

VARIATION IN FLOWERING PHENOLOGY AND ITS CONSEQUENCES FOR LUPINES COLONIZING MOUNT ST. HELENS

JOHN G. BISHOP¹ AND DOUGLAS W. SCHEMSKE

Department of Botany, Box 355325, University of Washington, Seattle, Washington 98195-5325 USA

Abstract. Species colonizing large-scale disturbances face heterogeneous environmental conditions that may strongly affect the relationship between phenotypic variation and reproduction. We investigated spatiotemporal variation in individual plant flowering phenology, flower and fruit predation, plant size, and fruit production in populations of *Lupinus lepidus* colonizing landscapes created by the 1980 eruption of Mount St. Helens. We quantified these variables in three populations in 1990, one that survived the 1980 eruption and two newly founded colonizing populations, and continued study of one newly founded population through 1992. We used structural equation modeling (SEM) to analyze the direct and indirect effects of size, phenological variables, and predation on fecundity, and to compare path coefficients among years and populations. Flowering phenologies were constant among populations and years in colonizing populations, but plants in the surviving population flowered earlier, more synchronously, and for a shorter duration. Flower and fruit predation by lepidopteran herbivores varied substantially among populations and years, and phenological variables strongly influenced herbivore damage. Although mean flowering date had a direct positive effect on fruit number in all three years in the large colonizing population, the total effect of flowering date varied among years because later flowering resulted in greater fruit predation. In the surviving population more asynchronous individuals had more fruits, but mean date had no effect. We conclude that substantial spatiotemporal variability in optimal phenology may prevent fine-scale adaptation of flowering schedules, and that phenotypic variation and herbivory may affect the demography of colonization populations.

Key words: *colonization; herbivory; Lupinus lepidus; Mount St. Helens; path analysis; phenology; natural selection; structural equation modeling; synchrony.*

INTRODUCTION

Variation in community assembly and abiotic conditions during succession (del Moral and Wood 1993, Chapin et al. 1994) commonly presents colonizing species with heterogeneous and often unpredictable environmental conditions. Despite the expectation that such species have characteristics adapted to colonization (Baker 1965, Grime 1979, Brown and Marshall 1981), environmental heterogeneity may cause optimal trait values to change between episodes or at different stages and sites of colonization. In this case, individuals of even highly colonizing species are unlikely to possess the optimal phenotype for a particular colonizable habitat (Brown and Marshall 1981), a circumstance that may alter the demography of colonizing populations and result in variable selection pressures.

Phenology, the seasonal timing of life history events such as germination or reproduction, comprises a set of traits that may critically affect reproductive success (Rathcke and Lacey 1985) yet whose optima are likely to vary widely across colonizable habitats. Flowering

phenology is particularly important because it determines reproductive synchrony with potential mates (Augspurger 1981, Marquis 1988), synchrony with or attractiveness to pollinators (Schemske 1977, Augspurger 1981, Gross and Werner 1983), and utilization of seasonally available resources such as light or water (e.g., Schemske 1977, Schmitt 1983, Marquis 1988, Galen and Stanton 1991, Walker et al. 1995). Flowering time may also strongly affect reproductive success by determining synchrony with, and thus vulnerability to, floral herbivores and seed predators (e.g., Breedlove and Ehrlich 1968, 1972, Augspurger 1981, Schemske 1984, Pettersson 1991, English-Loeb and Karban 1992). If colonizing populations face heterogeneous and unpredictable assemblages of pollinators, herbivores, and resources, then individual variation in flowering phenology may have strong but spatially and temporally variable reproductive consequences.

Recent demographic analyses suggest that variation in fecundity, a component of female reproductive success, strongly affects the rate of population increase in growing (as opposed to stable or declining) populations (Bishop 1996, Oostermeijer et al. 1996, Parker 1996), indicating that spatiotemporal variation in average fecundity may affect the demography of colonizing populations. Because population growth is the best measure of fitness in organisms with overlapping genera-

Manuscript received 28 March 1996; revised 19 November 1996; accepted 10 March 1997; final version received 15 April 1997.

¹ Present address: Department of Botany, Washington State University, 14204 NE Salmon Creek Avenue, Vancouver, Washington 98686-9600 USA.

tions (Lande 1982), fecundity is likely to be an important component of fitness in growing populations. While spatial variation that is constant through time may result in locally adapted phenologies, temporal variation may prevent such local adaptation and lead to the evolution of increased phenotypic plasticity or the maintenance of genetic variation for these traits (Bradshaw 1965, Via and Lande 1987, Turelli 1988, Via et al. 1995). Although the importance of flowering time has been studied in early successional communities (Heinrich 1976, Gross and Werner 1983), we know of no studies that examine the spatiotemporal variability of the effect of flowering phenology on reproductive success following large-scale disturbances.

In this paper we examine the relationship between flowering phenology and fruit production in populations of a perennial lupine, *Lupinus lepidus* var. *lobbii*. These populations are colonizing primary successional landscape created by the 1980 eruption of Mount St. Helens (Washington, USA), and secondary successional habitat created by subsequent mudflows. Primary successional habitat was created by a massive debris avalanche that buried >60 km² to depths of >200 m, followed by blanketing flows of incandescent gas and pumice (Franklin et al. 1988). In 1981 a single individual of *L. lepidus* was found flowering on the debris avalanche deposits, 4 km from the nearest surviving population, and 200 m below its typical pre-eruption elevation (C. M. Crisafulli et al., *unpublished manuscript*). The resulting population has been the focus of numerous studies demonstrating the importance of *L. lepidus* in primary succession (e.g., Morris and Wood 1989, Halvorson et al. 1992; C. M. Crisafulli et al., *unpublished manuscript*).

The massive scale of the disturbance at Mount St. Helens is associated with striking spatiotemporal variation in pollinator and herbivore activity (Bishop 1996; J. G. Bishop, K. Werner, and D. W. Schemske, *unpublished manuscript*), plant community assembly (del Moral and Wood 1993), and resource availability (Braatne 1989, del Moral and Bliss 1993). In addition, the unusually low elevation of many colonizing lupine populations exposes them to higher temperatures, greater water availability, and longer growing seasons compared to those at pre-eruption elevations (Braatne 1989). These conditions have the potential to strongly affect flowering phenology and its effect on reproductive success in *L. lepidus*. In this paper we ask: (1) Is natural variation in flowering phenology related to female reproductive success (i.e., fecundity)? (2) Does flowering phenology indirectly affect fecundity by its effect on herbivore damage to reproductive structures? (3) Do populations differ in these relationships? and (4) Do these relationships change between years? In our analysis we illustrate the use of structural equation modeling (SEM), a generalized form of path analysis, for comparing path models among populations and

years, comparisons not made in previous ecological studies.

METHODS

Species and study areas

Lupinus lepidus var. *lobbii* is a short-lived (up to 5 yr) legume characteristically found on subalpine pumice substrates in the Pacific Northwest (Kruckeberg 1987). Seeds germinate in May and June and individuals flower in their 2nd yr. Mature plants are generally <10 cm high, with stems spreading from a caudex in a circular pattern up to 80 cm in diameter. As in some other lupine species, flowers of *L. lepidus* are self-compatible but require pollinator visitation (primarily bumblebees, *Bombus* spp.) or wind agitation to set seed (J. G. Bishop et al., *unpublished manuscript*). The reproductive structures are attacked by a wide variety of herbivores (Bishop 1996); most common during the current study were larvae of the butterfly *Plebejus icarioides montis* (Lycaenidae), which chew through flower parts to eat developing seeds.

In 1990 we quantified individual flowering phenology and female reproductive success in two newly founded (1984, 1987) populations on the debris avalanche (hereafter termed "large" and "small" colonizing populations), and one population that survived the 1980 eruption ("surviving population"). The vegetation in the vicinity of the colonizing populations is species poor (Wood and del Moral 1987), and dominated by *L. lepidus*. The large colonizing population, at 1030 m elevation, is 2 km from surviving vegetation, and 5 km from the nearest surviving populations of *L. lepidus*. In 1990 the population contained >10 000 individuals spread over ~1 ha. The small colonizing population is made up of five patches consisting of 17–40 individuals each. This population is at 1130 m, ~1.5 km from the large colonizing population and 500 m from surviving vegetation. The area encompassed by the small colonizing population is approximately equal to that of the large colonizing and surviving populations and represents an early stage in the formation of a population like the large colonizing one.

The surviving population was severely disturbed by the Pine Creek lahar, but it occurs in nearly continuous surviving vegetation and with numerous associated species, unlike the two colonizing populations (del Moral and Wood 1988). This site, at 1350 m, is 200–300 m higher than the colonizing sites and is within 800 m of coniferous forest remnants. As in the large colonizing population, the surviving population comprised >10 000 plants spread over ~1 ha.

Census protocol

The goal of our field protocol was to measure naturally occurring covariation in individual plant size, timing of reproduction, insect damage to reproductive structures, and fecundity. In June 1990, before the onset

of flowering, we established four 40-m transects in both the large colonizing and surviving populations, marking the plant nearest the transect at 2.0-m intervals for a total of 80 plants/population. All plants were studied in the small colonizing population, for a total of 144 plants. For each plant we estimated seven variables: (1) plant diameter, (2) total flower number, (3) flowering duration, (4) mean date of inflorescence production (mean date), (5) flowering asynchrony, (6) percentage flower damage, and (7) total fruit number.

Plant diameter, estimated at the beginning of the growing season, is an appropriate measure of size in this species because the plants are prostrate and their planar projection is roughly circular. To estimate reproductive and phenological variables, we censused and marked all new inflorescences and all infructescences bearing nearly mature fruits at approximately weekly intervals throughout the flowering season. A week was the approximate time needed for the inflorescences marked at the previous census to finish flowering. This schedule resulted in 12 censuses in each colonizing population and 8 in the surviving population, which finished flowering several weeks earlier. We counted the number of flower scars on five randomly selected inflorescence stalks/plant, then estimated flower number as flowers/inflorescence \times total inflorescences.

We summarized individual phenologies using three variables: duration of flowering, asynchrony, and mean date. We calculated duration as the number of days elapsed between a plant's first and last flowering date. Mean date was the mean of census dates, in day of year (day 1 = 1 January), weighted by the number of inflorescences produced on each date. Asynchrony was calculated as the absolute value of the difference between each plant's mean date and the mean date of the entire population. Other phenological variables such as the higher moments of the distribution (e.g., variance or skewness in flowering time), first flowering date, and peak flowering date were all highly correlated with duration, mean date, or asynchrony, indicating that including them in our analysis would not provide additional insight but might result in statistical problems due to collinearity among variables (Mitchell-Olds and Shaw 1987, Petraitis et al. 1996).

We quantified flower damage by counting damaged (i.e., missing tissue) and undamaged flowers on seven haphazardly chosen inflorescences/plant at each census, if available. Percentage flower damage is the average percentage damage across dates weighted by the number of inflorescences on each date. Fruits were counted on seven infructescences (if available) on each plant at each census. We calculated total fruit number as a plant's mean fruits/infructescence on a given census date multiplied by the number of infructescences on that date, then summed over all census dates. Although total seed production would be a better estimate of reproductive success, our data for seeds/fruit are

incomplete. However, in 64 plants for which seed information was available, regression analysis indicated that fruit number uniquely explained 97.1% of the variance in total seeds compared to 0.1% of the variance explained by seeds/fruit. Fruit number and total seeds are also highly correlated (Pearson correlation coefficient = 0.98, $P < 0.0001$). Thus, fruit number provides a very good indicator of total seed number per plant.

We continued studying the large colonizing population for two subsequent years (1991 and 1992) to quantify temporal variation in colonizing populations; resources did not permit longitudinal study of more than one population. All measurements were repeated using the same plants as in 1990, except that plants that died between summers were replaced with their nearest neighbor. The population was censused 9 times in 1991 and 11 times in 1992. Two protocol changes were made. First, in 1991 we did not score flowers/inflorescence, so we calculated flower number by substituting each plant's value for flowers/inflorescence from 1990 or 1992 (or the mean). This procedure is reasonable because a regression using 213 plants for which flowers/inflorescence was available indicated that number of inflorescences uniquely explained 71.6% of the variance in total flower number, compared to only 4.4% for flowers/inflorescence. Thus, error in the substituted values of flowers/inflorescence would have relatively little effect on total flower number. Second, in 1991 and 1992 we estimated an eighth variable, percentage fruit damage, by counting the proportion of ripe or nearly ripe pods with holes made by caterpillars of *P. icarioides*. Damage by this species was not observed in 1990, but caused significant damage in 1991 and was present in 1992. We scored damage on 15 fruits/plant, if available, sampled evenly across infructescences. Damaged fruits rarely contained viable seeds, so we calculated undamaged fruits (fruit number \times [1 - fruit damage/100]) as an indicator of postdamage reproductive success.

Analysis

Comparison of population means.—We compared population means for all variables using Tukey tests for multiple comparisons among means (Zar 1984). We checked variables for conformation to normal distributions and compared ranks rather than means for variables that appeared non-normal. Separate analyses were performed for comparisons among populations in 1990 and among years in the large colonizing population. Significance levels were adjusted using sequential Bonferroni correction for the total number of comparisons in each analysis (Rice 1989).

Path model specification.—We used path analysis to investigate how well the data support a set of hypothesized relationships among the variables. The structure of these relationships is illustrated in a path diagram (Fig. 1), in which an arrow indicates the causal effect of one variable on another. For our purposes the pri-

mary advantage of path analysis is that it allows quantification of indirect paths. For example, in our model flower number, mean date, and asynchrony have direct effects on fruit number, but they also affect fruit number indirectly by affecting percentage flower damage. Although our choice of phenological variables was based partly on the correlation structure of a host of phenological variables, the relationships illustrated in our path diagram arise primarily from a priori knowledge, based on other studies and field experience with *L. lepidus*. For example, we hypothesized that plants with a greater prereproductive diameter would have a higher flower number because larger plants are likely to have more meristems dedicated to reproduction. If onset of flowering depends on reaching a resource threshold (Lacey 1986), then larger diameter may also result in an earlier mean date and longer flowering duration, and small plants may display greater asynchrony with the population mean because they reach a threshold size late in the season. If flower number is influenced by factors other than diameter, such as microclimatic conditions, it may directly affect mean date and duration (Fig. 1).

Size is also likely to affect the attractiveness of a plant to herbivores; therefore, we include flower number and fruit number as the components of size influencing percentage flower damage and percentage fruit damage, respectively (Fig. 1). We also expect that mean date and asynchrony will affect herbivory by determining whether reproductive structures are present when herbivores can do the most harm (Breedlove and Ehrlich 1968, 1972). We hypothesized that fecundity (fruit number and undamaged fruits) will largely be a function of flower number, but because percentage flower damage and percentage fruit damage cause direct damage to reproductive structures they may also directly decrease fecundity (Fig. 1). Flowering duration, mean date, and asynchrony may directly affect fruit number by determining vulnerability to unmeasured herbivory and access to resources needed for fruit ripening.

Model estimation.—The relationship between each dependent variable in the path diagram and its predictors is modeled as a linear equation whose coefficients (i.e., the path coefficients) indicate the magnitude of the effect of each predictor on the dependent variable, with the other predictors statistically held constant (Loehlin 1987). In most biological applications of path analysis the set of equations, one for each dependent variable, is solved with a series of multiple regressions (Kingsolver and Schemske 1991, Mitchell 1993), a method that is frequently misused (Petraitis et al. 1996). An alternative is to recognize that the path model specifies a covariance structure among the variables by dictating which variables can and cannot covary. One can then estimate path coefficients by finding those values that maximize the likelihood of the observed covariance structure given the covariance structure hy-

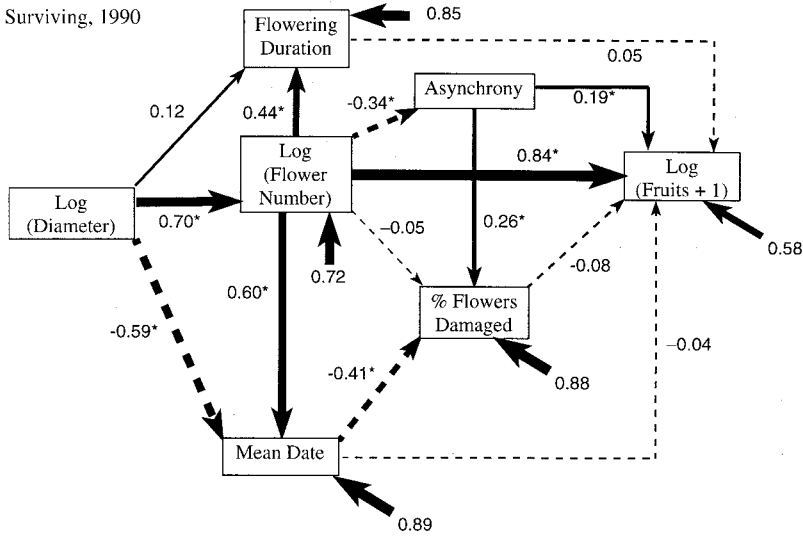
pothesized by the path model. These methods, implemented in structural equation modeling software such as LISREL or EQS 4.0 (Bentler 1989), have several advantages over ordinary path analysis, such as allowing confirmatory factor analysis and the evaluation of nested models (Loehlin 1987; see Mitchell 1992 and Pugusek and Tomer 1995 for biological applications). We utilize SEM in the current study because it allows simultaneous significance testing for the set of individual path coefficients, and allows an analysis of how multiple data sets differ when fit to the same path model, a procedure called “multisample analysis” (Bentler et al. 1987, Bentler 1989, known as a “stacked models” analysis in LISREL).

We used the maximum likelihood method in EQS 4.0 (Bentler 1989) to estimate standardized path coefficients in separate models for each population and year. These coefficients are equivalent to standardized partial regression coefficients. Correlation matrices used in this analysis are reproduced in the Appendix. We include in the analysis only plants that flowered. Diameter, flower number, fruit number, and undamaged fruits were log-transformed to meet the assumption of multivariate normality. No transformation normalized distribution of percentage fruit and flower damage, so these variables were left unaltered. We tested for collinearity among predictor variables, a common problem in path analyses, by calculating variation inflation factors (VIFs) for each independent variable (Petraitis et al. 1996). We also tested for nonlinear effects of predictor variables on fruit number using cubic spline regressions, with flower number as a covariate.

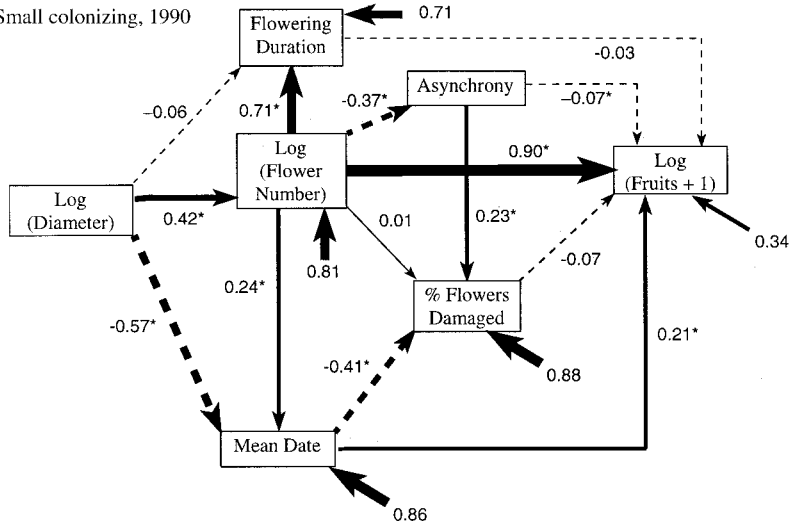
Models for the large colonizing population in 1991 and 1992 (Fig. 1d and e) contain additional paths to incorporate the effect of percentage fruit damage. However, we did not allow estimation of the path coefficients for the effect of percentage fruit damage and fruit number on undamaged fruits but instead fixed their values to their standardized partial regression coefficients. This was necessary because undamaged fruits was not measured independently, but calculated from percentage fruit damage and fruit number, and allowing these path coefficients to be freely estimated would artificially increase the model fit (Loehlin 1987). By fixing them in the model, we prevent them from entering the process of estimating model fit, but can still examine the indirect effect of other variables acting through these paths. Indirect effects of predictor variables on dependent variables were calculated by multiplying path coefficients involved in the indirect effect, and total effects were found by summing the direct and indirect effects of one variable on another.

Statistical criteria.—SEM allows assessment of the degree of fit between the observed and expected covariance structures, expressed as a goodness-of-fit χ^2 . A significant χ^2 indicates that the model does not fit the data. However, a significant χ^2 can also result from violation of several assumptions, and failure to reject

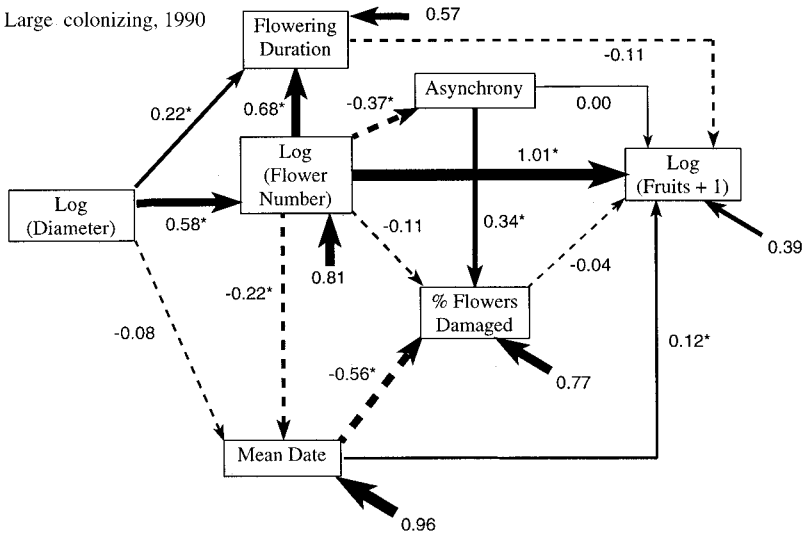
(a) Surviving, 1990



(b) Small colonizing, 1990



(c) Large colonizing, 1990



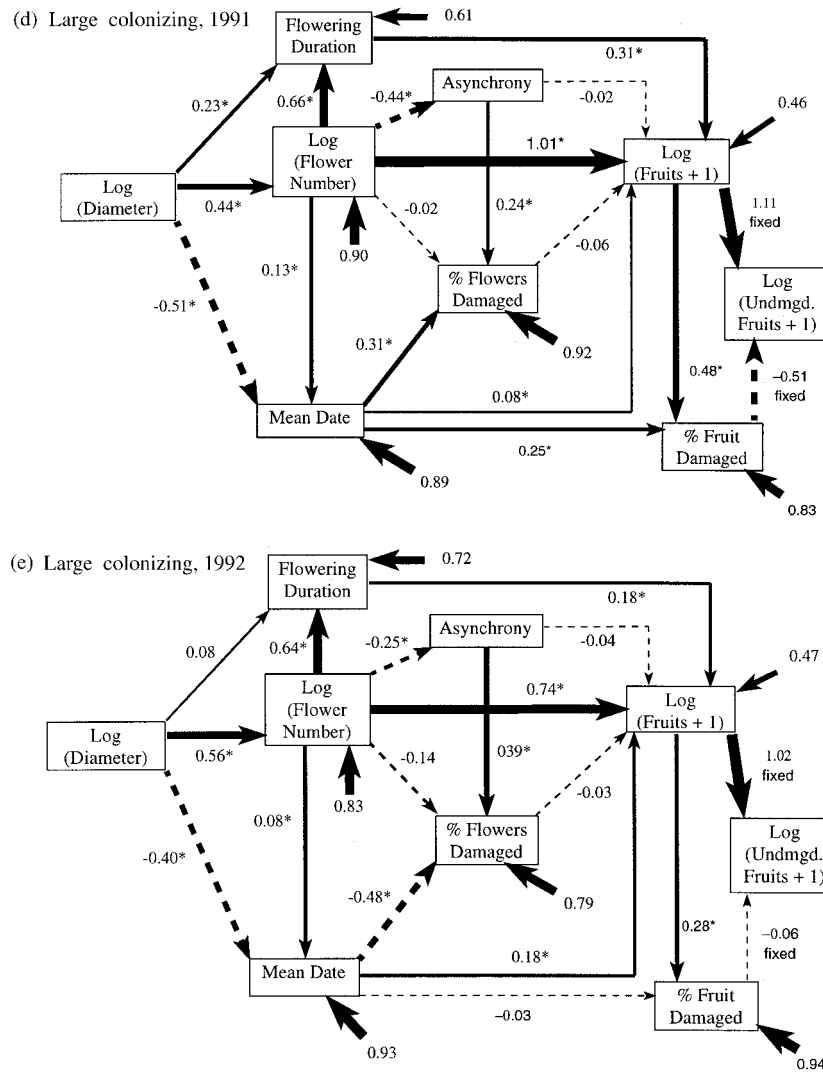


FIG. 1. Continued.

a model (a nonsignificant χ^2) may result from inadequate statistical power (Bentler 1989, Mitchell 1993). Therefore, we also report the Bentler-Bonett Normed Fit Index (NFI), which is based on the model χ^2 relative to that of a model that assumes independence of all variables. NFI ranges between 0 and 1, with NFI > 0.90 indicating a good fit (Bentler 1989), and tends to un-

derestimate model fit when sample sizes are small. We report overall fit to indicate that our models are a reasonable description of the processes that generate the observed correlations among variables, but our primary interest in model fit is in using it to assess the multivariate significance of individual path coefficients, and in the multisample analysis. It is worth noting that in-

←

FIG. 1. Path models for (a) surviving population, 1990; (b) small colonizing population, 1990; (c) large colonizing population, 1990; (d) large colonizing population, 1991; and (e) large colonizing population, 1992. Arrow widths are proportional to path coefficients. Coefficients indicate the expected change in the dependent variable if the predictor variable is changed one unit. Arrows not originating from a variable indicate the effect of unexplained causes. In 1991 and 1992 the path from asynchrony to percentage fruit damage was not significant and is omitted for clarity. Asterisks (*) denote path coefficients that are significantly different from 0. Goodness-of-fit statistics for each model are: (a) $\chi^2 = 6.3$, $df = 7$, $P = 0.50$, NFI = 0.97; (b) $\chi^2 = 15.4$, $df = 7$, $P = 0.03$, NFI = 0.96; (c) $\chi^2 = 6.1$, $df = 7$, $P = 0.52$, NFI = 0.98; (d) $\chi^2 = 14.1$, $df = 11$, $P = 0.22$, NFI = 0.95; (e) $\chi^2 = 9.4$, $df = 11$, $P = 0.52$, NFI = 0.96. NFI > 0.90 or a nonsignificant χ^2 indicates a good model fit.

TABLE 1. Comparison of variable means \pm 1 SD, made separately for large colonizing, small colonizing, and surviving populations in 1990 and across years for the large colonizing population.

Variable	Surviving 1990 N = 79	Small colonizing 1990 N = 119	Large colonizing		
			1990 N = 64	1991 N = 65	1992 N = 73
Fruit number*	46 ^b \pm 56	158 ^a \pm 184	115 ^a \pm 184	79 \pm 130	131 \pm 222
Undamaged fruits*				47 ^d \pm 103	124 ^c \pm 187
Diameter (cm)*	13.8 ^b \pm 9.0	9.6 ^a \pm 5.3	11.0 ^{abc} \pm 4.8	17.2 ^d \pm 9.0	12.5 ^c \pm 8.4
Flower number	535 \pm 751	661 \pm 770	757 \pm 1290	713 \pm 739	523 \pm 701
Duration (d)	28.2 ^b \pm 14.1	42.5 ^a \pm 19.9	40.4 ^a \pm 26.0	40.1 \pm 20.5	38.2 \pm 18.5
Mean date (d)	199 ^b \pm 8	211 ^a \pm 10	210 ^a \pm 13	205 \pm 10	211 \pm 9
Asynchrony (d)	5.5 ^b \pm 4.1	7.7 ^{ab} \pm 6.6	9.3 ^a \pm 8.6	7.9 \pm 6.2	6.9 \pm 5.8
Percentage flower damage*	3.8 ^b \pm 3	11.0 ^a \pm 13	9.4 ^{ac} \pm 16	11 ^c \pm 14	2 ^d \pm 6
Percentage fruit damage*	\sim 0	\sim 0	\sim 0	35 ^c \pm 38	4 ^d \pm 10

Note: Mean date is in day of year (day 200 = 18 July). Values that share the same or lack superscripts (a, b in 1990; and c, d in the large colonizing population) are not significantly different ($P > 0.05$, Tukey test for multiple comparisons among means or ranks [*], with sequential Bonferroni correction for 21 tests [1990] and 26 tests [large colonizing]).

terest in the significance of individual path coefficients does not depend on the degree of overall fit (Biddle and Marlin 1987). We used multivariate Wald tests (implemented in EQS 4.0) to assess the significance of individual path coefficients. The Wald test locates the set of path coefficients that can be considered zero simultaneously without worsening the fit (i.e., significantly increasing the χ^2) of the model (Buse 1982, Bentler 1989). Significance tests are possible only for direct effects.

Multisample analysis.—One goal of this study is to determine whether the relationships between variables differ between populations in 1990 or between years in the large colonizing population. In SEM, a multisample analysis allows one to ask whether sets of parameters in the model differ between groups, i.e., between populations or years (Bentler 1989). Multisample analysis is done by imposing cross-group constraints on the path models, in which the path coefficients of interest are constrained to be equal in all groups. EQS is used to simultaneously fit the model to the data from each group. The procedure is similar to fitting the model to a single group, except that the constrained paths must have the same coefficient in all groups. Next, a Lagrange multiplier test is used to identify the set of constraints that, if simultaneously released, would result in a significantly better model (i.e., a lower goodness-of-fit χ^2 ; Bentler 1989: Chapters 6 and 7). Constraints whose release causes a significant decrement in fit are eliminated and the model is reestimated and reevaluated iteratively until no additional significant decrements are found. The remaining constraints indicate the path coefficients that are statistically indistinguishable across groups. In this study we performed two multisample analyses, one to assess differences between populations, the other for differences between years. We first evaluated the restrictive hypothesis of equality of all path coefficients, then used the Lagrange multiplier test to narrow the set of constraints to those that indicate statistically identical path coefficients.

RESULTS

Comparison of population means

In 1990 the large colonizing, small colonizing, and surviving populations were similar in mean plant diameter and flower number (Table 1). However, plants in the surviving population flowered earlier, more synchronously, and for a shorter duration than those in the colonizing populations (Table 1, Fig. 2). The surviving population also suffered one-third the percentage flower damage, but produced only about one-third as many fruits as plants in the colonizing populations. These differences were significant in nearly all comparisons (Table 1). In contrast, there were no significant differences between the two colonizing populations.

Plants in the large colonizing population were significantly larger in diameter in 1991 than in 1990 or 1992 (Table 1), a consequence of retaining the previous year's plants in 1991 and 1992 and high turnover by 1992. However, there were no significant differences in flower number among years. Nor were there significant among-year differences in the means of the phenological variables, mean date, duration or asynchrony (Table 1, Fig. 2). In contrast, seed predation changed dramatically between years. In 1991 the lepidopteran *P. icarioides* was very abundant, causing on average 35% fruit damage and a corresponding drop in undamaged fruits. Percentage flower damage also changed significantly among years: in 1992 only 2% of flowers were damaged, whereas 9.4 and 11.0% were damaged in 1990 and 1991, respectively (Table 1). Thus, while flowering phenology in the large colonizing population was constant over a 3-yr period, herbivore damage, especially to fruits, fluctuated markedly.

Path analysis

Model fit.—Our path models provided a good overall fit to the data sets for all populations and years studied (Fig. 1). Four of the five models had a nonsignificant χ^2 indicating that the covariance structure specified by the model could not be rejected given covariance struc-

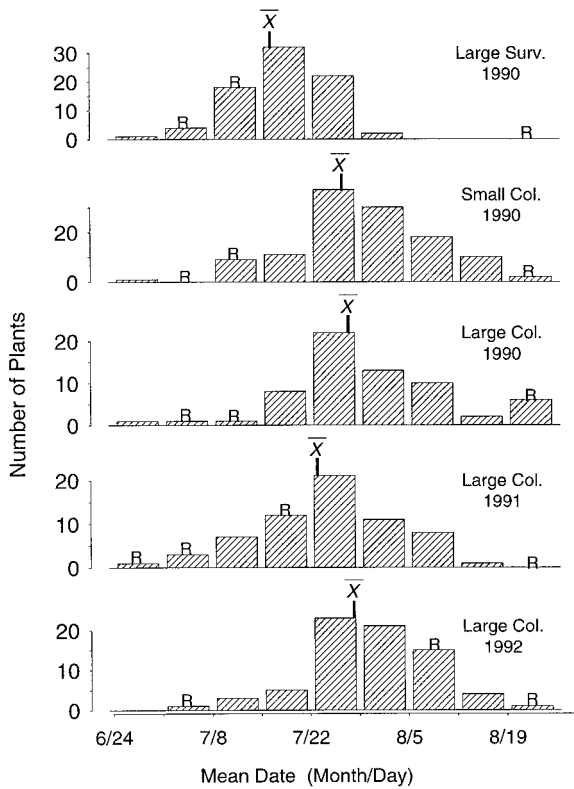


FIG. 2. Distribution of individual mean flowering dates for all three populations and years. \bar{X} denotes the mean date for each population. Surv. denotes surviving and Col. denotes colonizing populations. R denotes weeks with total rainfall >3 mm in Cougar, Washington, 18 km from the study sites.

tures of the data. All five models had Bentler-Bonett NFIs >0.90 indicating that the models provide an excellent fit compared to a null model that assumes independence among all variables. Because the one model rejected by the χ^2 test (Fig. 1b) was not rejected by the NFI, we conclude that this model is adequate, but that it may violate the assumption of multivariate normality, probably because we could not transform percentage flower damage to normality.

We found no evidence of significant nonlinearities in the effects of predictor variables on fruit number, based on cubic spline analysis. We also found little evidence of problems with collinearity of predictor variables. Although some predictor variables were very highly correlated (Appendix), they were even more highly correlated with the dependent variable, so that VIFs for the dependent variables do not exceed those of the model (see Petraitis et al. 1996). However, in three models there was evidence that collinearity may inflate the variance of factors affecting mean date, but this did not prevent the detection of significant path coefficients. Such collinearity may also inflate the value of path coefficients, but this will not affect our main conclusions.

Size affects most variables.—The excellent fit of the path models was due largely to strong relationships

between size (diameter and flower number) and most other variables. In all five models, flower number was strongly predicted by initial diameter, and had the largest direct effect on fruit number of any variable (Fig. 1). Larger plants also flowered earlier and longer, but with mean dates nearer to the population mean (i.e., less asynchronous), in all populations and in all years studied (Fig. 1). Although diameter was not allowed a direct effect on fruit number, it had strong indirect effects through all other variables. Summing the indirect effects of diameter for the five models yielded total effects on fruit number ranging from 0.31 in the small colonizing population to 0.60 in the surviving population. Note that because these are standardized coefficients, they indicate the average change in the dependent variable in units of standard deviation (SD) from the mean, given a one SD change in the predictor.

Factors affecting herbivory.—Flowering phenology (mean date and asynchrony) strongly influenced herbivore damage (percentage flowers damaged and percentage fruits damaged), even in populations or years where the average level of damage was relatively low (Fig. 1a–e). In all five models, increasing asynchrony led to an increase in percentage flower damage. Mean date also strongly affected damage levels: later-flowering plants experienced less flower damage in the small colonizing and surviving populations, and in the large colonizing population in 1990 and 1992. This pattern was reversed in the large colonizing population in 1991. In this year fruit damage by *P. icarioides* was extremely high, and later-flowering plants had greater damage to both fruits and flowers (Fig. 1d). Plant size (flower number) did not affect percentage flower damage in any of the five models. However, size (in terms of fruit number) did affect damage to fruits: larger plants sustained disproportionately higher percentage fruit damage by the lepidopteran *P. icarioides* in both 1991, when percentage fruit damage averaged 35%, and in 1992, when it was only 4% (Fig. 1d, e).

Factors affecting fruit production.—In all five models percentage flower damage had a negative effect on fruit number, but in no model was the path coefficient significantly different from 0 (Fig. 1). However, in 1991 the average percentage fruit damage was high, resulting on average in a 35% decrease in the final number of fruits (undamaged fruits). Because plants with more fruits were attacked more intensely (Fig. 1d), the overall decrease in fruits was $\sim 50\%$.

Our path analyses revealed a positive direct effect of mean date on fruit number in 1990 in the large and small colonizing populations, but not in the large surviving population. This path coefficient was also positive in the large colonizing population in 1991 and 1992. Thus, in the colonizing populations, once the effect of size (i.e., flower number) was statistically controlled for, plants that flowered later produce more fruits (mean path coefficient = 0.15). In contrast to

TABLE 2. Multisample comparison of path coefficients.

Path		χ^2 comparison					
Independent variable	Dependent variable	Large vs. small	Large vs. surviving	Small vs. surviving	1990 vs. 1991	1990 vs. 1992	1991 vs. 1992
Asynchrony	fruit number	0.97	4.68*	7.10**	0.58	0.01	0.01
Duration	fruit number	0.96	0.69	0.57	3.88*	0.53	7.30**
Mean date	fruit number	2.94	4.6*	7.71**	0.34	0.51	0.84
Flower damage	fruit number	0.22	0.13	0.11	0.29	0.11	0.02
Flower number	fruit number	0.02	2.15	1.18	5.44*	1.48	0.60
Diameter	duration	7.57**	10.97***	0.68	1.67	3.64	0.48
Flower number	duration	0.07	5.50*	12.63***	1.08	2.09	0.92
Flower number	asynchrony	0.87	1.03	0.08	0.18	0.87	0.70
Diameter	mean date	2.40	1.41	1.05	1.15	1.15	0.55
Flower number	mean date	5.81*	12.23***	12.90***	2.62	2.62	0.01
Asynchrony	percentage flower damage	1.03	0.15	0.01	0.96	1.43	0.11
Mean date	percentage flower damage	0.99	9.52**	38.41***	10.01***	7.70**	17.70***
Flower number	percentage flower damage	0.64	1.38	0.21	0.13	0.66	0.21
Diameter	flower number	4.00*	2.53	3.56	6.89**	6.89**	0.41

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, assessed by Lagrange multiplier test, with simultaneous significance tests. Coefficients with significant χ^2 differ between populations (1990) or years (large colonizing population). χ^2 is the increment in model χ^2 (i.e., worsening of model fit) caused by forcing that path coefficient to be equal in the two years being compared.

mean date, asynchrony had a significant effect on fruit number only in the surviving population.

In addition to direct effects on fruit production, our models specify that phenology could affect fruit number indirectly through percentage flower damage or affect undamaged fruits indirectly through percentage fruit damage and fruit number. Mean date and asynchrony both had strong direct effects on percentage flower damage in all models, but because percentage flower damage never affected fruit number, no indirect effect of phenology on fruit number was realized through this path (Fig. 1). However, mean date did affect undamaged fruits indirectly in the large colonizing population in 1991 because plants that flowered later sustained significantly greater fruit damage (Fig. 1d). As a result, the total effect of mean date on ln fruit number in 1991 was -0.07 , effectively reversing the direct effect of 0.08 .

Multisample analyses.—The multisample analysis of the 1990 populations rejected the hypothesis that the three populations could be described by identical models. The Lagrange multiplier test rejected 14 of 42 possible constraints indicating that the constraints resulted in a significantly higher χ^2 (Table 2; a higher χ^2 makes it more likely that the path model will be rejected). For example, if the path coefficient between mean date and percentage flower damage is constrained to be equal in the small colonizing and surviving populations, the model χ^2 increases by 38.4, a highly significant decrease in fit (Table 2). Although 11 of the 14 rejected constraints were between the large and small colonizing populations, this difference was not significantly different than the two-thirds expectation. However, 10 of the rejections occurred in pairs such that if the path coefficient for one colonizing population differed from the surviving population, then the other colonizing population also differed (Table 2). This further indi-

cates that the colonizing populations are more similar to each other than either is to the surviving population. In addition, differences in paths involving mean date contributed disproportionately to the total number of rejected constraints ($P = 0.006$, by Fisher's exact test) and to the differences between colonizing and surviving populations ($P = 0.03$, by Fisher's exact test). In fact, only 1 of the 14 rejected constraints did not involve a phenological variable, significantly fewer than expected ($P = 0.01$, Fisher's exact test). Thus, populations differed primarily in relationships involving phenological variables, especially mean date.

The hypothesis of equivalent models also was rejected in the temporal comparisons of the large colonizing population. In this analysis, 8 of 42 equality constraints were rejected (Table 2). In addition, constraints between 1991 and 1992 were rejected for the effects of mean date and fruit number on percentage fruit damage. Of particular interest was the effect of mean date on fruit number, which did not change between years, but differed between the colonizing and surviving populations (Table 2).

DISCUSSION

Demographic analysis of colonizing *L. lepidus* populations at Mount St. Helens, including those in the current study, demonstrates that they have sustained rapid population growth over a 10–15 yr period (Bishop 1996; C. M. Crisafulli et al., unpublished manuscript) and that fecundity contributes more than other life cycle components to population growth under these conditions (Bishop 1996). This result implies that factors affecting the average fecundity (i.e., fruit number) of populations will affect the growth of colonizing populations. Moreover, because fitness in populations with overlapping generations is best measured as an individual's contribution to population growth (Lande 1982), fecundity is an es-

pecially important component of fitness in lupines colonizing Mount St. Helens, and traits affecting fecundity may experience phenotypic selection.

Spatiotemporal variation in selection.—The direct positive effect of flowering time (mean date) on fecundity (fruit number) was remarkably consistent between the two colonizing populations and across years in the large colonizing population. Coefficients for this path ranged from 0.08 to 0.21, indicating relatively strong phenotypic selection for later flowering. However, later flowering plants also experienced much greater seed predation in 1991 (total effect = 0.29), when >50% of fruits were attacked by *P. icariodes* (Fig. 1d). As a result, the net effect of mean date in 1991 was reversed, resulting in selection for an earlier, rather than later, mean date. Duration of flowering also had large, positive direct effects on fruit production in 1991 (0.31) and 1992 (0.18), and its direct effect also was partially negated in 1991 by indirect effects through fruit number and percentage fruit damage. Thus, over the three years of this study there was strong but temporally variable selection on two phenological variables in colonizing populations. Spatial variation in the effect of phenological variables was also apparent. Whereas mean date strongly affected fruit number in colonizing populations in 1990, it had no effect in the surviving population, and asynchrony had a positive effect only in the surviving population (Fig. 1a).

These patterns of spatial and temporal variation were confirmed by the multisample analysis, which provided a method for judging the equality of path coefficients. The analysis indicated that colonizing populations differed from the surviving population in the effects of asynchrony and mean date, and that the effect of mean date and fruit number on percentage fruit damage was greater in 1991 than in 1992.

What unmeasured factor is responsible for the positive relationship between flowering date and reproductive success in colonizing populations, and its absence in the surviving one? Flowering phenology is commonly thought to affect reproduction through its role in achieving pollination, either by determining attractiveness to pollinators or determining synchrony with potential mates (Rathcke and Lacey 1985). Bee visitation patterns were consistent with the hypothesis of pollination failure in 1990 and 1991, when little bumblebee visitation occurred in colonizing populations until late in the season, but not in 1992 when bee visitation was uniformly high (J. G. Bishop, K. Werner, and D. W. Schemske, *unpublished manuscript*). Moreover, *L. lepidus* is capable of autogamy (in the presence of wind agitation) and a pollen addition experiment in 1991 provided no evidence for pollen limitation (J. G. Bishop, K. Werner, and D. W. Schemske, *unpublished manuscript*). Therefore, it seems unlikely that the advantage of later flowering is simply a result of early season pollination failure. A more likely explanation is that soil moisture conditions favored fruit maturation late in the summer. Maximum vapor pressure deficits at

Mount St. Helens are highest and soil water potentials lowest in late July and early August (Braatne 1989, del Moral and Bliss 1993). In 1990 it did not rain from July 8 until August 14, and midsummer precipitation was similarly lacking in 1991 and 1992 (Fig. 2, National Climate Data Center 1994). Increased precipitation and decreased temperatures after early August provide better conditions for ripening of fruit (Braatne 1989) and probably are responsible for the positive direct effect of both mean date and duration on fruit number. Plants in the surviving population were not able to take advantage of improved conditions because they finished flowering and setting fruit before late-August rains (Fig. 2).

Alpine and subalpine plants often experience summer drought conditions that may affect phenological patterns (Jackson and Bliss 1984, Galen and Stanton 1991, Walker et al. 1995), and early cessation of flowering in the surviving populations may also derive from more extreme soil moisture conditions. Braatne (1989) found that, due to steeper slopes and other factors, soil water potential at the surviving site was often low enough to limit photosynthetic activity, but this rarely occurred in sites similar to the colonizing ones. Thus, in the surviving population, but not in the colonizing populations, rapid drying may attenuate flowering duration, thereby decreasing mean date and asynchrony. Whether these differences are genetically based is unknown.

Evolutionary implications.—Having studied only one surviving and two colonizing populations, we cannot conclude that the two types of populations are generally different. However, compared to colonizing populations, surviving populations around the volcano are at higher altitude, on better developed soils (del Moral and Bliss 1993), and in closer proximity to pre-eruption communities with richer assemblages of competitors (Wood and del Moral 1987, del Moral and Wood 1988) and arthropods. Therefore, we expect that the reproductive consequences of variation in flowering phenology will be spatially heterogeneous, but that there will be consistently greater differences between colonizing and surviving populations than among colonizing populations. Such spatial differences in selection could lead to evolutionary divergence in phenology. However, if herbivores frequently reverse the otherwise positive effect of later flowering, then optimal flowering phenology will shift frequently within generations. This may prevent any fine-scale adaptation of mean flowering date, tending instead to maintain within-population variation in phenological traits and possibly resulting in the evolution of increased phenotypic plasticity (Via et al. 1995). We expect great temporal fluctuation in optimal phenology at Mount St. Helens for three reasons. First, our results indicate considerable temporal variation in the reproductive consequences of phenology, due primarily to among-year fluctuation in herbivores. Such fluctuations appear to be common in this system (Bishop 1996; W. F. Fagan and J. G. Bishop, *unpublished manuscript*). Second, *L. lepidus* populations probably persist for only a few tens of generations

due to succession. This process also causes a gradual increase in the average elevation of lupine populations. Third, Mount St. Helens is a young volcano, with an eruption return interval of ~ 150 yr (Harris 1988). As a result, both treeline and *L. lepidus* were ~ 600 – 1000 m below the local norm even before the 1980 eruption (Lawrence 1938). Overall, repeated disturbance, succession, and small-scale environmental variation are likely to result in frequent shifts in optimal phenology that may be difficult to track genetically. Although phenologies in colonizing and surviving populations already differ in the direction predicted by phenotypic selection and in accord with seasonal soil moisture availability, whether these differences stem from local adaptation or phenotypic plasticity (or both) is unknown.

Herbivory, phenology, and colonization

In 1991 fruit predation by the lepidopteran *P. icarioides* led to a 50–60% decrease in fruit production in the large colonizing population relative to 1990 and 1992. Given the demographic importance of fecundity in this system, if this level of seed loss occurs frequently, it may decrease the rate of population founding and growth in *L. lepidus*. In fact, *P. icarioides*, along with several other seed predators, decreased seed production by as much as 50% in the three years subsequent to this study (1993–1995, Bishop 1996). The demographic effects of these and other herbivores appear to be greater and more highly episodic in newly founded populations than in older ones (Bishop 1996; W. F. Fagan and J. G. Bishop, *unpublished manuscript*), possibly due to a lack of natural enemies in newly founded populations, and one may also expect strong, but variable, selection for herbivore resistance. Heavy seed predation by *P. icarioides* (Breedlove and Ehrlich 1968, 1972) and other lepidopterans (Harrison and Maron 1995) has been documented in other *Lupinus* species, but was thought not to affect population dynamics due to extensive seed banks.

Variation in phenology may also influence population dynamics through its effect on fecundity. In 1990 and 1992, when seed predation was low, plants in the colonizing population produced 2–3 times more fruits on average than those in the surviving population (Table 1). Because plants in the surviving population were as large or larger than those in colonizing populations, this increase in fruit production presumably is the benefit of later and longer flowering, possibly combined with a shift in resource allocation toward fecundity. Thus, assuming that the pre-1980 ancestors of the colonizing populations were similar to plants in the surviving population, flowering phenologies have already shifted in a manner that will increase rates of reproduction and hence colonization. However, even within populations, variation in phenology contributes significantly to variation in fruit number in the colonizing populations, suggesting that nonoptimal phenologies may decrease rates of colonization. Although this affect

is diminished in some years by the effects of fruit damage, it demonstrates the importance to colonizing species of a rapid response to environmental variability.

ACKNOWLEDGMENTS

We thank the Schemske Lab group, K. Karoly, R. Mitchell, J. Kingsolver, K. Schwaegerle, S. Armbruster, and an anonymous reviewer for many helpful comments on the manuscript. Many thanks go to B. Cook, D. McCrumb, B. Bishop, J. Agren, D. Lello, A. Mooney, B. Nakamura, I. Parker, M. Ruckelshaus, J. Titus, A. Wagner, and R. Williamson for field assistance. This work was supported by a grant to D. W. Schemske from the University of Washington (U.W.) Graduate School Research Fund, and fellowships and support to J. G. Bishop from the U.W. Plant Molecular Integration and Function Committee, and N.S.F. Grants DEB 9213143 and BIR 9256532.

LITERATURE CITED

- Augsburger, C. K. 1981. Reproductive synchrony of a tropical shrub: Experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* **62**:775–778.
- Baker, H. 1965. Characteristics and modes of origin of weeds. Pages 147–169 in H. G. Baker and G. L. Stebbins, editors. *The genetics of colonizing species*. Academic Press, New York, New York, USA.
- Bentler, P. M. 1989. EQS structural equations program manual. BMDP Statistical Software, Los Angeles, California, USA.
- Bentler, P. M., S. Y. Lee, and L. J. Weng. 1987. Multiple population covariance structure analysis under arbitrary distribution theory. *Communications in Statistics—Theory* **16**:1951–1964.
- Biddle, B. J., and M. M. Marlin. 1987. Causality, confirmation, credulity, and structural equation modeling. *Child Development* **58**:4–17.
- Bishop, J. G. 1996. Demographic and genetic variation during colonization by the herb *Lupinus lepidus* on Mount St. Helens. Dissertation. University of Washington, Seattle, Washington, USA.
- Braatne, J. 1989. Comparative physiological and population ecology of *Lupinus lepidus* and *Lupinus latifolius* colonizing early successional habitats on Mount St. Helens. Dissertation. University of Washington, Seattle, Washington, USA.
- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**:115–155.
- Breedlove, D. E., and P. R. Ehrlich. 1968. Plant–herbivore coevolution: lupines and lycaenids. *Science* **162**:671–672.
- Breedlove, D. E., and P. R. Ehrlich. 1972. Coevolution: Patterns of legume predation by a lycaenid butterfly. *Oecologia* (Berlin) **10**:99–104.
- Brown, A. H. D., and D. Marshall. 1981. Evolutionary changes accompanying colonization in plants. Pages 351–363 in G. C. E. Scudder and J. L. Reveal, editors. *Evolution today*. Proceedings of the II International Congress on Systematic and Evolutionary Biology, Vancouver, British Columbia, Canada.
- Buse, A. 1982. The likelihood ratio, Wald and Lagrange multiplier tests: An expository note. *American Statistician* **36**:153–157.
- Chapin, F. S. III, L. R. Walker, C. L. Fastie, and L. C. Sharmar. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**:149–173.
- del Moral, R., and L. C. Bliss. 1993. Mechanisms of primary succession: Insights resulting from the eruption of Mount St. Helens. *Advances in Ecological Research* **24**:1–66.

- del Moral, R., and D. M. Wood. 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio* **74**:11–27.
- del Moral, R., and D. M. Wood. 1993. Early primary succession on a barren volcanic plain at Mount St. Helens, Washington. *American Journal of Botany* **80**:981–992.
- English-Loeb, G. M., and R. Karban. 1992. Consequences of variation in flowering phenology for seed head herbivory and reproductive success in *Erigeron glaucus* (Compositae). *Oecologia* **89**:588–595.
- Franklin, J. F., P. M. Frenzen, and F. J. Swanson. 1988. Recreation of ecosystems at Mount St. Helens: Contrast in artificial and natural approaches. Pages 1–37 in: *Rehabilitating damaged ecosystems*. Volume 2. Ed. by J. Cairns Jr. CRC Press, Boca Raton, Florida, USA.
- Galen, C., and M. L. Stanton. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany* **78**:978–988.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, Chichester, UK.
- Gross, R. S., and P. A. Werner. 1983. Relationships among flowering phenology, insect visitors, and seed-set of individuals: Experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs* **53**:95–117.
- Halvorson, J. J., E. H. Franz, J. L. Smith, and R. A. Black. 1992. Nitrogenase activity, nitrogen fixation, and nitrogen inputs by lupines at Mount St. Helens. *Ecology* **73**:87–98.
- Harris, S. L. 1988. *Fire mountains of the west: The Cascade and Mono Lake volcanoes*. Mountain Press, Missoula, Montana, USA.
- Harrison, S. J., and J. Maron. 1995. Impacts of defoliation by tussock moths (*Orgyia vetusta*) on growth and reproduction of bush lupine (*Lupinus arboreus*). *Economic Entomology* **20**:223–229.
- Heinrich, B. 1976. Flowering phenologies: Bog, woodland, and disturbed habitats. *Ecology* **57**:890–899.
- Jackson, L. E., and L. C. Bliss. 1984. Phenology and water relations of three plant life forms in a dry tree-line meadow. *Ecology* **65**:1302–1314.
- Kingsolver, J., and D. W. Schemske. 1991. The measurement of natural selection by path analysis. *Trends in Ecology and Evolution* **6**:276–280.
- Kruckeberg, A. R. 1987. Plant life on Mount St. Helens before 1980. Pages 3–17 in D. Bilderback, editor. *Mount St. Helens 1980*. University of California Press, Berkeley, California, USA.
- Lacey, E. P. 1986. Onset of reproduction in plants: Size-versus age-dependency. *Trends in Ecology and Evolution* **1**:72–76.
- Lande, R. 1982. A quantitative genetic theory of life history evolution. *Ecology* **63**:607–615.
- Lawrence, D. B. 1938. Trees on the march: Notes on the recent volcanic and vegetational history of Mount St. Helens. *Mazama* **20**:49–57.
- Loehlin, J. C. 1987. *Latent variable models*. Lawrence Erlbaum, Hillsdale, New Jersey, USA.
- Marquis, R. J. 1988. Phenological variation in the neotropical understory shrub *Piper arieianum*: Causes and consequences. *Ecology* **69**:1552–1565.
- Mitchell, R. J. 1992. Testing evolutionary and ecological hypotheses using path analysis and structural equation modeling. *Functional Ecology* **6**:123–129.
- . 1993. Path analysis: Pollination. Pages 211–231 in *Design and analysis of ecological experiments*. S. M. Scheiner and J. G. Gurevitch, eds. Chapman and Hall, New York, New York, USA.
- Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: Statistical inference and biological interpretation. *Evolution* **41**:1149–1161.
- Morris, W. F., and D. M. Wood. 1989. The role of lupine in succession on Mount St. Helens: Facilitation or inhibition? *Ecology* **70**:697–703.
- National Climate Data Center. 1994. *Climate data 1980–1994 (CD-ROM)*. Hydrosphere Data Product, Boulder, Colorado, USA.
- Oostermeijer, J. G. B., M. L. Brugman, E. R. de Boer, and H. C. M. den Nijs. 1996. Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology* **84**:153–166.
- Parker, I. M. 1996. *Ecological factors affecting rates of spread in Cytisus scoparius, an invasive exotic shrub*. Dissertation. University of Washington, Seattle, Washington, D.C.
- Petraitis, P. S., A. E. Dunham, and P. H. Niewiarowski. 1996. Inferring multiple causality: the limitations of path analysis. *Functional Ecology* **10**:421–431.
- Pettersson, M. W. 1991. Flower herbivory and seed predation in *Silene vulgaris* (Caryophyllaceae): Effects of pollination and phenology. *Holarctic Ecology* **14**:45–50.
- Pugusek, B. H., and A. Tomer. 1995. Determination of selection gradients using multiple regression versus structural equation models (SEM). *Biometrical Journal* **4**:449–462.
- Rathcke, B. J., and E. P. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**:179–214.
- Rice, W. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- Schemske, D. W. 1977. Flowering phenology and seed set in *Claytonia virginica* (Portulacaceae). *Bulletin of the Torrey Botanical Club* **104**:254–263.
- . 1984. Population structure and local selection in *Impatiens pallida* (Balsaminaceae), a selfing annual. *Evolution* **38**:817–832.
- Schmitt, J. 1983. Individual flowering phenology, plant size, and reproductive success in *Linanthus androsaceus*, a California annual. *Oecologia* (Berlin) **59**:135–140.
- Turelli, M. 1988. Phenotypic evolution, constant covariances and the maintenance of additive variance. *Evolution* **43**:1342–1347.
- Via, S., R. Gomulkiewicz, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: Consensus and controversy. *Trends in Ecology and Evolution* **10**:212–217.
- Via, S., and R. Lande. 1987. Evolution of genetic variability in a spatially heterogeneous environment: Effects of genotype-environment interaction. *Genetical Research* **49**:147–156.
- Walker, M. D., R. C. Ingersoll, and P. J. Webber. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* **76**:1067–1083.
- Wood, D. M., and R. del Moral. 1987. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. *American Journal of Botany* **76**:1228–1237.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

APPENDIX

A) Correlations between all variables included in the path analyses for 1990

	Mean date	Percentage flower damage	Duration	ln(diameter)	ln(flowers)	ln(fruiets)	Asynchrony
1990 large colonizing ($N = 64$)							
Mean date	1.000						
Percentage flower damage	-0.511	1.000					
Duration	-0.230	-0.018	1.000				
ln(diameter)	-0.203	-0.024	0.606	1.000			
ln(flowers)	-0.266	-0.089	0.803	0.576	1.000		
ln(fruiets)	-0.107	-0.188	0.686	0.568	0.908	1.000	
Asynchrony	0.054	0.347	-0.195	-0.144	-0.374	-0.367	1.000
1990 large surviving ($N = 79$)							
Mean date	1.000						
Percentage flower damage	0.344	1.000					
Duration	0.091	0.029	1.000				
ln(diameter)	-0.171	-0.100	0.422	1.000			
ln(flowers)	0.189	-0.064	0.518	0.696	1.000		
ln(fruiets)	0.051	-0.105	0.434	0.590	0.792	1.000	
Asynchrony	-0.250	0.181	-0.207	-0.087	-0.338	-0.110	1.000
1990 small colonizing ($N = 119$)							
Mean date	1.000						
Percentage flower damage	-0.389	1.000					
Duration	0.174	-0.115	1.000				
ln(diameter)	-0.464	0.266	0.296	1.000			
ln(flowers)	0.000	-0.057	0.709	0.424	1.000		
ln(fruiets)	0.224	-0.213	0.666	0.307	0.907	1.000	
Asynchrony	0.095	0.188	-0.133	-0.162	-0.282	-0.316	1.000

B) Correlations between all variables included in the path analyses for 1991–1992

	Mean date	Percentage flower damage	Duration	ln(diameter)	ln(flowers)	ln(fruiets)	Asynchrony	Undamaged fruits	Percentage fruit damage
1991 large colonizing ($N = 65$)									
Mean date	1.000								
Percentage flower damage	0.314	1.000							
Duration	-0.123	0.025	1.000						
ln(diameter)	-0.447	-0.066	0.524	1.000					
ln(flowers)	-0.091	-0.121	0.766	0.444	1.000				
ln(fruiets)	-0.031	-0.106	0.779	0.468	0.865	1.000			
Asynchrony	0.034	0.243	-0.382	-0.209	-0.440	-0.423	1.000		
Undamaged fruits	-0.163	-0.107	0.661	0.337	0.777	0.866	-0.377	1.000	
Percentage fruit damage	0.234	0.025	0.437	0.314	0.392	0.490	-0.237	0.021	1.000
1992 large colonizing ($N = 73$)									
Mean date	1.000								
Percentage flower damage	-0.491	1.000							
Duration	-0.233	-0.074	1.000						
ln(diameter)	-0.356	-0.034	0.442	1.000					
ln(flowers)	-0.142	-0.164	0.688	0.559	1.000				
ln(fruiets)	0.056	-0.271	0.657	0.478	0.853	1.000			
Asynchrony	-0.187	0.488	-0.207	-0.083	-0.253	-0.313	1.000		
Undamaged fruits	0.058	-0.271	0.648	0.469	0.848	0.996	-0.310	1.000	
Percentage fruit damage	-0.029	-0.061	0.235	0.212	0.261	0.282	-0.101	0.194	1.000