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## FLOWERING PATTERNS OF UNDERSTORY HERBS 30 YEARS AFTER DISTURBANCE OF SUBALPINE OLD-GROWTH FORESTS BY TEPHRA FROM MOUNT ST. HELENS

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*Premise of research.* We sought to determine the role of flowering in recovery of understory herbs from a major disturbance and to determine the effects of plant and environmental factors on flowering patterns.

*Methodology.* We counted flowering and nonflowering shoots in permanent plots eight to 10 times over a 30-year period for all 48 understory herb species in four subalpine old-growth conifer forests that received tephra (aerially transported volcanic ejecta) from the 1980 eruptions of Mount St. Helens, Washington. We defined two measures of flowering and related them to environmental and plant characteristics.

*Pivotal results.* Patterns of flowering varied widely among species both among and within growth forms. Flowering increased with time, especially where it was initially low (for evergreen clonal plants, species that also grow in early seral habitats, and plants in deep tephra and from herb-poor sites). Some significant differences that occurred during the first 20 years disappeared by year 30. Percent of shoots flowering declined as shoot density increased, but the significance of this relationship declined until it became nonsignificant by year 25. There was a significant but weak relationship between the proportion of shoots flowering for a species and its proportional increase in shoot numbers during the 30 years of vegetation redevelopment; some species expanded populations only by flowering, while others became dominant while flowering little.

*Conclusions.* Flowering patterns changed with time; this constitutes an important aspect of successional change. Studies of flowering and other aspects of sexual reproduction are important for understanding mechanisms of succession.

*Keywords:* coniferous forest, flowering, forest herbs, Mount St. Helens, succession, volcanic tephra.

### Introduction

Plant reproduction, either from seed or via clonal growth, allows recovery of vegetation following disturbance. Thus, to fully understand succession, one must understand the processes of regeneration. For forest understory herbs—a key component of temperate forests (Gilliam 2007)—revegetation is often due primarily to clonal spread rather than sexual reproduction (Bierzychudek 1982; Whigham 2004; Nelson et al. 2007). Clonal spread is limited by the annual extension of rhizomes and stolons (Antos and Zobel 1984, 1985a, 1985b, 1985c, 2005; Antos 1988; Lezberg et al. 1999, 2001; Nelson et al. 2007) and by barriers to spread. Other forest herbs lack clonal spread (Antos and Zobel 1984; Jules 1998; Lezberg et al. 1999). Thus, reproduction from seed is required for spread at all spatial scales for some forest herbs and required for spread beyond local patches for almost all.

Many forest herbs spread slowly into areas from which they have been extirpated (Brunet et al. 2000; Verheyen et al. 2003; Verheyen and Hermy 2004; Matlack 2005). Even within established forests, seed supply often limits spread at the scale of a local patch (Ehrlén and Eriksson 2000; Albrecht and McCarthy 2009). Because sexual reproduction is critical to spread into new stands and across barriers to clonal growth, and because it is limiting for many species in mature forests, we must evaluate it to understand population dynamics of forest herbs. Flowering is the critical first stage for sexual reproduction and thus is required for substantial spread of most understory herbs; without substantial flowering, good seed set, seed dispersal, and seedling establishment cannot happen in situations such as ours (Zobel and Antos 1997) where seed banks are not effective. Yet flowering is typically infrequent in many forest understory species (Bierzychudek 1982; Whigham 2004; Lindh 2005). Thus, low rates of flowering are likely to be an important limitation for recovery of forest herbs from disturbance.

One may view flowering from the standpoint of differences among individual species or among growth forms or from the standpoint of the community as an assemblage of species (Caradonna et al. 2014). Flowering may differ among species because of species' attributes and in relation to environmental

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conditions (Helenurm and Barrett 1987; Kawarasaki and Hori 2001; Cook et al. 2012; CaraDonna et al. 2014). Because environmental conditions change during succession, flowering patterns will change along with other conditions and processes, such as species cover and density, diversity, productivity, and nutrient cycling. As succession continues, flowering may change in several ways: increase or decline in general or differentially among growth forms or species, or reach its greatest intensity under different environmental conditions.

During succession following volcanic disturbance, as with other disturbances, propagule availability is often limiting and strongly influences succession, as shown at Mount St. Helens (Dale et al. 2005b; del Moral et al. 2012; Titus and Bishop 2014) and at other volcanos (Tsuyuzaki 2009; del Moral and Magnusson 2014; Efford et al. 2014). Flowering, as the first stage of sexual reproduction, thus influences succession in volcanic landscapes. We have previously reported flowering patterns and regeneration of understory herbs on sites buried by volcanic tephra (aerially transported volcanic ejecta) at Mount St. Helens in 1980 (Zobel and Antos 2007, 2009, and references cited therein). In our 20-year community-wide study (Zobel and Antos 2007), flowering of herbs differed among species, growth forms, and environments. Species that flowered more also left fewer survivors and had higher turnover of individuals. Some growth forms flowered consistently, and others not at all. Some species became dominant on the basis of only seedling establishment (e.g., *Tiarella unifoliata*); others, however, dominated despite having little or no sexual reproduction (e.g., *Rubus lasiococcus*). These 2 decades, although longer than most studies of flowering and successional change, did not allow a complete recovery of herbs where tephra was deep (Antos and Zobel 2005; D. B. Zobel and J. A. Antos, unpublished data); thus, our assessment of the role of flowering in succession there remained incomplete. The third decade of understory succession at our sites contrasted in several ways with that in the first 20 years. Between years 20 and 30, forest floor development was pronounced, secondary disturbances continued, some growth forms exceeded their original importance while others plateaued far below their pre-eruption importance, some species that previously failed to flower began to flower abundantly, and new species established (D. B. Zobel and J. A. Antos, unpublished data).

In this study, we emphasize changes in flowering patterns from year 20 to year 30 and the apparent role of flowering

in succession. We answer the following questions, using our 30-year record of flowering of understory herbs affected by tephra. (1) Did species that flowered proportionately more contribute more to vegetation recovery? (2) Did the proportion of shoots flowering for a species change significantly with the density of shoots present? (3) Did the patterns of flowering among years differ among species? (4) What environmental and plant characteristics had significant relationships with the incidence and intensity of flowering? (5) How did patterns of flowering in the third decade after disturbance differ from earlier in succession? (6) How did the influence of the factors related to incidence of flowering change with time?

## Material and Methods

### Study Sites and Species

We sampled the understories of four sites in old-growth conifer forests in the *Abies amabilis* vegetation zone (Franklin and Dyrness 1973) in the Cascade Range, Washington State (table 1). All sites received tephra from the 1980 eruptions of Mount St. Helens (Swanson and Major 2005), but the tree canopy remained intact. Shallow tephra had relatively little effect on herb cover and richness; in contrast, 12–15 cm of tephra almost obliterated the herbaceous understory, which still had only 23%–52% of pre-eruption cover in 2010. Damage from tephra (table 1) and subsequent changes in the cover, density, and species richness of the herb layer at these sites were summarized by Antos and Zobel (1985b, 1986, 2005) and Zobel and Antos (1997, 2009). All data reported here came from plots on natural tephra, except at Site DR, where we also sampled flowering in plots from which tephra was cleared in 1982 to simulate erosion. We refer to sampling years by time elapsed after the 1980 eruption; for example, 1980 is year 0, 2010 is year 30.

We collected data from 48 species. Nomenclature follows Hitchcock and Cronquist (1973) for consistency with our earlier reports, but we provide revised names in parentheses at their first use (Cook et al. 2013). The herbs we studied are almost all perennial; however, they differ greatly in growth form, reproductive characteristics (60% of species spread effectively by vegetative means), and responses to burial (Antos and Zobel 1985a, 1985c, 1986; Zobel and Antos 1986, 1992, 2009). They showed comparable variation in sexual repro-

Table 1

Study Site Characteristics				
Site code	Tephra depth (cm)	Elevation (m)	No. herb species	Reduction in herb cover (%)
SP	4.5	1245	9	41
SR	4.5	1290	26	0
DP	15	1160	12	99+
DR	15	1240	32	99+

Note. Sites DP and DR were 22 km from the crater near Mosquito Meadows, and sites SP and SR were 58 km from the crater near Chambers Lake (Antos and Zobel 1985b). Site codes: S = shallow tephra, D = deep, P = herb poor, R = herb rich. Herb species numbers are pre-eruption values based on plots cleared in 1980. Reduction in herb cover (%) refers to the effect of the tephra deposit; it is based on 1981 cover in natural tephra plots compared with an estimate of pre-eruption cover (1981 data from plots cleared of tephra in 1980; Antos and Zobel 1985b).

duction (Zobel and Antos 2007). In this article, we extended our study for 10 years, during which new species began to flower and the patterns of flowering changed. We report results of classifying species based on habitat breadth as well as on growth form.

We grouped species by habitat breadth (i.e., whether they grow in forest only, in forest + meadow, or in forest + early seral habitats) on the basis of our observations, other studies in our region, and regional floras (Hitchcock et al. 1955–1969; Dyrness 1973; Halpern and Harmon 1983; Stickney 1986; Halpern 1989; del Moral 1998; Biek 1999; del Moral and Jones 2002; Dale et al. 2005a, Frenzen et al. 2005). We classified species into six growth forms: mycotrophic achlorophyllous angiosperms, graminoids, deciduous nonclonal forbs, deciduous clonal forbs, evergreen nonclonal plants, and evergreen clonal forbs. Graminoids included grass, sedge, and rush species. Mycotrophic achlorophyllous angiosperms (Furman and Trappe 1971) emerge from soil only when flowering, so the proportion of shoots flowering always equals 1.0. Evergreen nonclonal data are mainly from the robust, grass-like lily *Xerophyllum tenax*. This growth form never flowered in our plots during sampling years (proportion of shoots flowering = 0), although *X. tenax* occasionally did flower in years between samples, as indicated by old flowering stalks. The two growth forms with invariable levels of flowering were excluded from statistical analyses and graphs, although their means were included in tables.

#### Methods of Sampling and Analysis

At each study site, we used 100 permanent 1-m<sup>2</sup> plots on undisturbed (natural) tephra, located every 3 m along several transects on level topography (Antos and Zobel 1985b). At site DR only, we cleared tephra from an additional 50 plots in year 2; cleared plots were located at 6-m intervals on transects interspersed among those with natural tephra (Zobel and Antos 1986).

We counted the number of nonseedling shoots of all understory herbs during years 0–3, 20, 25, and 30 at all sites (except year 25 at site SR); in deep tephra in years 4, 7 and 10; and in shallow tephra in year 9. We recorded all shoots with flower buds, flowers, or fruits (both healthy and aborted) as flowering. We sampled once per sampling year; the chances of missing signs of flowering were small, given the short growing season at these high-elevation sites with a late-melting snow pack.

We examined two different measures of the importance of flowering. (1) At each site, in what proportion of plots (with a given species present) did flowering occur (flowering incidence)? (2) In plots where flowering did occur, what proportion of the shoots flowered at each site (flowering intensity)? For both measures, we usually analyzed data for all species, regardless of how few plots or plants were involved. Each case was the mean value for one species at one site in 1 yr. Throughout all analyses, we used  $P \leq 0.05$  as the criterion for significance but deemphasized factors with marginal  $P$  values because we carried out several analyses

We coded whether a species flowered in a given plot in a given year (i.e., 1 = flowering, 0 = not flowering); the mean value (between 0 and 1) for all plots including the species at a

site at that time was flowering incidence. Frequent zeros (absence of flowering) prevented this variable from being transformed to normality. To determine flowering intensity, we calculated the mean of the proportion of shoots flowering, for all plots at a site where a species was flowering in a given year. Flowering intensity values were normally distributed following a log transformation.

We used two subsets of data with balanced designs. (1) All-sites data: natural tephra plots at all sites for years 0–3, 20, 25, and 30 (for flowering intensity, we omitted year 25, when total shoots was not counted at site SR). (2) Site DR data: site DR for years 3, 4, 7, 10, 20, and 30 to test shoot density, plot treatment (natural tephra or plots with tephra cleared in year 2), habitat breadth, growth form, and year. We excluded year 25, when cleared plots were not measured. This analysis allowed a test of the influence of delayed erosion (i.e., year 2 removal) of tephra.

We used several statistical analyses to answer the questions we posed above. To determine whether species with more flowering had a greater increase in shoot density from 1981 to 2010 (question 1), we related flowering by each species to its change in shoot density by plotting change over flowering intensity. Change in density was defined in two ways: (1) by difference (year 30 density – year 1 density) and (2) by ratio (year 30 density/year 1 density). The Spearman rank correlation coefficient was used to determine significance of each relationship. For this analysis, we used only species with >9 shoots in year 30 and, for the ratio, with >0 shoots in year 1.

To determine whether flowering intensity was related to shoot density (question 2), we calculated the Spearman rank correlation coefficient, with one data point per year per species and using all cases where flowering occurred. A separate correlation was developed for each year and another for all years together. For our compilation of flowering percentages among species and years (question 3), we used all available data from natural tephra (all sites and years where a species was present), which provided the best estimate for overall flowering behavior after the eruption.

The effects of plant, site, and environmental factors on flowering (question 4) were tested in a variety of ways for both flowering incidence and intensity. For incidence, we used logistic regression (modified to account for repeated measurement of the same species-site combinations) and all-sites data to examine the influence of four categorical factors (tephra depth = deep or shallow, herb richness of the site = poor or rich [table 1], species' growth form, and species' habitat breadth) and two quantitative factors (year and number of shoots). Using site DR incidence data, we used repeated-measures logistic regression to examine the effect of tephra removal in year 2, growth form, and habitat breadth; year and number of shoots were also included in the model. We used a repeated-measures ANOVA to analyze flowering intensity, using the same factors as for incidence but treating number of shoots as a covariate. The relationships of tephra depth and herb richness to flowering incidence were also tested for 10 individual species that had at least 12 cases in both deep and shallow tephra, using a logistic regression model that included year and the number of shoots of the species present.

Data were divided into three sets: to year 20 (summarized by Zobel and Antos [2007]), year 25, and year 30. Simple

regressions were run among the sets for species with data in two or more sets to determine how closely third-decade flowering was related to earlier data (question 5).

We used two methods to describe when various factors related to flowering became significant (question 6). Logistic regressions were run for each individual year to determine in which years a factor significantly influenced flowering incidence (question 6, part 1). Another logistic regression analysis used all data for a given year and all previous sampling years to determine how long it took before accumulated data produced significance for each factor (question 6, part 2).

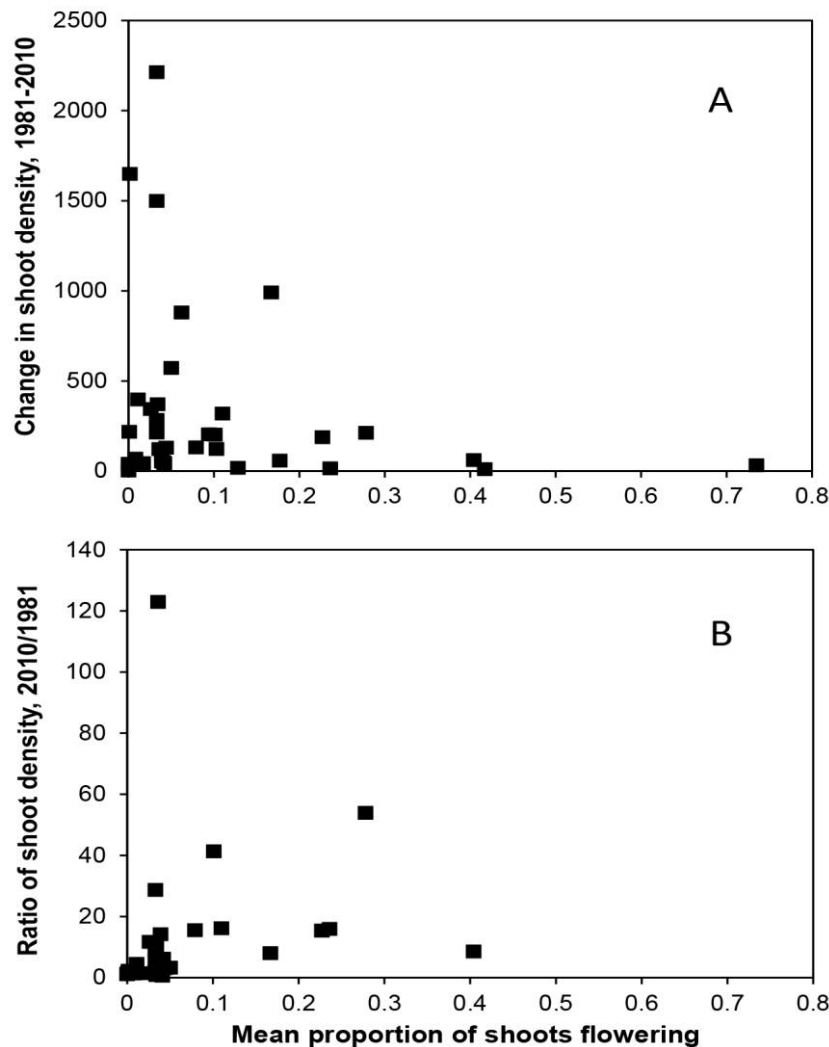
We differentiated sites by their tephra depth and herb species richness (table 1). Tephra depth affected plant survival and rates of recovery and thus shoot density and the age and size structure of populations, which may have had direct effects on flowering. Herb species richness may be viewed as a general indicator of site quality; herb-rich sites had less dominance of

evergreen species, later snow melt, more concave microtopography, and higher levels of Ca, Mg, and total N in the buried pre-eruption soil (Zobel and Antos 1991).

## Results

### *Comparison of Results from Two Data Sets*

We analyzed 452 cases in the all-sites data set (with each case being the mean value for a single species from all plots at one site in 1 yr) and 259 cases from site DR. All-sites data were limited to years at the beginning and end of our study but included all tephra depths and degrees of herb richness. Site DR data were limited to one deep tephra, herb-rich site but included plots cleared in year 2, in addition to those on natural tephra, and data from years 4, 7, and 10, years not included in the all-sites data. These data sets usually provided



**Fig. 1** Relationship between flowering intensity (the proportion of shoots flowering) for a given species at a given site and the change in shoot density for that species at that site from year 1 to year 30. Each data point represents one species at one site. Points with zero shoots in year 1 were omitted from B. A, Change in actual density (Spearman rank correlation coefficient  $r = -0.058$ ,  $P = 0.75$ ). B, Proportional change in density ( $r = 0.47$ ,  $P = 0.011$ ).



**Table 2**  
Relationship between Total Number of Shoots (Flowering + Not Flowering) and Flowering Intensity

Year	<i>r</i>	<i>P</i>	<i>N</i>
0	-.85	.007	11
1	-.87	.003	13
2	-.71	.0003	27
3	-.67	.0002	32
20	-.49	.002	40
25	-.29	.14	27
30	-.27	.0505	52
All	-.56	<.0001	202

Note. *r* values are Spearman rank correlation coefficients, with one coefficient for each sampling year and one for all years together. Each data point used in the correlation was the mean for a given species at one site in one year, using all-sites data. Cases without flowering were excluded. *N* = number of cases.

similar results, and they will be mentioned separately only where results differed.

*Relationship of Flowering Intensity to Species Increase after Disturbance*

**Question 1: Did species that flowered proportionately more contribute more to vegetation recovery?** The result differed depending on how we defined the 1981–2010 increase in species importance. The numerical increment in plant density did not change significantly as flowering intensity increased (fig. 1A). In contrast, the proportional change in shoot density increased significantly as intensity of flowering increased, even though species differed widely (fig. 1B).

*Relationship of Flowering to Shoot Density*

**Question 2: Did the proportion of shoots flowering for a species change significantly with the density of shoots present?**

For all-sites data, cases that lacked flowering averaged 52 shoots each, whereas cases with flowering had 242 shoots each ( $P < 0.0001$ ). On the other hand, in those cases where flowering occurred, the proportion of shoots flowering declined with increasing shoot density (table 2); this relationship was initially strong but declined with time. The correlation was no longer significant in years 25 and 30.

*Flowering within a Whole Community*

**Question 3: Did the patterns of flowering among years differ among species?** Several analyses indicated that species differed in their year-to-year flowering patterns. For three of 48 species, no shoots flowered during any sample year: *Xerophyllum tenax*, *Epilobium angustifolium* (*Chamerion angustifolium* var. *canescens*), and *Luetkea pectinata*. Three species first flowered in year 25, three first in year 30. For 10 major species, flowering occurred somewhere in our plots during 42%–100% of sampling years; most species flowered in most years (table 3). The mean intensity of flowering (table 3) varied from 0.04 to 0.19; the highest values were for *Tiarella unifoliata* (*Tiarella trifoliata* var. *unifoliata*), *Osmorbiza purpurea*, and *Mitella pentandra*. The maximal intensity of flowering (table 3) ranged from 0.08 (*Chimaphila umbellata*) to 0.56 (*O. purpurea*); there was little year-to-year consistency, with maximal flowering occurring in seven different years among the 10 species.

Among 30 species-pair combinations with data for >5 yr, only three pairs showed similar patterns with time, that is, had a significant correlation coefficient, all positive: *Rubus pedatus* and *Streptopus roseus* (*Streptopus lanceolatus* var. *curvipes*;  $r = 0.96$ ,  $P = 0.0006$ ), *Rubus lasiococcus* and *S. roseus* ( $r = 0.92$ ,  $P = 0.003$ ), and *R. lasiococcus* and *R. pedatus* ( $r = 0.70$ ,  $P = 0.023$ ).

Fourteen species showed a significant rank correlation coefficient of flowering with year (table 4); all except *Arnica latifolia* and *Oxalis trilliifolia* increased with time. Only two species (*R. lasiococcus* and *T. unifoliata*) showed significance

**Table 3**

Flowering Intensity for 10 Major Species for All Sample Years at All Sites

Year	Rula	Pyse	Mipe	Tiun	Rupe	Ospu	Vasi	Vise	Stro	Chum
0	.07	.50	.17	.11	.04		.02			.08
1	.006	.04	.47	.13	.008	.10	.06		.006	
2	.03	.03	.26	.32	.04	.12	.03	.11	.03	
3	.02	.04	.29	.25	.06	.30	.02	.04	.09	
4	.02	.10	.04	.15	.08	.56		.11	.03	
7	.08	.26	.04	.20	.11	.15	.04	.10		
9	.04	.02								.01
10	.14	.05	.21	.15	.22	.19	.04	.07	.40	
20	.02	.01	.05	.10	.05	.05	.004	.02	.01	
25	.08	.02	.02	.25	.29	.12		.04		.07
30	.06	.04	.06	.18	.04	.22	.14	.04	.03	.03
Mean	.05	.07	.17	.19	.07	.18	.04	.06	.11	.05
Percent	100	100	92	92	92	83	75	75	67	42

Note. Blank cells indicate that the species was not recorded in the plots sampled that year. Species abbreviations: Rula = *Rubus lasiococcus*, Pyse = *Pyrola secunda*, Mipe = *Mitella pentandra*, Tiun = *Tiarella unifoliata*, Rupe = *Rubus pedatus*, Ospu = *Osmorbiza purpurea*, Vasi = *Valeriana sitchensis*, Vise = *Viola sempervirens*, Stro = *Streptopus roseus*, Chum = *Chimaphila umbellata*. Mean is the average proportion of shoots that flowered across all sampling years. Percent is the percentage of years during which the species flowered somewhere within our plots.

**Table 4**  
Signs Indicating Whether Incidence and Intensity Increased or Declined during Succession for 12 Species

Species	Incidence		Intensity	
	All sites	Site DR	All sites	Site DR
<i>Arnica latifolia</i>	–		–	
<i>Deschampsia</i> sp.		+		+
<i>Epilobium alpinum</i> ( <i>Epilobium anagallidifolium</i> )				+
<i>Erythronium montanum</i>				+
<i>Gaultheria humifusa</i>	+		+	
<i>Hieraceum albiflorum</i>	+		+	
<i>Linnaea borealis</i>	+		+	
<i>Oxalis trilliifolia</i>				–
<i>Pyrola secunda</i>	+			
<i>Rubus lasiococcus</i>	+	+	+	
<i>Rubus pedatus</i>	+			
<i>Stellaria</i> sp.		+		+
<i>Tiarella unifoliata</i>	+	+		+
<i>Viola sempervirens</i>		+		

Note. Data show the sign of significant Spearman rank correlation coefficients with year for individual species for both incidence and intensity of flowering, for both all-sites and site DR data. Blank cells indicate not significant.

in both the all-sites data and site DR data. Significance was more common for flowering incidence than for flowering intensity.

#### Factors Related to Incidence of Flowering

*Question 4 (part 1): What environmental and plant characteristics had significant relationships with the incidence of flowering?* Logistic regression (adjusted for repeated measurements) on presence-absence data indicated that all factors tested were associated with significant differences, except for habitat breadth in the all-sites data and growth form at site DR (table 5). In the all-sites data, graminoids and deciduous nonclonal species flowered more than clonal species; plants from herb-rich more than those from herb-poor sites; and plants from shallow tephra more than those from deep tephra. At site DR, species that grew in early seral habitats flowered less than other species. Flowering increased after the first 2 yr of measurement in both data sets.

However, the means in table 5 did not reflect several important changes in patterns as succession proceeded (fig. 2). The overall temporal increase in flowering incidence (table 5) was significant only in conditions in which flowering was initially low: deep tephra (fig. 2A), herb-poor communities (fig. 2B), plants that also occur in early seral sites and plants confined to forest (fig. 2C), and evergreen clonal and graminoid plants (fig. 2D). In these cases, flowering reached levels similar to that for other levels of the factor and was continuing to increase after year 20, while the factor levels with higher initial incidence had reached a plateau (fig. 2). For habitat breadth (fig. 2C), forest + early seral plants had near-zero flowering until year 3 but reached the level of other plants by year 20, and flowering of forest-only plants was continuing to increase, in contrast to other plants.

The effect of early erosion was measured for plots cleared in year 2 at site DR. Flowering incidence in cleared plots (mean = 0.19,  $N = 124$ ) differed significantly from natural plots at the same site (mean = 0.24,  $N = 135$ ,  $P = 0.006$ ).

Among 10 species that were important across the range of tephra depths, the degree of herb richness, or both, tephra depth was associated with a significant difference for three species, and herb richness for four (table 6). For each factor, one species showed the opposite pattern from the averages for growth forms shown in table 5: *Viola sempervirens* flowered more in deep than in shallow tephra, and *Pyrola secunda* (*Orthilia secunda*) flowered more in herb-poor than in herb-rich sites.

#### Factors Related to Intensity of Flowering

*Question 4 (part 2): What environmental and plant characteristics had significant relationships with the intensity of flowering?* Flowering intensity was significantly related to flowering incidence (all-sites data,  $r = 0.60$ ; site DR data,  $r = 0.49$ ;  $P < 0.0001$  for both). Intensity of flowering varied significantly with growth form (table 7). Like incidence, intensity was greater for graminoid and deciduous nonclonal plants than for clonal forbs. Otherwise, however, incidence and intensity provided different information about flowering patterns: unlike incidence, flowering intensity did not differ with species' habitat breadth, tephra depth, herb richness of the site, or year. Apparently, flowering occurred more widely with time, while the proportion of shoots flowering remained the same. Flowering intensity of natural and year 2 cleared plots at site DR did not differ significantly ( $P = 0.17$ ).

#### Consistency of Flowering Patterns with Time

*Question 5: How did patterns of flowering in the third decade after disturbance differ from earlier in succession?* Among 33 species with data for flowering intensity in at least two of three periods (to year 20, year 25, and year 30), the relationships among periods were significant but not strong. Simple regressions of data from year 20 and earlier with year 25 showed adjusted  $r^2 = 0.37$ ,  $P = 0.0003$ ; with year 30, values were lower but still significant ( $r^2 = 0.12$ ,  $P = 0.027$ ). The relationship between years 25 and 30 was not significant ( $r^2 = 0.09$ ,  $P = 0.054$ ).

#### Changing Influence of Factors as Succession Proceeded

*Question 6: How did the influence of the factors related to incidence of flowering change with time?* The logistic regression model relating factors to flowering incidence was significant for all individual sampling years (table 8). Growth form was significant after year 2; its influence seemed robust. Tephra depth was significant only in early years. Habitat breadth of species became more significant with time. Herb species richness was significant only once, late in the study.

When we accumulated the data for flowering incidence across years, there was more consistent significance of factors than when considering individual years (tables 8, 9). The influence of some factors related to flowering incidence became

**Table 5**  
**Relationship of Flowering Incidence to Plant Factors, Environmental Factors, and Year**

Factor and level	<i>P</i>		All sites		Site DR	
	All sites	Site DR	<i>N</i>	Mean	<i>N</i>	Mean
Growth form	.001	.17				
Mycotrophic achlorophyllous			2	1.0	...	...
Deciduous clonal			156	.46	97	.41
Deciduous nonclonal			119	.61	72	.49
Evergreen clonal			142	.46	47	.45
Evergreen nonclonal			15	0	...	...
Graminoid			18	.61	43	.58
Habitat	.07	.0003				
Forest only			282	.54	110	.54
Forest and early seral			23	.43	33	.27
Forest and meadow			146	.41	116	.46
Herb richness	<.0001	...				
Herb rich			315	.57	...	...
Herb poor			137	.32	...	...
Tephra depth	.004	...				
Deep			221	.43	...	...
Shallow			231	.55	...	...
Year	<.0001	.0006				
0			37	.30	...	...
1			51	.25	...	...
2			55	.49	...	...
3			58	.55	30	.27
4			...	...	30	.27
7			...	...	38	.50
10			...	...	43	.53
20			76	.53	54	.46
25			80	.58	...	...
30			95	.56	64	.59

Notes. Data are the sample size ( $N$  = number of cases) and mean of flowering incidence for each factor level, with the level of significance for factors, based on a likelihood ratio test from a logistic regression run for repeated measures, for both the all-sites and site DR data. Number of shoots is a quantitative variable that was also included in the models ( $P < 0.0001$ ); it is the number of shoots, flowering plus nonflowering, for each case. All factors in the table are categorical except year. Site DR data also include plots with tephra removed in year 2. The effect of year 2 tephra removal was significant ( $P = 0.006$ ). Means: natural, 0.55; 1982 cleared, 0.38.

significant early, while others required decades and hundreds of data points for their influence to appear (table 9). Number of shoots was significant every year, growth form after year 0, and tephra depth and habitat breadth after year 3, but herb species richness did not become significant until year 25. Part of the reason for the gain in significance with time was the increasing sample size, but part also may have been due to changes in flowering behavior as succession proceeded, as noted above (table 8). Accumulating data over multiple years increased significance for the patterns but may have masked changes in flowering behavior that developed during succession (fig. 2; table 8).

## Discussion

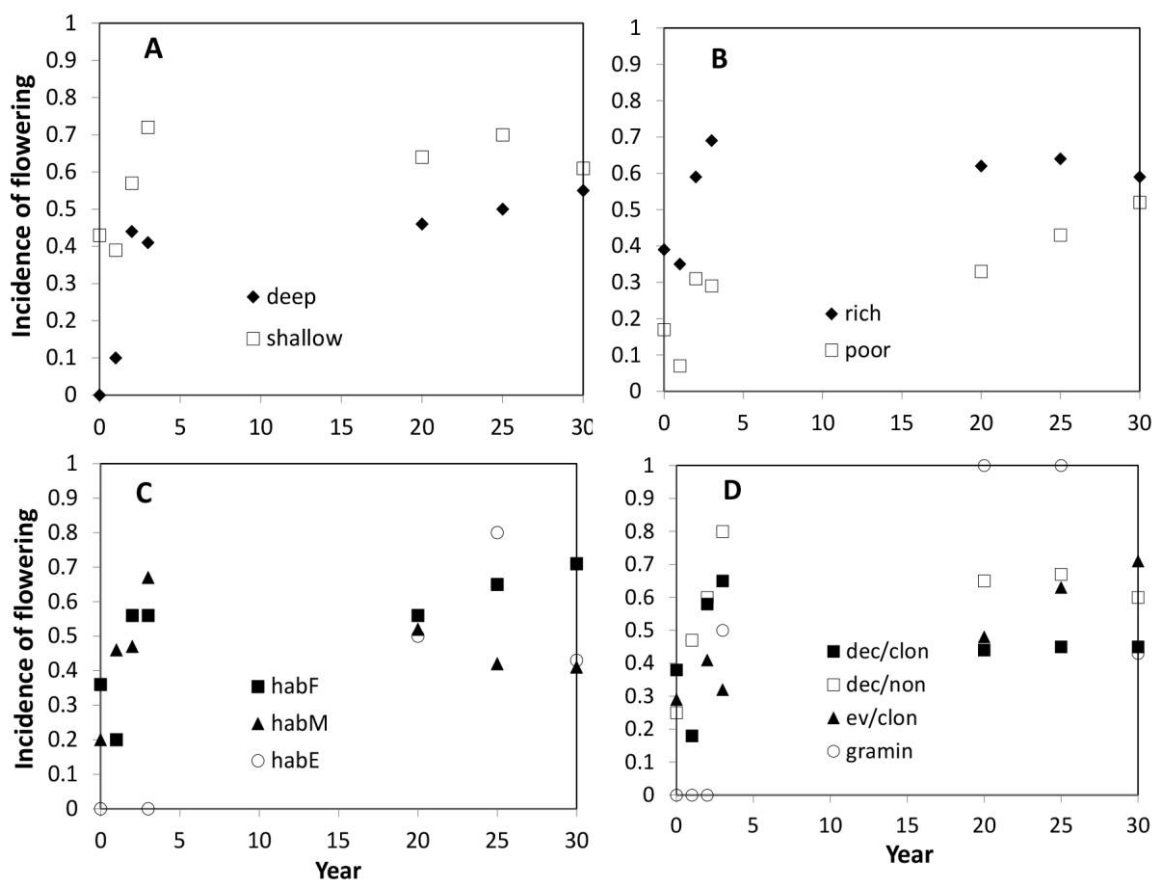
### *The Importance of Flowering during Vegetation Redevelopment*

Limited seed production and dispersal of understory herbs have been cited as causes limiting herb distribution, including their failure to occupy suitable habitat in stable forests, their

limited ability to colonize, and their uncertain persistence in a changing landscape (e.g., Cain et al. 1998; Ehrlén and Eriksson 2000; Verheyen et al. 2003; Matlack and Monde 2004). Our results up to year 20 indicated that sexual reproduction was critical for some species—but not others—during revegetation of habitat damaged by tephra (Zobel and Antos 2007).

The relative amount of flowering was weakly related to the success of a species at establishing individuals following the tephra deposit (fig. 1). This result does not mean, however, that we can ignore flowering when considering the basis for species' differential colonization of the 1980 tephra; rather, the lack of a clear general relationship comes from the variation in the importance of sexual reproduction among species. Some species—for example, *Tiarella unifoliata* (which left no survivors in our deep tephra plots)—became important only through regeneration from seed. In contrast, *Rubus lasiococcus* produced few flowers and no seedlings but was an important early colonizer of tephra at all sites. In general, species differences in reproduction are critical to succession on volcanic deposits (e.g., Dale et al. 2005a; Tsuyuzaki 2009; del Moral and Magnusson 2014; Efford et al. 2014).





**Fig. 2** Incidence of flowering by year in deep versus shallow tephra (A), in herb-rich versus herb-poor communities (B), for groups of species with different habitat breadths (habF = forest only, habM = forest and meadow, habE = forest and early seral; C), and for different herb growth forms (dec/clon = deciduous and clonal, dec/non = deciduous nonclonal, ev/clon = evergreen and clonal, gramin = graminoid; D). Evergreen nonclonal plants (which never flowered in our plots) and mycotrophic achlorophyllous angiosperms (which always flowered) were excluded from the graphs.

Flowering itself does not necessarily reflect the impact of sexual reproduction (Silvertown et al. 1993). Stages of the sexual reproductive process besides flowering may differentiate species in their success: at our sites, species with higher production of seedlings per flowering incident produced a greater

increase in year 20 density than those with lower seedling production (Zobel and Antos 2007).

Sexual reproduction should not be considered separately from other aspects of the reproductive process. Forest herbs often flower little, relying on vegetative production of new

**Table 6**

**Significance of the Relationship of Flowering Incidence to Tephra Depth and Herb Richness of the Site for Six Species**

Species	$N_{\text{deep}}$	$N_{\text{shallow}}$	Model $P$	Mean			
				Shallow	Deep	Poor	Rich
<i>Streptopus roseus</i>	22	12	<.0001	.75	.14	.27	.39
<i>Tiarella unifoliata</i>	22	12	.015	.82	.73		
<i>Viola sempervirens</i>	21	14	.0002	.36	.52		
<i>Osmorhiza purpurea</i>	14	12	.005			0	.67
<i>Pyrola secunda</i>	14	12	<.0001			.50	.45
<i>Rubus pedatus</i>	22	12	<.0001			.42	.73

Notes. Data are for single species that were important at both levels of either tephra depth or herb richness. Blank cells indicate not significant. The model also included year and number of plots where the species was present.  $N_{\text{deep}}$  = number of cases in deep tephra,  $N_{\text{shallow}}$  = number of cases in shallow tephra.

**Table 7**  
**Relationship of Flowering Intensity to Growth Form**

Level	All sites		Site DR	
	N	Mean	N	Mean
Mycotrophic achlorophyllous	2	1.0	...	...
Deciduous clonal	145	.044	40	.117
Deciduous nonclonal	110	.129	36	.152
Evergreen clonal	136	.044	21	.069
Evergreen nonclonal	14	0	...	...
Graminoid	18	.143	25	.235

Notes.  $P$  values: all sites,  $P = 0.006$ ; site DR,  $P = 0.006$ . Means are of flowering intensity (proportion of shoots flowering in plots where flowering occurred). Levels of significance are based on a repeated-measures, multifactor ANOVA on log-transformed data, with number of shoots as a covariate ( $P < 0.0001$  for all-sites analysis,  $P = 0.008$  for site DR). Levels of habitat breadth, herb richness, tephra depth, year, and 1982 tephra removal (for site DR data) did not differ significantly.  $N$  = number of cases.

ramets (Bierzychudek 1982; Whigham 2004). Flowering and other aspects of regeneration are related among our species (Zobel and Antos 2009): species that flowered more were those that left fewer survivors and that had higher shoot turnover in shallow tephra, that is, those that tended to have a more variable population size. Changes after year 20 reinforced this idea: several graminoids that established late had high proportions of shoots flowering in years 25 and 30. These continuing changes in species composition and relative flowering success of different types of plants (fig. 2) should lead to continuing shifts in species composition for at least the near future. Our earlier conclusion that understanding variation in flowering is necessary to understand this example of vegetation change remains intact.

The shifts with time in success of initial establishment, flowering, and eventual population size may reflect a changing environment. In particular, the recent increased flowering of groups of plants that initially flowered little (fig. 2)—evergreen clonal and those that can be early seral—seems likely to be associated with an increasing availability of nutrients and perhaps light. Clonal plants often concentrate flowering in a few ramets when resources are limited; with more resources, flowering within a genet should increase. Nutrient availability has probably increased with accumulation of over-

story tree litter and the establishment of a continuous, consolidated forest floor organic layer that is densely populated with roots, a major change from earlier years when much of the tephra surface was barren (Zobel and Antos 1991). Continuing secondary disturbances, especially tree mortality (e.g., for younger trees because of heavy snow or ice; some old-growth *Abies amabilis* at site DR, apparently associated with retention of tephra on foliage [Segura et al. 1994]), increased understory light and reduced root competition. A few weedy species (mostly native) not in the original forest have invaded by seed, perhaps also reflecting greater resource availability. On the other hand, continuing spread of shrubs, tree seedlings, and larger herbs will increase competition, and expansion of the still-reduced bryophyte layer may further modify seedbed conditions. One can expect flowering and seedling establishment patterns to continue to change with the understory environment. Should our herbs be seed limited, as is typical in old forests (e.g., Ehrlén and Eriksson 2000), these relative changes in flowering are likely to lead to changes in species composition.

#### *Changes in the Third Decade after Disturbance*

The patterns of flowering at our sites were continuing to change decades after disturbance. Our results contrasted substantially with those based on the first 20 years of succession (Zobel and Antos 2007), including changes in some conclusions. Major differences were as follows. (1) Flowering increased after year 20: only three of 48 species failed to flower by year 30 compared with five of 41 species 10 yr earlier; the proportion of shoots flowering for most species was 0.02–0.04 (maximum of 0.15) up to year 20, whereas in our data (table 3), the comparable values were 0.04–0.10 (maximum of 0.19); and 12 species had a significant increase in flowering related to year (table 4) compared with six in the earlier data. (2) Deciduous nonclonal species flowered more than clonal forms in both the 20- and 30-yr data, but the situation was changing. Graminoids, which we previously lumped with forb growth forms, added flowering species and flowered equally or more than deciduous nonclonal forbs (tables 5, 7). More importantly, flowering of evergreen clonal species increased substantially (fig. 2D), reducing the differential among growth forms. (3) Our previous conclusion (Zobel and Antos 2007) that flowering increased as shoot density increased was contradicted by our current result that, before year 25, flowering

**Table 8**  
**Differences among Single Sampling Years in Significance of Factors Influencing Flowering Incidence**

Year	df	Model $P$	Tephra depth	Herb richness	Growth form	Habitat breadth	No. shoots
0	36	.03	.06	.95	.63	.24	.03
1	50	.0002	.02	.21	.004	.18	.002
2	54	.04	.87	.16	.21	.09	.14
3	57	.0001	.02	.29	.002	.008	.44
20	75	<.0001	.36	.88	.002	.72	<.0001
25	79	.004	.13	.045	.045	.03	NA
30	93	.007	.68	.052	.03	.005	.29

Notes. Data are significance ( $P$ ) values based on logistic regression on flowering presence-absence data. Regressions were run using data for the listed year only. All four sites were sampled during these years. NA = not available (shoots were not counted at site SR in year 25).

Table 9

Differences among Years, Using Cumulative Data, in Significance of Factors Influencing Flowering Incidence								
Year	df	Model <i>P</i>	Tephra depth	Herb richness	Growth form	Habitat breadth	Year	No. shoots
0	36	.03	.06	.95	.63	.24	NA	.03
1	87	<.0001	.01	.35	.008	.54	.62	.0002
2	142	<.0001	.15	.08	.008	.06	.008	.0004
3	200	<.0001	.02	.056	.0002	.002	.0005	.0008
20	276	<.0001	.01	.09	<.0001	.02	.006	<.0001
25	329	<.0001	.008	.03	<.0001	.02	.002	<.0001
30	423	<.0001	.02	.003	<.0001	.007	.001	<.0001

Notes. Data are significance (*P*) values based on logistic regression on flowering presence-absence data and are based on cumulative data for the listed year and all previous sample years in which all four sites were sampled.

declined significantly with increasing density (table 2). The difference in sign reflected how the analysis was done: for the 2007 article, we used both cleared and natural tephra plot data and all cases instead of only cases with flowers. When we include nonflowering cases for our current data set, the Spearman rank correlation coefficient (*r*) became positive (all-sites data set,  $r = 0.34$ ,  $P < 0.0001$ ). A major reason for the difference in sign is that cases without flowering have few shoots (52) compared with flowering cases (242): thus, about half the data points have zero flowering and a low shoot number, while many cases with flowers have high shoot numbers, producing a positive relationship. We believe our current approach is more useful. (4) The reduction in proportion of shoots flowering as shoot density increased (table 2) has at least three possible explanations. (a) It may reflect competition or other forms of interference among shoots, which seems most tenable in shallow tephra, where shoot density was reduced moderately to none by the tephra. (b) Second, denser populations may have included many young, preflowering plants of these slow-growing perennials, which seems likely in deep tephra, where few shoots survived and most current shoots developed after the eruption. (c) Third, the few survivors in deep tephra tended to be large, of flowering size, contributing to the negative trend in table 2. The decrease with time in the significance of the negative relationship suggests that the process of filling of open space by new plants (producing small, nonflowering shoots) has declined as succession proceeded; furthermore, there may be less competitive effect in dense herb stands as the nutrients N and P accumulated in the tephra (Zobel and Antos 1991). (5) The relationship of some factors to flowering changed during the third decade: the effect of year 2 tephra removal on flowering intensity changed from negative in year 20 to nonsignificant in year 30, and the relationship of herb richness to flowering incidence changed from nonsignificant in year 20 to positive in year 30 (table 9).

#### *Flowering as a Component of Successional Change*

Ecologists traditionally study change during succession in a variety of attributes and processes, such as community structure, species composition, productivity, and nutrient cycling. The change in patterns of flowering is worthy of similar consideration. To summarize the results during the third decade after tephra emplacement: with time, flowering increased, more for some growth forms and species than for others; the

negative influence of shoot density on flowering intensity disappeared; and year 2 tephra removal no longer reduced flowering intensity, while flowering incidence now was higher where herb richness was high. As noted in the introduction, flowering is required for spread beyond the local patch, flowering in understory herbs is often rare, and thus low flowering may lead directly to seed limitation of succession, as found in understory herbs. In our situation where late snow melt synchronizes species' phenology, sampling of flowering is easier than sampling of seedling establishment and survival, which requires data from consecutive years. Although it provides only a partial picture of the sexual reproductive process, flowering makes a convenient and important indicator of how reproduction is changing.

The relationship of growth form to incidence and intensity of flowering was initially strong (tables 5, 7, 8). However, some of these differences disappeared with time (fig. 2), as flowering continued to increase for evergreen clonal species, plants of forest-only and forest + early seral habitats, and plants in herb-poor and deep tephra sites. This modification of the relative degree of flowering is a part of successional change that eventually may lead to increases in importance of at least some of those species with a recent increase in flowering success, as CaraDonna et al. (2014) suggest for shifts in phenology during climatic warming. Flowering and seed production will likely continue to have an important influence on species composition and spatial patterns of herbs among patches as succession proceeds, which is consistent with patterns observed for many older forests (Valverde and Silvertown 1998; Ehrlén and Eriksson 2000; Albrecht and McCarthy 2009; Burton et al. 2011). Thus, flowering is a process that warrants consideration during all stages of succession.

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