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Individual flower demography, floral phenology and floral display size in *Silene latifolia*

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ABSTRACT

Flowers, as repeated modules on a plant, may show population dynamics that correspond to ecological models for population growth. We hypothesized that rate of flower production (birth rate), number of open flowers per day (population size) and flower duration (longevity) should be related to plant resource status. With dioecious species, resource demands of male or female function would contribute to sex-specific floral demographics. For example, fruit production in females imposes a resource cost that is absent in males. We recorded individual flower dynamics for 1200 flowers on 85 female plants and 11,179 flowers on 94 male plants in the dioecious species *Silene latifolia*. For males, resource availability was manipulated by defoliating a subset of plants (1587 flowers on 18 plants). For females, resource availability and usage was manipulated as follows: 0% pollinated (401 flowers on 16 plants), 50% pollinated (118 non-pollinated and 131 pollinated flowers on 17 plants), 100% pollinated (470 flowers on 46 plants) and 100% pollinated and defoliated (80 flowers on 6 plants). Populations of flowers on individual plants showed a good fit to the logistic population growth model. Estimated carrying capacities for flowers decrease with decreasing resource availability (males > defoliated males > 0% pollinated females > 50% pollinated females > 100% pollinated females > 100% pollinated and defoliated females). Pollinated flowers had shorter longevity than non-pollinated flowers. Non-pollinated flowers on plants with 50% pollination had shorter longevity than non-pollinated flowers on plants with 0% pollination. Thus, flower population dynamics within plants do show evidence of resource-based dynamics.

Keywords: demography, exponential growth, floral longevity, logistic growth, phenology, resource allocation, *Silene latifolia*.

INTRODUCTION

The phenology of flowering on an individual plant, and the resulting overall floral display, can be viewed as a population process. Onset and cessation of flowering, and the number of open flowers at any given time, are determined by the balance between initiation (=birth) and senescence (=death) of individual flower modules. Following an initial study by Bazzaz

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and Harper (1977), population dynamics models have been applied to a range of modular plant parts, including leaves and tillers (for a review, see McGraw and Garbutt, 1990). It has also been suggested that flower production, as a resource-based phenomenon, might also be usefully studied as a population process (Lovett Doust and Easton, 1982). However, population dynamics models have yet to be used to explore overall flowering phenology. The aim of this study was to explore the analogy between population dynamics models and the dynamics of flowers within individual plants.

As plants increase in size, and thus in photosynthetic area and root volume, resource acquisition capacity increases in correspondence to growth. At the same time, plants are investing resources in new activities, such as future growth, biomass maintenance and reproduction, all of which are based on different rates of resource utilization. Thus, the overall growth dynamics of a plant represents interplay among a range of competing rates of resource acquisition and usage. Plant growth is an inherently exponential process. Although most plants are indeterminate in growth, they do not increase in size indefinitely. One possible explanation for limitations on plant growth is that rates of resource utilization overtake resource acquisition, so that plant growth may enter a logistic phase of growth or eventually senescence. This basis for plant growth is the conceptual model that underlies the present study.

Within a plant, individual flowers open, have a certain lifespan and senesce. The rate at which flowers are produced on a plant is analogous to an intrinsic rate of increase of a population of organisms and may be determined by the available resource base for flower production in the same manner that resource availability can limit birth rate in a population. Similarly, the maximum number of flowers that will be supported by a plant – its 'carrying capacity' – could be determined by the rate of resource utilization for flower production and support in balance with the resource acquisition capacity of the plant (Burd and Head, 1992; Ashman, 1994). Finally, maintenance of an open flower imposes a resource cost such that flower longevity will be influenced by the overall resource capacity of the plant (Ashman and Schoen, 1994; Schoen and Ashman, 1995).

Several factors can influence the resource status of a plant and thus the population dynamics of flowering. First, as noted above, plant size is an important factor in that it directly influences the rate of resource acquisition through photosynthetic capacity. Photosynthetic capacity can be experimentally manipulated by defoliating the plant (e.g. Elmqvist and Gardfjell, 1988; Spears and May, 1988; Lubbers and Lechowicz, 1989; Tuomi *et al.*, 1989; Delph, 1990; Delph *et al.*, 1993). The resource consumption rate of a plant can also be experimentally manipulated by varying the percentage of flowers pollinated (e.g. Lubbers and Lechowicz, 1989; Delph and Meagher, 1995; Laporte and Delph, 1996). A flower that does not set fruit incurs a much lower eventual resource cost than a flower that sets fruit.

Finally, in a dioecious species, the sex of the plant plays an important role in floral dynamics. In some dioecious species, the differential costs of male and female reproduction have resulted in differential life-history patterns, where female plants exhibit a higher vegetative growth rate or delay onset of flowering until they reach a greater overall vegetative size than males (Meagher and Antonovics, 1982; Allen and Antos, 1988, 1993; Meagher, 1999). In many cases, individual male flowers are less costly (Meagher, 1992, 1994; Ågren and Schemske, 1995; Carroll and Delph, 1996) or represent a much lower 'risk' in terms of later costs of fruit set (Wallace and Rundel, 1979; Meagher and Antonovics, 1982; Meagher, 1984). Thus, independently of plant size, the following factors influence resource status in

relation to flowering of dioecious plants in particular: sex of the plant (male *vs* female) and pollination status and resource costs of fruit set within females.

Here, we present a model of floral display as a consequence of the population dynamics of individual flower life histories in the dioecious species *Silene latifolia*. This species is characterized by a marked sexual dimorphism in overall flower number and flower size (Meagher, 1992, 1994), and resource allocation patterns associated with overall plant size and flowering have been studied extensively (Gehring, 1993; Delph and Meagher, 1995; Carroll and Delph, 1996; Laporte and Delph, 1996). We focus on the relationship between photosynthetic resource acquisition capability, manipulated through defoliation, and resource costs of fruit set on flower population dynamics within plants. The main aim of the study is to examine the efficacy of the logistic model for population growth in describing flower and floral display dynamics on a plant. We address the following specific questions: How does overall resource status influence flower population dynamics? How does sex influence phenological patterns (timing and longevity of flowers)? How does pollination affect phenological patterns in females, in both pollinated and non-pollinated flowers?

MATERIALS AND METHODS

In this study, we used a greenhouse population of *Silene latifolia*. These plants were established as part of a series of experiments to examine relationships between resource utilization patterns and sex (Delph and Meagher, 1995). The seeds originated from a single natural population located in a pasture near Blacksburg, VA. We planted the seed in the Rutgers University greenhouse on 10 July 1989, treated as day 0 in the following analysis, and maintained the plants as described by Delph and Meagher (1995) through to harvesting on 13–15 December 1989. Thus, the life span of the plants ranged from 156 to 158 days, with the first onset of flowering occurring on day 68 (16 September).

Each flower that appeared on a plant was tagged and monitored for each day that it was open. Thus birth date and longevity were recorded for each individual flower on each plant (Table 1). The plants fell into six resource categories. First, unmanipulated males ($n = 76$) were regarded as having the highest available resource for flower production, as the cost (and potential future cost) per flower was the lowest for this group. Next, males that were defoliated on the day of first flowering ($n = 18$) were regarded as having the next highest resource availability for flower production because the flowers were still relatively inexpensive but the productivity of the plant was limited. Females were generally regarded as incurring a greater resource cost per flower, since female flowers are larger and there is the added risk of pollination and subsequent cost of fruit set. Thus, females fell into three cost-of-flowering groups depending on pollination status: 0% of the flowers pollinated ($n = 16$), 50% of the flowers pollinated ($n = 17$) and 100% of the flowers pollinated ($n = 46$). Finally, females that were 100% pollinated and that were defoliated on the first day of flowering ($n = 6$) were regarded as having the lowest resource capacity for flowering.

The overall number of open flowers on a given plant was modelled using the logistic population growth equation, in which an exponential growth rate of the population is limited as the maximum number of flowers that can be supported is reached. The standard equation for logistic growth of ecological populations (Ricklefs, 1990) is:

$$dN/dt = rN((K - N)/K) \quad (1)$$

Table 1. Outline of flower data used in the present analysis

		Number		Birth date		Longevity	
	N	NP	P	NP	P	NP	P
Males							
Normal	76	9592		133.5		3.33	
Defoliated	18	1587		136.3		3.26	
Females							
0% pollinated	16	401		135.9		5.88	
50% pollinated	17	118	131	136.7	134.4	5.67	2.71
100% pollinated	46		470		126.3		2.87
100% pollinated and defoliated	6		80		130.4		2.70

Note: *N* is the number of plants in each category, number is the total number of flowers observed over all plants in each category, birth date is the mean number of days from date of planting until the flower opened, longevity is the mean number of days that the flower was open; NP = flowers not pollinated, P = flowers pollinated.

where N is the total number of individuals in a population (in the present case, flowers on a plant), t is a measure of time, r is the per individual (flower) rate of increase in number, and K is the maximum number of individuals (flowers) that can be supported by the population. In the case of flower production on a plant, flowers do not give birth to other flowers, but rather flowers develop at a rate determined by the resource status and overall development of the plant. Thus, in this case, flowers and flower production are manifestations of an underlying potential for investment in reproduction by the plant, and r and K are measures of the rate and eventual capacity of that investment. The observation base for this analysis was the cumulative number of open flowers on each plant for each day, and values for r and K were determined from non-linear regression analyses for each plant using the following solution to equation (1):

$$N_t = K/[1 + \{(K - N_0)/N_0\}e^{-rt}] \quad (2)$$

where N_t is the observed number of open flowers on day t, N_0 is a hypothetical starting value for flower production, r is the exponential rate of increase in flower number, and K is the maximum number of flowers that can be supported on a plant. Estimates of N_0, r and K were obtained for each plant using the procedure NLIN in SAS (SAS Institute Inc., 1996), which uses arbitrary initial values for parameters of interest (N_0, r and K) and iterates to obtain a least squares best fit to the non-linear regression model. Not all initial values enable successful convergence; initial values were varied until optimal starting points were determined for each plant. A lack of successful convergence was manifested by a failure to meet convergence criteria (least squares best fit) or by unbounded and extreme solutions (such as $K = 10^{42}$); both of these inappropriate outcomes result in warning messages from SAS. Results from regressions that converged successfully were compiled for subsequent analysis. Regressions for each plant were based on daily flower counts, starting from the date of first flowering for that plant. Time t was recorded as number of days from date of first flowering, such that values of t ranged from 1 to as high as 91 for each plant. This was done

so that the ordinal day within the sequence of flowering would be measured as the same for each plant. Significance tests for goodness of fit of the overall non-linear regressions were based on analysis of variance (ANOVA) using the sum of squares for the convergent parameter estimates. Significance tests of individual regression parameters were based on *t*-tests using the fitted values and their standard errors.

The compiled set of estimates of *r* and *K* was subjected to ANOVA to assess impacts of resource category (e.g. sex, defoliation and fruit set) on flower population dynamics. To ensure that more accurate estimates had a greater impact on the ANOVA, the WEIGHT option was used in SAS so that the analyses were weighted by the degree of statistical significance of departure of the parameter estimate from zero as determined by *t*-tests, with less significant estimates contributing less to the ANOVA.

Floral life history was summarized both on a per plant level and a per flower level within plants. On a per plant level, the overall resource status of the plants was determined by a measure of the final above-ground biomass of the plant at the end of the experiment, including all flowers produced and shed over the course of the experiment. Another per plant measure used was the date of first flowering, which, in turn, reflects the resource status of the plant early in the experiment. Per flower measures included the ordinal birth date of the flower (measured as number of days following the date of first flowering) and the longevity of the flowers (number of days that the flower remained open).

RESULTS

The general trend in flowering was that plants showed a gradual increase in flower production throughout the study (Fig. 1). Although there was no difference between the sexes in average date of onset of flowering, males produced substantially more flowers and maintained a larger standing population of flowers on any given day than females. There was also a general impact of resource status on flower production, with a clear trend towards decreased flower production with either an increase in cost (females with increasing levels of pollination) or a decrease in resources available (defoliation). It is also clear from inspection of the overall phenological pattern that sexual dimorphism in flower production is sharply enhanced by pollination of female flowers. The 0% pollinated females were much more male-like in their overall phenology than females that were pollinated at rates of 50% or 100%.

Most of the plants analysed also showed a significantly good fit to a logistic growth curve (Figs 2 and 3), so that it was possible to evaluate flower population growth rates and carrying capacities (Fig. 4). Unmanipulated males showed the lowest flower population growth rate and the highest carrying capacity. Defoliated males had a slightly lower carrying capacity and they reached it faster, reflecting a slightly higher flower population growth rate. This trend continued through successively increasing resource cost in females, so that plants that experienced 100% pollination as well as defoliation had a very low carrying capacity (essentially one flower at a time). Thus, as plants become more resource-stressed, the ability to fit a population growth model becomes diminished because the standing population of flowers is so small. The ANOVA of *r* estimates showed significant heterogeneity among resource categories, with a general tendency towards an increase in *r* with decreasing resource status (Table 2). The ANOVA of *K* estimates across the resource categories showed significant heterogeneity, with a general tendency towards a decrease in *K* with decreasing resource status (Table 2). For both population growth parameters, there was a substantial

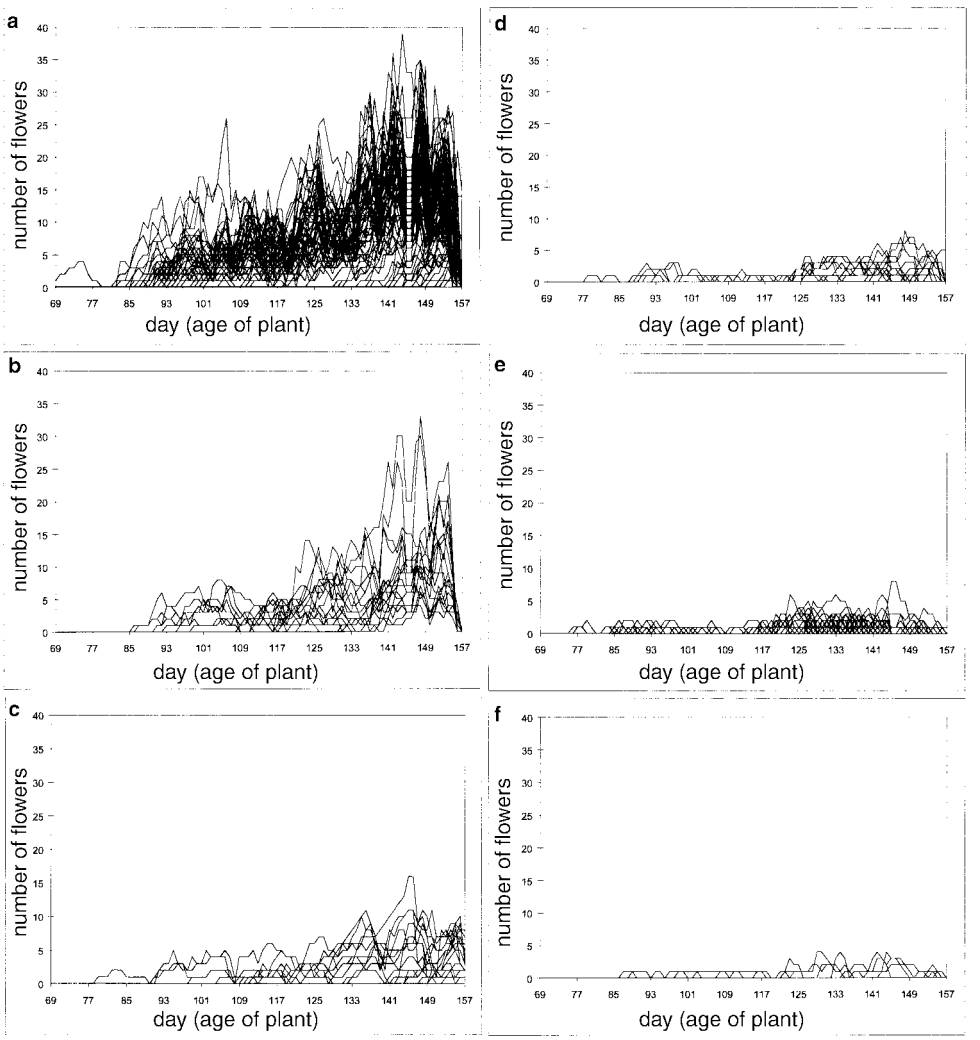

Fig. 1. Flowering phenology patterns for plants in the six resource categories (from lowest to highest): (a) unmanipulated males, (b) defoliated males, (c) 0% pollinated females, (d) 50% pollinated females, (e) 100% pollinated females, (f) defoliated 100% pollinated females.

impact of plant sex (male *vs* female) in addition to the impact of resource status, and the impact of plant sex was consistent with the apparent impact of resource status variation within sex: modifying the cost of flower production in relation to available resources, either by increasing flower size, eventual cost due to fruit production, or by reducing resource assimilation (defoliation), has a significant impact on the population dynamics parameters underlying flower production.

The resource status of the plant also influenced flower birth date (Table 3) and flower longevity (Table 4). The earliest average flower initiation took place in the 100% pollinated females, reflecting the fact that flower production in females shuts down very quickly if

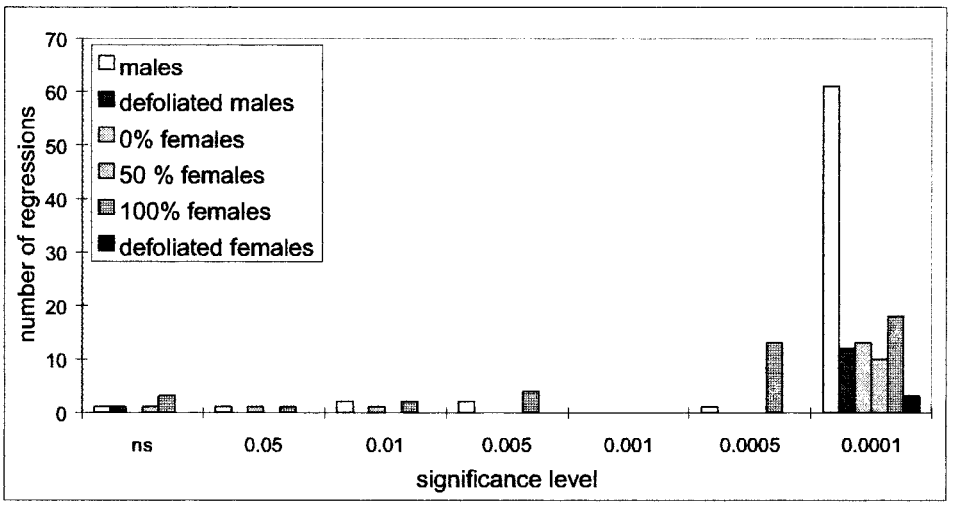

Fig. 2. Frequency distributions of statistical significance levels for non-linear regressions on flowering phenology patterns over the six resource categories.

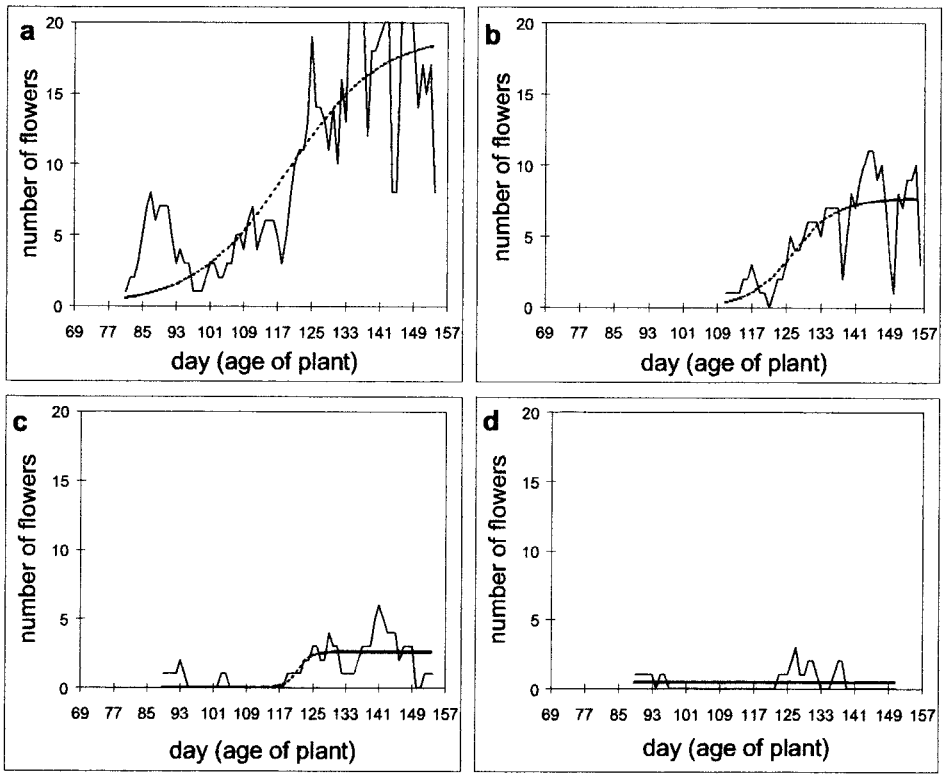

Fig. 3. Selected individual flowering phenology patterns and fitted logistic growth curves for plants falling into four resource categories: (a) unmanipulated males, (b) defoliated males, (c) 0% pollinated females, (d) 50% pollinated females.

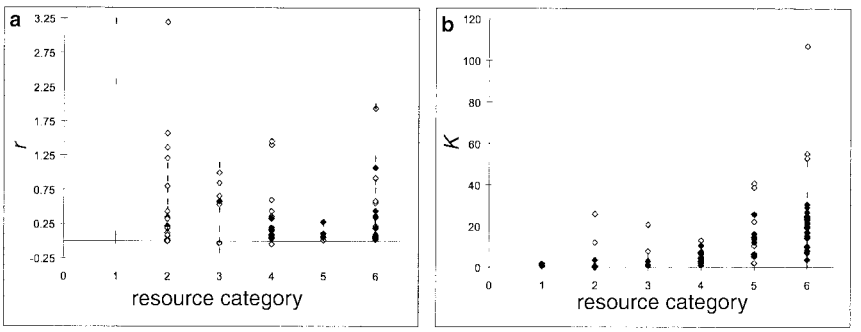

Fig. 4. Estimates of r (a) and K (b) obtained from the non-linear regression analysis for plants in each of the six resource categories. Sample sizes for the numbers of plants in each resource category are shown in the first column of Table 1. ◆, estimates that were significantly different from 0 at the 5% significance level; ◇, estimates that were not statistically significant.

Table 2. Multiple range test results from an ANOVA of population projection parameters weighted by level of statistical significance

	r ($F_{5,144} = 3.16$, $P < 0.0097$)			K ($F_{5,144} = 19.19$, $P < 0.0001$)		
Resource category	Mean	Duncan group	Scheffé group	Mean	Duncan group	Scheffé group
Males						
Normal	0.25	B	B	17.54	A	A
Defoliated	0.12	B	B	17.28	B	A
Females						
0% pollinated	0.32	B	B	5.94	B	AB
50% pollinated	0.56	B	AB	2.44	B	B
100% pollinated	0.47	B	A	0.63	B	B
100% pollinated and defoliated	1.11	A	A	1.19	B	B

Note: Letter codes for Duncan and Scheffé indicate means that were not significantly different.

flowers are pollinated. Male plants also had a relatively early average birth date of flowers, suggesting that they had more flowers earlier on in their flowering sequence. This reflects the fact that males had a higher K, so they achieved a higher standing population of flowers earlier on in their life cycle, whereas in general females with a low K had their flowering more evenly distributed, with a higher percentage of their flowers being initiated later. In terms of longevity, pollinated female flowers had the lowest longevity, followed by male flowers and then non-pollinated female flowers. Within female plants, pollination of other flowers on the same plant resulted in a shorter life span for non-pollinated flowers, as shown by the observed lower longevity of non-pollinated flowers on 50% pollinated females in comparison with non-pollinated flowers on 0% pollinated females. Pollinated flowers also

tend to shut down quickly, so that pollinated flowers on females had the lowest longevity of all flower types. Thus, pollination and the resulting resource cost of fruit set have consequences at the level of the whole plant in terms of flower production as well as at the level of the individual flower in terms of flower longevity.

Finally, we explored relationships between two whole plant measures of resource status (date of first flowering and final above-ground dry weight) and average flower life histories (birth date and longevity) for plants in the different resource categories (Table 5). For all resource categories, larger plants showed a non-significant trend towards earlier onset of flowering, as shown by the negative correlations between these characters. Plants that had an earlier onset of flowering tended to have later average flower birth dates, as reflected in the negative correlations between these variables, which can be attributed to the fact that larger plants had a greater overall flower production and continued to produce more and more flowers, so that their average flower birth date was later. The correlation between date of first flowering and longevity was not consistent, being positive for defoliated plants and negative for the other groups. This suggests that flower longevity is influenced by both the strength of the resource base, as reflected in variation in onset of flowering, and ongoing input into the resource base, which would be more limited in defoliated plants of either sex. This is also influenced by defoliation taking place at the onset of flowering. Plants that started flowering later had a greater reserve of resources for maintaining flower longevity, so that defoliation did not have as much time to result in an adverse effect on flower longevity as for plants that began flowering earlier and hence were defoliated earlier. The other correlation that varied was the one between final dry weight and longevity, which was

Table 3. Results of an ANOVA among individual flower birth dates

Source	d.f.	MS	*F*-ratio
Resource category	6	5298.68	2.6 ($P < 0.0500$)
Plants(resource category)	132	1902.78	6.5 ($P < 0.0001$)
Error	12 222	290.90	

Resource category	Mean	Duncan group	Scheffé group
Males			
Normal	133.5	AB	AB
Defoliated	136.3	A	AB
Females			
0% pollinated	135.9	A	AB
50% pollinated [non-pollinated flower]	136.7	A	A
50% pollinated [pollinated flower]	134.4	A	AB
100% pollinated	126.3	C	C
100% pollinated and defoliated	130.4	B	BC

Note: Data for flowers from different plants are nested within resource category. Significance tests for differences among flowering category use the MS for plants nested within flowering category as the error MS. Letter codes for Duncan and Scheffé indicate means that were not significantly different.

Table 4. Results of an ANOVA among individual flower longevities

Source	d.f.	MS	*F*-ratio
Resource category	6	194.52	20.6 ($P < 0.0001$)
Plants(resource category)	131	9.45	10.0 ($P < 0.0001$)
Error	11 373	0.95	

Resource category	Mean	Duncan group	Scheffé group
Males			
Normal	3.32	C	B
Defoliated	3.26	C	B
Females			
0% pollinated	5.88	A	A
50% pollinated [non-pollinated flower]	5.67	B	A
50% pollinated [pollinated flower]	2.71	D	C
100% pollinated	2.87	D	C
100% pollinated and defoliated	2.70	D	C

Note: Data for flowers from different plants are nested within resource category. Significance tests for differences among flowering category use the MS for plants nested within flowering category as the error MS. Letter codes for Duncan and Scheffé indicate means that were not significantly different.

positive for males and negative in 100% pollinated females. For males, it would seem that bigger plants produced longer-lived flowers, which makes sense in that bigger plants would be better able to maintain the flowers for longer. In contrast, the 100% pollinated females shut their flowers down faster if they were bigger, as shown by the negative correlation between dry weight and longevity, suggesting that bigger plants, operating with a larger resource base, were faster at initiating fruit development.

DISCUSSION

The population dynamics analogy appears to provide an effective description of flower dynamics in *Silene latifolia*. Furthermore, the population dynamics of flowers responds to underlying changes in plant resources, particularly in terms of the eventual number of flowers supported on a plant (K), suggesting that flower populations are subject to logistic resource constraints in much the same way that a population of organisms might ultimately be limited by its ecological carrying capacity as determined by resource availability. Such logistic constraints on flower population growth would, of course, be determined by per flower resource costs. Indeed, *S. latifolia* manifests a size–number trade-off in flower production when per flower costs are driven to extremes by selection on flower size (Meagher, 1994).

Various models have been proposed for the timing of flowering in relation to resource availability in plants (Burd and Head, 1992; Ashman, 1994; Ashman and Schoen, 1994; Schoen and Ashman, 1995). Specifically, in addition to an initial cost, flowers produced

Table 5. Correlations among dry weight and flower life-history variables

	First flowering	Relative birth date	Longevity
Males			
Dry weight	−0.212[a] (69)	+0.232[a] (69)	+0.075[a] (68)
First flowering		−0.992[e] (76)	−0.335[d] (74)
Relative birth date			+0.303[c] (74)
Defoliated males			
Dry weight	−0.318[a] (16)	+0.366[a] (16)	+0.225[a] (16)
First flowering		−0.975[e] (18)	+0.156[a] (18)
Relative birth date			−0.243[a] (18)
0% pollinated females			
Dry weight	−0.095[a] (13)	+0.136[a] (13)	+0.134[a] (13)
First flowering		−0.991[e] (16)	−0.331[a] (16)
Relative birth date			+0.306[a] (16)
50% pollinated females, flower not pollinated			
Dry weight	−0.413[a] (14)	+0.557[b] (14)	−0.082[a] (14)
First flowering		−0.922[e] (17)	−0.468[a] (16)
Relative birth date			+0.395[a] (16)
50% pollinated females, flower pollinated			
Dry weight	−0.413[a] (14)	+0.605[b] (14)	−0.049[a] (14)
First flowering		−0.934[e] (17)	−0.468[a] (16)
Relative birth date			+0.342[a] (16)
100% pollinated females			
Dry weight	−0.217[a] (44)	+0.251[a] (44)	−0.055[a] (44)
First flowering		−0.919[e] (46)	−0.245[a] (46)
Relative birth date			−0.265[a] (46)
100% pollinated and defoliated females			
Dry weight	−0.448[a] (6)	−0.019[a] (6)	−0.118[a] (6)
First flowering		−0.684[a] (6)	+0.477[a] (6)
Relative birth date			−0.489[a] (6)

Note: Sample sizes are in parentheses. [a] Not significant; [b] $P < 0.05$; [c] $P < 0.01$; [d] $P < 0.005$; [e] $P < 0.0001$.

have an ongoing maintenance cost due to nectar production, respiration, transpiration, and so on. Thus, the dynamics and longevity of flowers on a plant is determined jointly by the required capital investment of resources and the diminishing effectiveness of flowers as pollen sources or recipients in relation to their maintenance cost. The differential capital cost of male flowers and female flowers has been determined for *S. latifolia* (Carroll and Delph, 1996), and an impact of this difference is evident in the eventual difference in flower carrying capacity between the sexes (males have a higher carrying capacity). Diminishing returns on maintenance costs of flowers might also be the basis for the observed sexual

dimorphism in floral longevity. Males, as pollen donors, would be expected to undergo a loss of effectiveness as more and more of the pollen is removed, whereas non-pollinated female flowers remain reproductively viable. Thus, shedding flowers to prevent resource drain and enable the production of new flowers might be more pronounced in males. This effect is seen in our results quite clearly: male flowers are indeed short-lived in comparison with non-pollinated female flowers. Indeed, reduced longevity in male flowers is a general trend in dioecious plant species (Primack, 1985; Carr, 1991), and a similar shorter period of male activity relative to female function has even been reported in hermaphroditic flowers (Preston, 1991).

Resource dynamics may provide a mechanism for floral turnover on a plant, but it does not necessarily account for evolutionary causality. The manner in which resources are accumulated and allocated is also subject to natural selection and could change over time to maximize fitness in response to other ecological factors influencing a plant. In the case of *Silene latifolia* and related species in the Caryophyllaceae, one such ecological factor is the widespread occurrence of the smut disease *Microbotryum violaceum* (= *Ustilago violacea*), which is transmitted via pollinators from plant to plant. This disease and its epidemiology have been viewed by many as a plant-based model for sexually transmitted diseases (Skogsmyr, 1993; Alexander *et al.*, 1996). In general, increased visitation by pollinators enhances the probability of infection, such that later flowering and reduced flower production are favourable (Thrall and Jarosz, 1994; Alexander and Antonovics, 1995; Biere and Antonovics, 1996; Biere and Honders, 1996). In a population infested with *M. violaceum*, rapid turnover of male flowers might also be favoured by selection to reduce the probability of infection by shedding the flower before the fungal spores can germinate and spread into the plant (Shykoff *et al.*, 1996).

Our previous results have suggested that sexual dimorphism in *Silene latifolia* is strongly related to differences in resource utilization between the sexes (Delph and Meagher, 1995). In addition to a difference in capital cost of flowers, there is a substantial difference between the sexes in the risk of future cost; female flowers, if pollinated, will incur the cost of fruit set and seed production. Plants appear to respond to this differential risk in terms of the reduced longevity of non-pollinated flowers on plants that have some flowers pollinated compared to plants in which no flowers have been pollinated. It would also appear that the overall sexual dimorphism in the dynamics of flower production is determined in part by this differential risk of cost of fruit set. Specifically, female plants with no flowers pollinated were markedly more male-like in their overall phenological pattern.

Differences in ultimate costs of flowering in male and female plants are a major factor underlying sexual dimorphism in plants. The fact that female flowering ultimately results in a higher resource cost to the plant has been well documented in many species (Meagher and Antonovics, 1982; Meagher, 1984; Delph, 1990; Korpelainen, 1992; Gehring, 1993; Cippolini and Whigham, 1994; Costich, 1995). In terms of phenology, this not only impacts flower production within a season as shown here, but among seasons as well. Females have been shown to flower less frequently over a span of years than males in several dioecious species (Meagher and Antonovics, 1982; Meagher, 1984; Cippolini and Stiles, 1991; Thomas and Lafrankie, 1993; Garcia and Antor, 1995). Thus, increased resource cost of flowering in females manifests itself on a range of levels, from competition for resources within seasons to longer-term dynamics of plant resources among seasons.

Another way of considering the dynamics of flowering is that observed flowers on a plant represent a physical manifestation of the resource capacity to produce flowers. Thus, the

models we impose on flower population dynamics are an indirect measure of the dynamics of underlying resource units. For example, initiation of a flower will only occur when the underlying critical accumulation of resource units needed has occurred, and this critical accumulation will be lower for males than for females in *S. latifolia*. Differences in critical accumulation between the sexes might contribute to the earlier onset of flowering in males of *S. latifolia* as observed in previous studies (Meagher, 1992; Purrington, 1993). The effects of critical resource accumulation might also explain why the population model analogy breaks down for increasingly resource-stressed female plants, such that the population growth rate estimate for this group is the highest. A useful way to envision this is that we are actually measuring the population dynamics of abstract growth units, where flowers are only produced when a critical number of growth units has accumulated. Since male flowers ultimately tie up fewer growth units, the population dynamics of male flowers more closely models the dynamics of the underlying units. For females, with more resource-costly flowers, we may only be measuring a more truncated portion of the resource dynamics; the full curve would include the accumulation of resource units building up to the point where an actual flower is generated.

In summary, we have shown that the phenology of flowering over the course of a season shows a good fit to a resource-based population growth model. This interpretation of flower production and longevity provides a very reasonable framework for the analysis of patterns of flowering in relation to resource availability in *Silene latifolia*. The applicability of this model has further implications for plant growth and development. For example, the population dynamics of resource units that underlie population growth of flowers on an individual can be influenced in a variety of ways. Our results show that changes in resource accumulation (defoliation) or utilization (sex or pollination level) status have such an impact. Other external influences on resource availability, such as fertilizer levels or light and water availability, might be expected to influence such patterns as well. Furthermore, internal variation in photosynthetic capacity, water utilization and metabolic efficiency would also have an impact on the growth rate of resource units.

Variation in the underlying growth rate of resource units for flowering could account for a number of different phenological patterns observed in plants. We have already seen here an example of logistic patterns of flower population growth. Another possibility is that, if the resource growth rate were driven to high levels, and if the cost per flower were greater than each individual resource unit, then it would be possible for plants to overshoot their capacity for flower production. This would open the possibility that plants might show other aspects of non-linear dynamics (e.g. May, 1981; Godfray and Blith, 1990) in flowering, such as cyclical flowering or chaotic fluctuation in flower number. One such effect would be plants that produce a flush of flowers, shut down for a while and then produce a later flush of flowers. If the resource growth rate were high enough, the plants might even fluctuate so widely as to produce a flush of flowers and then die, as is observed in monocarpic species.

Future work on the relationships between growth rates of flower populations on plants could include additional manipulations of resource availability to mimic various ecological factors. In the case of *Silene latifolia*, one such factor in females might be predation of fruit or seed (Wright, 2000). If such predation took place early in fruit development, it might relax the resource stress of setting fruit and promote additional flowering. It would also be interesting to explore the underlying resource currency that is the limiting factor for flower production. Various workers have investigated this in terms of the energy or nutrient

content of mature flowers (e.g. Ashman, 1994), but this addresses the finished product, not necessarily the cost of production. Relating flower initiation and longevity to measures of the growth rate of underlying resource units could provide valuable insight not only into flower production, but also into other aspects of plant growth. Finally, one could explore the relationship between ecological adaptation to different background environments and primary resource availability and its ultimate impact on flower population dynamics.

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REFERENCES

Ågren, J. and Schemske, D.W. 1995. Sex allocation in the monoecious herb *Begonia semiovata*. *Evolution*, **49**: 121–130.

Alexander, H.M. and Antonovics, J. 1995. Spread of anther smut diseases (*Ustilago violacea*) and character correlations in a genetically variable experimental population of *Silene alba*. *J. Ecol.*, **83**: 783–794.

Alexander, H.M., Thrall, P.H., Antonovics, J., Jarosc, A.M. and Oudemans, P.V. 1996. Population dynamics of plant disease: a case study of anther smut disease. *Ecology*, **77**: 990–996.

Allen, G.A. and Antos, J.A. 1988. Relative reproductive effort in males and females of the dioecious shrub *Oemleria cerasiformis*. *Oecologia*, **76**: 111–118.

Allen, G.A. and Antos, J.A. 1993. Sex ratio variation in males and females of the dioecious shrub *Oemleria cerasiformis*. *Am. Nat.*, **141**: 537–553.

Ashman, T.-L. 1994. A dynamic perspective on the physiological cost of reproduction in plants. *Am. Nat.*, **144**: 300–316.

Ashman, T.-L. and Schoen, D.J. 1994. How long should flowers live? *Nature*, **371**: 788–790.

Bazzaz, F.A. and Harper, J.L. 1977. Demographic analysis of the growth of *Linum usitatissimum*. *New Phytol.*, **78**: 193–208.

Biere, A. and Antonovics, J. 1996. Sex-specific costs of resistance to the fungal pathogen *Ustilago violacea* (*Microbotryum violaceum*) in *Silene alba*. *Evolution*, **50**: 1098–1110.

Biere, A. and Honders, S.J. 1996. Impact of flowering phenology of *Silene alba* and *S. dioica* on susceptibility to fungal infection and seed predation. *Oikos*, **77**: 467–480.

Burd, M. and Head, G. 1992. Phenological aspects of male and female function in hermaphroditic plants. *Am. Nat.*, **140**: 305–324.

Carr, D.E. 1991. Sexual dimorphism and fruit production in a dioecious understory tree, *Ilex opaca* Ait. *Oecologia*, **85**: 381–388.

Carroll, S.B. and Delph, L.F. 1996. The effects of gender and plant architecture on allocation to flowers in dioecious *Silene latifolia* (Caryophyllaceae). *Int. J. Plant Sci.*, **157**: 493–500.

Cipollini, M.L. and Stiles, E.W. 1991. Costs of reproduction in *Nyssa sylvatica*: sexual dimorphism in reproductive frequency and nutrient flux. *Oecologia*, **86**: 585–593.

Cipollini, M.L. and Whigham, D.F. 1994. Sexual dimorphism and cost of reproduction in the dioecious shrub *Lindera benzoin* (Lauraceae). *Am. J. Bot.*, **81**: 65–75.

Costich, D.E. 1995. Gender specialization across a climatic gradient: experimental comparison of monoecious and dioecious *Ecballium*. *Ecology*, **76**: 1036–1050.

Delph, L.F. 1990. Sex-differential resource allocation patterns in the subdioecious shrub *Hebe subalpina*. *Ecology*, **71**: 1342–1351.

Delph, L.F. and Meagher, T.R. 1995. Sexual dimorphism masks life history trade-offs in the dioecious plant *Silene latifolia*. *Ecology*, **76**: 775–785.

Delph, L.F., Lu, Y. and Jayne, L.D. 1993. Patterns of resource allocation in a dioecious *Carex* (Cyperaceae). *Am. J. Bot.*, **80**: 607–615.

Elmqvist, T. and Gardfjell, H. 1988. Differences in response to defoliation between males and females of *Silene dioica*. *Oecologia*, **77**: 225–230.

Garcia, M.B. and Antor, R.J. 1995. Sex ratio and sexual dimorphism in the dioecious *Borderea pyrenaica* (Dioscoreaceae). *Oecologia*, **101**: 59–67.

Gehring, J.L. 1993. Temporal patterns in the development of sexual dimorphisms in *Silene latifolia* (Caryophyllaceae). *Bull. Torrey Bot. Club*, **120**: 405–416.

Godfray, H.C.J. and Blith, S.P. 1990. Complex dynamics in multispecies communities. *Phil. Trans. R. Soc. Lond. B*, **330**: 221–223.

Korpelainen, H. 1992. Patterns of phenotypic variation and sexual size dimorphism in *Rumex acetosa* and *R. acetosella*. *Bot. Helv.*, **102**: 109–120.

Laporte, M.M. and Delph, L.F. 1996. Sex-specific physiology and source–sink relations in the dioecious plant *Silene latifolia*. *Oecologia*, **106**: 63–72.

Lovett Doust, J. and Easton, G.W. 1982. Demographic aspects of flower and fruit production in bean plants, *Phaseolus vulgaris* L. *Am. J. Bot.*, **69**: 1156–1164.

Lubbers, A.E. and Lechowicz, M.J. 1989. Effects of leaf removal on reproduction *vs* belowground storage in *Trillium grandiflorum*. *Ecology*, **70**: 85–96.

May, R.M. 1981. *Theoretical Ecology: Principles and Applications*, 2nd edn. Boston, MA: Blackwell.

McGraw, J.B. and Garbutt, K. 1990. Demographic analysis. *Ecology*, **71**: 1199–2004.

Meagher, T.R. 1984. Sexual dimorphism and ecological differentiation of male and female plants. *Ann. Missouri Bot. Gard.*, **71**: 254–264.

Meagher, T.R. 1992. The quantitative genetics of sexual dimorphism in *Silene latifolia*. I. Genetic variation. *Evolution*, **46**: 445–457.

Meagher, T.R. 1994. The quantitative genetics of sexual dimorphism in *Silene latifolia*. II. Responses to sex-specific selection. *Evolution*, **48**: 939–951.

Meagher, T.R. 1999. The quantitative genetics of sexual dimorphism. In *Sexual Dimorphism in Plants* (M. Geber, T. Dawson and L. Delph, eds), pp. 275–294. New York: Springer-Verlag.

Meagher, T.R. and Antonovics, J. 1982. The population biology of *Chamaelirium luteum*, a dioecious lily. III. Life history studies. *Ecology*, **63**: 1690–1700.

Preston, R.E. 1991. The intrafloral phenology of *Streptanthus tortuosis* (Brassicaceae). *Am. J. Bot.*, **81**: 1044–1053.

Primack, R.B. 1985. Patterns of flowering phenology in communities, populations, individuals, and single flowers. In *The Population Structure of Vegetation* (J. White, ed.), pp. 571–593. Dordrecht: Dr W. Junk.

Purrington, C.B. 1993. Parental effects on progeny sex ratio, emergence, and flowering in *Silene latifolia* (Caryophyllaceae). *J. Ecol.*, **81**: 807–811.

Ricklefs, R.E. 1990. *Ecology*, 3rd edn. New York: W.H. Freeman.

SAS Institute Inc. 1996. *The SAS® System for Windows™, release 6.11*. Cary, NC: SAS Institute Inc.

Schoen, D.J. and Ashman, T.-L. 1995. The evolution of floral longevity: resource allocation to maintenance versus construction of repeated parts in modular organisms. *Evolution*, **49**: 131–139.

Shykoff, J.A., Bucheli, E. and Kaltz, O. 1996. Flower lifespan and disease risk. *Nature*, **379**: 779.

Skogsmyr, I. 1993. Male reproductive investment and venereal diseases in plants: the case of the sticky catch-fly, *Lychnis viscaria*. *Oikos*, **66**: 209–215.

Spears, E.E., Jr. and May, P.G. 1988. Effect of defoliation on gender expression and fruit set in *Passiflora incarnata*. *Am. J. Bot.*, **75**: 1842–1847.

Thomas, S.C. and Lafrankie, J.V. 1993. Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain forest. *Ecology*, **74**: 1529–1537.

Thrall, P.H. and Jarosz, A.M. 1994. Host pathogen dynamics in experimental populations of *Silene alba* and *Ustilago violaceae*. I. Ecological and genetic determinants of disease spread. *J. Ecol.*, **82**: 549–559.

Tuomi, J., Vuorisalo, T., Niemelä, P. and Haukioja, E. 1989. Effects of defoliation on female inflorescences in mountain birch, *Betula pubescens* subs. *tortuosa*. *Can. J. Bot.*, **67**: 334–338.

Wallace, C.S. and Rundel, P.W. 1979. Sexual dimorphism and resource allocation in male and female shrubs of *Simmondsia chinensis*. *Oecologia*, **44**: 34–39.

Wright, J.W. 2000. Pollination, seed predation and floral character evolution in *Silene latifolia*. Doctoral dissertation, Rutgers University, New Brunswick, NJ.