set. No experimental tests

have demonstrated that longer durations of floral life increase fruit or seed set of flowers in the field.

Here I present an experimental test of the pollination benefit of long floral duration for mountain laurel, *Kalmia latifolia* L. (Ericaceae). Flowers can remain viable for 2–3 wk if unpollinated, and they rapidly senesce after pollination (Rathcke, 1988a; Nagy et al., 1999). I reduced the functional longevity of flowers by clipping stigmas and then compared fruit sets (fruits initiated per number of flowers) of experimental and control flowers. I also did procedure controls, and I tested whether control (naturally pollinated) flowers were pollination limited by augmenting flowers with cross-pollen. I compare the floral longevity of *K. latifolia* with other shrub species growing in the same habitat and for different flowering seasons (spring and summer). I discuss possible reasons for the maintenance of long floral duration in this species.

MATERIALS AND METHODS

This study was done in the Great Swamp, Rhode Island, USA (41°29' N, 72°32' W) (for a description of the site, see Rathcke [1988a, b]). *Kalmia latifolia*, mountain laurel, is a tall evergreen shrub that grows in the understory of forests and on mountains in eastern North America. Shrubs have tubular, pink-white flowers displayed in inflorescences (corymbs) of 10–300 flowers, and individual shrubs may have thousands of flowers open at the same time. Bumble bees were the only flower visitors and pollinators of *K. latifolia* (Rathcke, 1988a, b). In this low elevation habitat, flowers do not self-pollinate (Rathcke, 1988a), although flowers can self-pollinate at the end of flower life in a montane habitat in Virginia (Rathcke and Real, 1993; Levri, 1998; Nagy et al., 1999). Fruits are dry capsules with hundreds of tiny seeds.

Reduction of floral duration—For the experiment, I tagged four budded inflorescences on each of 14 shrubs. For each shrub, two inflorescences were assigned to controls and two were assigned to experimental treatments. For each assigned inflorescence, new flowers (in anthesis) were tagged with color-coded yarn every 2 d throughout the flowering season (12–29 June). To reduce the functional floral longevity for female function, I clipped the stigmas of all flowers after they had been receptive (glistening and sticky) for 3–4 d. I

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TABLE 1. Percentage fruit sets of *Kalmia latifolia* flowers with natural floral longevities and with reduced functional longevities (3–4 d) created by clipping stigmas (means \pm 1 SD). Fruit set = 100 (fruit/flowers), N = number of plants (number of flowers). Difference between control and treatment was tested using Friedman's non-parametric t test with plant as the sample unit. The asterisk denotes a significant difference; probability level is shown.

Treatment	N	Fruit set (%)	P
Natural longevity	14 (612)	65 \pm 17.7*	<0.0001
Reduced longevity	14 (568)	10 \pm 8.3	

chose 3–4 d because most other shrubs that cflowered with *K. latifolia* in June had floral longevities of 3–4 d (Rathcke, 1988b). Stigmas were clipped with scissors just below the sticky surface, and the scissors were sterilized with ethanol after each use. Experimental flowers and control flowers were exposed to natural pollination, and subsequent fruit sets were measured and compared.

I also did a procedural control treatment to ascertain whether stigma clipping harmed flowers or normal fruit development. I augmented other flowers with cross-pollen and clipped their stigmas the following day. To determine whether stigma clipping would preclude subsequent pollination and fertilization as assumed, I clipped stigmas of virgin flowers and immediately added pollen to the remaining styles. Fruit sets were compared between these treatments and controls.

Fruit set—Fruit set was calculated as the percentage of flowers that initiated fruits. Percentage fruit set was calculated for each inflorescence, and a mean was calculated for each individual shrub for each treatment. Fruit initiation after a month of development was assumed to indicate that flowers had been successfully pollinated and fertilized. Previous studies showed that little fruit abortion occurs after initiation, so these values also closely reflect final fruit set (Rathcke, 1988a). Seeds were not measured.

Pollination limitation—To test for pollination limitation of fruit set of flowers, I compared the fruit set of naturally pollinated flowers to the fruit set of flowers augmented with cross-pollen. In the pollen-augmentation treatment, all open flowers on one inflorescence on each of the experimental shrubs were augmented every 2 d with cross-pollen mixed from four other distant shrubs. The pollination limitation of entire plants was not determined because each shrub typically has thousands of flowers. It is known that augmented pollination of a subset of flowers on a plant may influence the fruit set of other flowers or may reduce fruit set in subsequent years because of resource reallocation (Zimmerman and Pyke, 1988). However, the experimental flowers in these shrubs were usually <1% of the total flowers on a shrub and seem unlikely to have strongly affected the fruit set of other inflorescences.

A relative index of pollination limitation (PL) was calculated based on fruit sets (FS) of control flowers with natural longevity (control) and of experimental flowers with shortened longevity (experimental) as follows:

$$PL = 100 (\% \text{ FS of control} - \% \text{ FS of experimental}) / (\% \text{ FS of control})$$

If the fruit sets of control and experimental flowers are equal, then PL = 0%. If fruit set were zero for experimental flowers and 100% for control flowers, then PL would equal 100% (Rathcke, 2000).

Comparisons of floral longevities—In a previous study, longevities of bagged flowers were measured for other shrub species growing in this site (Rathcke, 1988b). Flowers were bagged with bridal veiling to exclude pollinators, and flowers were individually tagged, color-coded by day of opening, and monitored daily until flowers senesced. For five of these species, the floral longevities of naturally pollinated flowers were also measured and compared with that of unpollinated flowers (Rathcke, 1988b).

For this study, the mean floral longevities of spring and summer flowering shrubs were compared to each other and to *K. latifolia*. To test whether the floral longevity of *K. latifolia* reflected a trait shared with other species in the

TABLE 2. Percentage fruit sets of *Kalmia latifolia* flowers in controls and in two experimental treatments: (1) with stigmas pollinated and subsequently clipped and (2) with stigmas clipped and styles immediately pollinated (means \pm 1 SD). Fruit set = 100 (fruit/flowers), N = number of plants (number of flowers). Difference between control and treatment was tested using Friedman's non-parametric t test with plant as the sample unit. NS indicates no significant difference.

Treatment	N	Fruit set (%)	Significance
Control	14 (612)	65 \pm 17.7	NS
Pollinated, then clipped	9 (224)	61 \pm 16.2	
Control	14 (612)	65 \pm 17.7	not tested
Clipped, then pollinated	9 (149)	0	

same family (Ericaceae), the same comparisons were made using only ericaceous shrubs.

Statistical analyses—Differences in fruit sets among different treatments were tested with nonparametric Friedman's paired-sample sign tests because percentage data are not distributed normally and because individual shrubs can differ in fruit set for other reasons and can be considered blocks. In this test, the ranking in one block (plant) is independent of the ranking in another block (Sokal and Rohlf, 1981). Tests are based on plants (blocks), not flowers, although the numbers of flowers are shown. Differences in floral longevities of different species were tested with Student's t tests because the data met the assumption of homogeneity of variances based on Bartlett's tests. Statistical analyses were done using SYSTAT, version 5.01 (Systat Inc., Evanston, Illinois, USA).

RESULTS

Floral longevity experiment—Flowers with reduced functional floral longevity had only 10% fruit set, whereas control flowers with natural longevities had 65% fruit set (Table 1). Reduced floral longevity resulted in 85% pollination limitation of fruit set. Stigma clipping did not harm flowers or fruit development. The mean fruit set of flowers that were hand-pollinated and then clipped on the following day was not significantly different from the mean fruit set of hand-pollinated, unclipped flowers (Table 2). Stigma clipping precluded subsequent pollination and fertilization as assumed; stigmas of virgin flowers that were clipped and the styles pollinated produced no fruit (Table 2).

Pollination limitation—Mean fruit sets of naturally pollinated flowers and pollen-augmented flowers were not significantly different, indicating that fruit set was not limited by pollination (Table 3).

Comparisons of floral longevities—Shrubs that flowered in spring had longer floral longevities of 6–9 d (Table 4) and a

TABLE 3. Percentage fruit sets of *Kalmia latifolia* flowers with natural pollination and with augmented cross-pollen (means \pm 1 SD). Fruit set = 100 (fruit/flowers), N = number of plants (number of flowers). Difference between the control and treatment was tested using Friedman's nonparametric t test with plant as the sample unit. NS indicates no significant difference.

Treatment	N	Fruit set (%)	Significance
Natural pollination	14 (612)	65 \pm 17.7	NS
Augmented pollination	14 (537)	50 \pm 16.2	

TABLE 4. Floral longevities for shrubs flowering in spring (May) and summer (June and July) in the Great Swamp, Rhode Island, USA. Modes in days shown. (Table modified from Table 3 in Rathcke, 1988b).

Family	Species	No. days
Spring-flowering shrubs		
Ericaceae	<i>Gaylussacia baccata</i>	6
Ericaceae	<i>Vaccinium atrococcum</i>	8
Ericaceae	<i>Vaccinium corymbosum</i>	9
Caprifoliaceae	<i>Viburnum cassinoides</i>	6
Summer-flowering shrubs		
Ericaceae	<i>Kalmia latifolia</i>	8
Ericaceae	<i>Kalmia angustifolia</i>	4
Ericaceae	<i>Rhododendron viscosum</i>	4
Ericaceae	<i>Gaylussacia frondosa</i>	3
Ericaceae	<i>Lyonia ligustrina</i>	4
Clethraceae	<i>Clethra alnifolia</i>	3
Aquifoliaceae	<i>Ilex glabra female</i>	5
Aquifoliaceae	<i>Ilex opaca female</i>	4
Liliaceae	<i>Smilax glauca male</i>	2

mean of 7.2 d (Table 5), whereas shrubs that flowered in summer had floral longevities of 3–4 d (Table 4) and a mean of 3.4 d (Table 5). The mean floral longevities were significantly different for summer- and spring-flowering shrubs (Table 5). The floral longevity of *K. latifolia* was significantly longer than that of other summer-coflowering shrubs (Table 5). The floral longevity of *K. latifolia* was not significantly different from the mean floral longevity of spring-flowering shrubs (Table 5), but the maximum floral longevity of *K. latifolia* (21 d) was much longer than that found for any other shrub species in this community.

Shrubs in the Ericaceae showed a similar seasonal pattern in floral longevities; spring-flowering species had longer floral life spans than summer-flowering species (Table 6). The floral longevity of *K. latifolia* was significantly longer than that of other summer-flowering ericaceous shrubs and was similar to that of spring-flowering ericaceous shrubs (Table 6).

DISCUSSION

These experimental results demonstrate that long floral duration can significantly increase successful pollination and fruit set in *K. latifolia*. Flowers with natural longevities were not pollination-limited, whereas flowers with reduced longevities (3–4 d) showed 85% pollination limitation of fruit set. Long floral duration lasting up to 21 d is clearly advantageous to female fitness in *K. latifolia*, and is unique in this site. Other shrubs that coflower in summer with *K. latifolia* had a mean life span of only 4.2 d for bagged flowers. Spring-flowering

shrubs had longer mean floral durations (7.2 d) than summer-flowering shrubs. This seasonal difference in floral duration may reflect the seasonal change in pollinator abundance observed in this habitat. In spring, all pollinators are scarce and bees are infrequent, consisting mostly of a few queen bumble bees starting their colonies and a few species of solitary bees, mostly *Andrena*. In addition, weather is often unfavorable to pollinator activity. In contrast, bee pollinators are abundant in summer because bumble bee colonies have produced many workers and many solitary bee species are present (Rathcke, 1988a, b). Low pollinator abundance in different habitats has often been related to longer floral durations in these habitats (Arroyo et al., 1981; Primack, 1985; Stratton, 1989; Bingham and Orthner, 1998; Blionis et al., 2001; Blionis and Vokou, 2001). In this one habitat, the seasonal change in pollinator abundance is accompanied by a seasonal change in floral longevities, but it cannot explain the long floral duration of *K. latifolia* because it blooms in summer when its bumble bee pollinators are abundant.

Although pollinator abundance is lower in spring, the longer floral life spans of spring-flowering shrubs could also reflect cooler temperatures, which may reduce metabolism and slow development. Arroyo et al. (1981) reported that mean longevity of flowers was 4.1 d at a low elevation site (2320 m asl) and 9.0 d at a high elevation site (3550 m asl) in the Andes, and they attributed the difference to slower floral development at cooler temperatures. However, cooler temperatures could be a proximate cue for the ultimate factor of low pollinator availability. In either circumstance, *K. latifolia* again is an exception because it blooms during the warmer days of June but has long floral duration.

The long floral duration of *K. latifolia* is not a trait shared by other shrubs in the same family (Ericaceae) that were growing in this site. *Kalmia latifolia* has greater floral longevity than other ericaceous species that coflower in summer, including one congeneric species, *K. angustifolia* (Table 6). Although the mean floral longevity (8 d) of *K. latifolia* was not significantly different from spring-flowering Ericaceae, the maximum floral longevity for *K. latifolia*, up to 21 d, was much longer than the floral maximum of any other shrub in the community.

The long floral duration of 21 d in *K. latifolia* is unusual for plant species in general. Floral longevities of 2 wk or longer have been reported for relatively few species. These species include some orchids (Primack, 1985), two fig species (Khadari et al., 1995), and some wind-pollinated species (Primack, 1985), and their long flower durations have been attributed to low probabilities of pollination (Primack, 1985). Most plant species have floral longevities of 2–4 d (Primack, 1985; Stratton, 1989). Tropical species often have floral longevities

TABLE 5. Comparisons of floral longevities of shrubs in the Great Swamp, Rhode Island, USA, between different seasons and with *Kalmia latifolia* (means \pm 1 SD). Significant differences were tested by Student's *t* tests. Asterisks denote significant differences; probability levels are shown. NS indicates no significant difference. See Table 4 for species names.

Comparison	N (species)	Floral longevity (d)	P
Spring-flowering shrubs	4	7.2 \pm 1.50*	<0.01
Summer-flowering shrubs, <i>K. latifolia</i> excluded	8	3.4 \pm 1.06	
Summer-flowering shrubs, <i>K. latifolia</i> excluded	8	3.4 \pm 1.06*	<0.01
Summer-flowering <i>K. latifolia</i>	1	8	
Spring-flowering shrubs	4	7.2 \pm 1.50	NS
Summer-flowering <i>K. latifolia</i>	1	8	

TABLE 6. Comparisons of floral longevity of ericaceous shrubs in the Great Swamp, Rhode Island, USA, between different seasons and with *Kalmia latifolia* (Ericaceae) (means \pm 1 SD). Significant differences were tested by Student's *t* tests. Asterisks denote significant differences; probability levels are shown. NS indicates no significant difference. See Table 4 for species names.

Comparison	N (species)	Floral longevity (d)	P
Spring-flowering shrubs	3	7.7 \pm 1.53*	<0.01
Summer-flowering shrubs, <i>K. latifolia</i> excluded	4	3.8 \pm 0.50	
Summer-flowering shrubs, <i>K. latifolia</i> excluded	4	3.8 \pm 0.50*	<0.01
Summer-flowering <i>K. latifolia</i>	1	8	
Spring-flowering shrubs	3	7.7 \pm 1.53	NS
Summer-flowering <i>K. latifolia</i>	1	8	

of only 1 d, possibly because of high rates of predation or bacterial and fungal decay (Primack, 1985). Risk of disease has been proposed to shorten floral longevity (Shykoff et al., 1996). In this study, neither flower predation nor infection of flowers was evident for any of the species, although fungal pathogens on leaves have been shown to increase fruit abortion and affect mating in *K. latifolia* in Virginia (Levri and Real, 1998). The apparent lack of floral predation or disease may allow long floral duration of *K. latifolia* in this site.

What is a possible explanation for the long floral duration of *K. latifolia*? I propose that long floral duration is advantageous because *K. latifolia* is a poor competitor for pollinators and that it is a mechanism for competitive avoidance. Flowers of *K. latifolia* produce little nectar and are infrequently visited by bumble bees when other shrub species are flowering (Rathcke, 1988a). Bumble bees are the only pollinators of *K. latifolia* in this habitat, and they preferentially visit species with higher nectar rewards. The long floral duration of *K. latifolia* increases the probability that flowers will be pollinated after competing species cease flowering (Rathcke, 1988a). Because unpollinated flowers remain viable, they extend the flowering phenology of *K. latifolia* into a competition-free period. In addition, long floral duration may provide pollination assurance when pollinators are scarce and allow *K. latifolia* to tolerate conditions of low pollinator activity. Such tolerance of low pollinator activity may be an alternative strategy to having greater attraction or rewards and greater competitive ability for pollinators (Rathcke, 1988a).

Species that tolerate low resources have been termed "good response competitors" in contrast to "good effect competitors" that can deplete resources effectively (Goldberg, 1990; Miller and Travis, 1996). The ability of *K. latifolia* to tolerate low rates of pollinator visitation and its inability to compete effectively for pollinators make it a good response competitor. Why is *K. latifolia* a good response competitor, rather than a good effect competitor for pollinators? Higher nectar production per flower would make it more competitive with coflowering species (Rathcke, 1988a). However, greater nectar rewards would probably cause bees to forage longer within individual shrubs and would promote geitonogamy (within-plant pollination) and selfing (Rathcke and Real, 1993). Because *K. latifolia* shows strong inbreeding depression with selfing, a strategy of higher nectar rewards could be detrimental to both female and male reproductive success (Rathcke, 1992; Rathcke and Real, 1993). Higher nectar production would also be costly in resources. Other traits could also increase attractiveness (Waser, 1983; Caruso, 2000), but higher rewards would be necessary to increase the ability of *K. latifolia* to compete effectively for pollinators.

Another benefit of long floral duration can be to increase

the size of the floral display and attract more pollinators (Ishii and Sakai, 2001). However, large floral displays can also increase geitonogamy (within-plant pollination), which would be detrimental to *K. latifolia* because of strong inbreeding depression (Rathcke and Real, 1993). The cost from geitonogamy can be reduced by pollination-induced senescence, which removes flowers from the display when they are pollinated. Flowers of *K. latifolia* show pollination-induced senescence; corollas wilt and fall the day after they are successfully pollinated (Rathcke, 1988a). Pollination-induced senescence can also direct pollinators to viable flowers and increase the effectiveness of pollinator visits (van Doorn, 1997). In addition, flexible floral longevity can decrease transpirational water loss and energy costs of maintaining flowers (Primack, 1985; Stratton, 1989), which have been shown to be substantial in some species (Ashman and Schoen, 1997; Galen et al., 1999).

Whether the long floral duration of *K. latifolia* evolved as a response to competition for pollinators remains speculative. Instead, this trait may have evolved in areas such as montane habitats, where pollinators are sparse or unpredictable as has been reported for other species (Arroyo et al., 1981; Stratton, 1989; Bingham and Orthner, 1998; Blionis and Vokou, 2001; Blionis et al., 2001). The trait may have been maintained when it proved to be advantageous in more favorable sites where competition for pollinators was strong. Other species have evolved self-pollination, rather than long floral duration, for reproductive assurance in situations in which pollinators are sparse (Baker, 1955; Lloyd, 1980; Fausto et al., 2001). Self-pollination has also been invoked as a mechanism for competitive avoidance in *Arenaria uniflora* (Fishman and Wyatt, 1999). This study suggests that long floral life span can be an alternative to self-pollination under conditions of uncertain pollination and competition. In fact, *K. latifolia* exhibits both long floral duration and the ability to self-pollinate in a montane site in Virginia where pollinators are more unpredictable and where competition with other shrubs is also strong (Rathcke and Real, 1993; Nagy et al., 1999; B. J. Rathcke, unpublished data). Despite having both of these mechanisms for reproductive assurance, fruit set was pollination-limited in Virginia (Rathcke and Real, 1993). In contrast, fruit set was not pollination-limited in this habitat in Rhode Island, indicating that pollinators were more available, especially after competing shrubs ceased flowering. This greater availability of pollinators may explain why *K. latifolia* does not self-pollinate and has only prolonged floral duration as a mechanism for reproductive assurance in this Rhode Island habitat.

Floral senescence in *K. latifolia* is induced by pollen deposition, rather than pollen removal, which suggests that female function is less rapidly completed than male function (Proctor and Harder, 1995; Bell and Cresswell, 1998; Evanhoe

and Galloway, 2002). This response supports the assumption made here that female function and maintenance of fruit set is the important factor selecting for long floral duration in *K. latifolia*. Whatever the benefits and the adaptive origin of long floral duration of *K. latifolia*, these results demonstrate that long floral duration can function as a mechanism to avoid competition for pollinators and provide reproductive assurance. Whether long floral duration serves this function in other species remains to be determined.

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