

## The effects of fire on scarlet gilia: an alternative selection pressure to herbivory?

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**Summary.** The primary goals of this paper were to experimentally assess the relative importance of fire, a potentially important selective agent involved in shaping scarlet gilia's compensatory response and, in general, determine scarlet gilia's response to fire. Burn treatment results demonstrated that fire was not an important selective agent involved in shaping scarlet gilia's compensatory response. The most common response to fire was the production of one or more new clonally derived rosettes. This was an unexpected result; this typically monocarpic herb rarely produces clonal offspring. Although rosette production lessened the detrimental effects of fire by giving plants that cloned a second chance to flower, these newly formed rosettes delayed flowering for at least one year and had significantly higher overwinter mortality rates than rosettes from unburned control plots. In addition, significantly fewer individuals from the burn treatments flowered and there was significantly higher immediate mortality. There was, however, no detrimental effect on the reproductive success (seed production) of individuals that flowered following the burn. Overall, cumulative estimates of plant performance suggest that at the population level fire results in a 4.5-fold decrease in relative plant fitness. However, fire-induced seed germination could negate the detrimental effects of fire on the population dynamics of scarlet gilia. In the year of the burn there was a 116-fold increase in the number of germinating seeds and by the second year this translated into an approximate 6-fold difference in the number of surviving rosettes. Two alternative candidates, frost damage and ungulate trampling, can cause the removal of apical dominance and a response similar to that generated by ungulate and insect herbivores. However, they are probably minor factors favoring selection toward growth compensation; experimental and observational results demonstrate that apical dominance was removed in only 3% of plants exposed to freezing temperatures and ungulate trampling caused breakage and release of apical dominance in only 0.2% of plants.

Recent studies have shown that when mule deer and elk browsed the monocarpic biennial scarlet gilia, *Ipomopsis aggregata*, relative fitness in terms of seed production and subsequent seedling survival averaged 2.4 times that of the uneaten controls (Paige and Whitham 1987a; Whitham et al. 1991; Paige 1992). The increase in relative fitness was largely due to an architectural change in the plant; ungulate removal of scarlet gilia's single inflorescence resulted in the production of multiple flowering stalks due to the release of apical dominance. From an evolutionary perspective, given that herbivory is predictably high on these sites each year (on average 77% of all plants are browsed during the flowering season), it is tempting to surmise that scarlet gilia's compensatory response is an evolutionary adaptation to herbivory.

But before we can begin to understand the evolutionary interactions between plants and herbivores it is necessary to ascertain whether there are other selection pressures, both past and present, involved in generating the observed plant response patterns. Apical damage, for example, can be caused by a number of factors other than herbivory, including frost damage, fire, pathogen attack, trampling and breakage by wind (Benner 1988).

Prior to fire suppression programs beginning in the early 1900's, fire was an important historical component of the forest/grassland community of which scarlet gilia is a part. Low intensity surface fires occurred at regular intervals of 2–10 years, burning through all parts of the community (Cooper 1960; White 1985). These lightning-induced fires predominate during the monsoon season (beginning in early July) and coincide with the period of stem elongation and flowering in scarlet gilia. Thus, fire represents a relatively predictable and potentially important selection pressure. Therefore, the primary goals of this paper are to assess the relative importance of fire as a selective agent in shaping scarlet gilia's compensatory response and, in general, determine scarlet gilia's response to fire. The interactive effects of fire and herbivory are also assessed.

In addition, the effects and relative importance of a number of other potential selective agents (in particular, ungulate trampling and frost damage) may be involved in the release of apical dominance. On Fern Mountain, where

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these studies were carried out, large herds of elk (85–250 individuals) and small herds of mule deer (5–15 individuals) migrate into the area each year, potentially exposing scarlet gilia to trampling. Furthermore, this high elevation (2500 m) population usually experiences freezing temperatures well into May, exposing rosettes and newly elongating shoots of scarlet gilia to the potentially damaging effects of frost. These additional hypotheses, that stem damage by trampling or freezing may be important in shaping scarlet gilia's compensatory response, will also be tested.

## Methods and materials

Studies on the effects of fire and its relative importance as a selective agent in shaping scarlet gilia's compensatory response were conducted during the summers of 1989 through 1991 at the Museum of Northern Arizona (elevation 2133 m), near Flagstaff, Arizona. Scarlet gilia, *Ipomopsis aggregata* (Polemoniaceae), is a red flowered monocarpic biennial herb of western montane regions that flowers from early-mid July through late September (Hainsworth et al. 1985; Paige and Whitham 1985, 1987a, b; Paige 1992). Following seed germination, scarlet gilia develops into a leafy rosette and after 1–8 years of vegetative growth a single paniculate-racemose inflorescence is produced (Paige and Whitham 1987a). Following stem elongation the plant flowers, reproduces and then dies.

To test the effects of fire on the growth response and reproductive success of scarlet gilia, two 10 m<sup>2</sup> natural plots in which 80 plants were tagged (42 and 38 plants/plot) were burned in early June, 1989. Fire breaks were created around each of the plots and the dry litter was ignited with a match. Two 10 m<sup>2</sup> plots in which 114 plants (56 and 58 plants/plot) were tagged served as controls. In all 4 plots about one half of the elongating plants had been browsed and had multiple stems (Table 1A and B). In early August survival and growth form of individual plants were assessed (Table 1). Because there were no significant differences in plant responses between the two burn treatment plots ( $X^2 = 4.08$ ,  $df = 2$ ,  $p = 0.145$ ) or between the control plots ( $X^2 = 2.90$ ,  $df = 3$ ,  $p = 0.425$ ) plots within a treatment

were pooled for analyses. Comparisons between the burned plots included the number of plants that produced new rosettes, the number of plants that produced multiple-stems, and the number of plants that died; no plants produced single-stems and none of the rosettes remained as they were prior to the fire (i.e., the "Same Rosette", Table 1), therefore these cells were not included. Comparisons between the control plots included the number of new rosettes produced, number of single-stemmed plants, number of multiple-stemmed plants and the number of rosettes that remained rosettes. Because no plants died in the control plots, these cells were not included in the comparison.

The separate and interactive effects of fire and herbivory on the reproductive success of scarlet gilia were assessed in both burned and unburned plots in early October of 1989 and 1991 and in burned plots only in 1990. Plants used for measurements of survival and reproduction were selected and matched across treatments on the basis of stem diameter (stem diameters covered the most common range of sizes within the populations, from 2–6 mm;  $F = 0.915$ ,  $df = 9, 102$ ,  $p = 0.52$  for all plants over three years, see below). Stem diameter is a relatively accurate measure of plant size (positively correlated with biomass,  $R^2 = .54$ ,  $N = 25$ ,  $p < .0001$ ; height,  $R^2 = .40$ ,  $N = 25$ ,  $p < .0007$ ; and flower production,  $R^2 = .66$ ,  $N = 25$ ,  $p < .0001$ , for example). Stem diameter measurements were taken from the base of the original (now burned) stem or stem scar so that plants could be accurately matched for initial size (prior to burning and browsing). In 1989 twenty-two plants (12 multiple-stemmed (browsed) plants and 10 single-stemmed (unbrowsed) plants) were selected from the two burn sites and twenty plants (10 multiple-stemmed plants and 10 single-stemmed plants) were selected from adjacent unburned sites (not all plants were tagged on all plots, hence the apparent discrepancy between the 9 multiple-stemmed plants surviving the burn in Table 1 and the 12 multiple-stemmed plants used for assessing the interactive effects of fire and herbivory). Plants were then compared in terms of the number of flowers produced, number of fruits produced, number of seeds per fruit and plant height. In 1990, another twenty-one plants (11 multiple-stemmed and 10 single-stemmed plants) were selected from the two burn sites to assess the effects of the previous year's burn on the current year's reproductive success. Control plot plants were, unfortunately, not measured in 1990. In 1991 twenty plants (10 multiple-stemmed and 10 single-stemmed plants) were selected from both burned and unburned sites, respectively. Plants were again selected on the basis of stem diameter;

**Table 1.** Regrowth response of scarlet gilia, *Ipomopsis aggregata*, between burn treatments (A) and unburned controls (B). Highly significant differences occurred between the treatment groups (i.e.,

burn versus unburned treatments;  $p < .0001$ , see results). Number and percentage of plants of a particular growth form following the burn treatments are shown

### A. Burn treatment

Plant form prior to burn		Growth form distribution after burn				
		New rosette	Same rosette	Single-stemmed	Multiple-stemmed (From fire)	Died
Rosette	20 <sup>a</sup>	13 (65%)	0 (0%)	0 (0%)	1 (5%)	6 (30%)
Single-stemmed	35	22 (63%)	–	0 (0%)	3 (9%)	10 (29%)
Multiple-stemmed (From herbivory)	25	8 (32%)	–	0 (0%)	5 (20%)	12 (48%)

### B. Non-burn treatment

Plant form prior to burn		Growth form distribution, controls				
		New rosette	Same rosette	Single-stemmed	Multiple-stemmed (From herbivory)	Died
Rosette	26 <sup>a</sup>	0 (0%)	26 (100%)	0 (0%)	0 (0%)	0 (0%)
Single-stemmed	54	1 (2%)	–	19 (35%)	34 (63%)	0 (0%)
Multiple-stemmed (From herbivory)	34	0 (0%)	–	0 (0%)	34 (100%)	0 (0%)

<sup>a</sup> Total number of plants prior to treatment

plants were similar in size to those measured in both 1989 and 1990. Measurements included the number of flowers produced, number of fruits produced and plant height.

Potential differences in relative fitness were assessed using an analysis of covariance with two treatment factors (burn treatment: burned or unburned; browsing level: browsed or unbrowsed) and one blocking factor (year). Basal stem diameter was used as a covariate to further adjust for the effects of plant size on yield. Tests were run on log-transformed or  $\log(Y+1)$ -transformed data to equalize variances. Alpha levels for the four variables measured were adjusted using a Bonferroni adjustment.

In an effort to see if average plant size was affected by the previous year's burn, stem diameters were measured on 100 haphazardly selected plants from the two treatment sites in 1990; 50 from the burn sites and 50 from adjacent unburned sites.

Overwintering survivorship of 39 tagged regrowth rosettes on burn sites was compared to the overwintering survivorship of 77 tagged rosettes on unburned sites the following spring to assess the effects of fire on the long term survival of rosettes.

To determine the effects of fire on seed germination and seedling establishment ten 0.3 m<sup>2</sup> plots were randomly selected within each of the treatment sites (burned and unburned control) and all seedlings were counted. Counts were conducted in early August (1989) prior to the current year's production and dispersal of seed. Overwintering survivorship of seedlings was measured on these plots the following year in early July.

To examine the effects of fire intensity on the survival and regrowth response of scarlet gilia, plants growing in approximately 13 cm of pine needle litter under ponderosa pines were compared to plants growing in sparsely distributed low growing vegetation (primarily grasses) away from the pines where fire intensity was not as great. These measures were made on one plot in August 1989. Although no direct measure on fire intensity was made, observationally the fires were higher, hotter and more damaging under pine than in the sparsely distributed low growing vegetation.

Studies on the importance of freeze damage and trampling in the release of apical dominance were conducted during the summers of 1987–1991 on Fern Mountain (elevation 2500 m), near Flagstaff, Arizona. To assess the effects of frost damage on the release of apical dominance 65 rosettes were covered with wire mesh cages in the fall of 1990 to exclude herbivores. The following summer when the plants began to bolt, the number of shoots produced by each plant were counted to see if frost damage played a role in releasing apical dominance under natural conditions of the field. To assess the effects of trampling on the release of apical dominance, 1,952 plants were surveyed for breakage by mule deer and elk early in the flowering season during the period of stem elongation prior to flowering. These studies were conducted during the summers of 1987–1991.

## Results

### *Effects of fire on plant growth form*

Burn treatment results demonstrate that fire was not an important selective agent involved in shaping scarlet gilia's compensatory response. The most common response to fire was the production of one or more new clonally derived rosettes by each of the three plant growth forms (rosettes, single-stemmed plants and multiple-stemmed plants), as opposed to causing the release of apical dominance (Table 1A and B). For example, among those plants that survived the burn, 93% of all rosettes produced one or more new rosettes, 88% of all single-stemmed plants produced one or more basal rosettes and 62% of all multiple-stemmed plants produced one or more basal rosettes by the end of the flowering season. Rosettes were generated from belowground root biomass, typically near

the top of the root; original meristems died as a result of the fire. Only 7% of all rosettes and 12% of all single-stemmed plants responded in a fashion similar to that generated by ungulate herbivores, producing multiple inflorescences in response to fire. Plants that were multiple-stemmed prior to the burn treatment had the highest probability of producing multiple-stemmed inflorescences following the burn; i.e., 38% of all multiple-stemmed plants produced multiple inflorescences in response to fire. No burn treatment plants produced single-stemmed plants following the fire, although when newly formed rosettes bolt single-stemmed plants will be produced, as demonstrated in the years following. Thirty-five percent of all plants (28 of 80) died in response to the burn treatment. Although plants that were browsed and burned experienced a higher percentage mortality than unbrowsed plants that were burned (48% versus 29%), the difference was nonsignificant ( $X^2 = 2.37$ ,  $df = 1$ ,  $p = 0.14$ ).

These results contrast sharply with the control plot plants in which 0% of the rosettes produced new rosettes, only 2% of the single-stemmed plants produced new rosettes and 0% of the multiple-stemmed plants (generated by insect or ungulate damage) produced new rosettes. Instead, all tagged rosettes remained as rosettes (i.e., no change in growth form), 35% of the tagged single-stemmed plants remained single-stemmed plants throughout the flowering season and 63% of the single-stemmed plants formed multiple stems due to insect or ungulate herbivory (see Paige and Whitham 1987a; Whitham et al. 1991; Paige 1992). All multiple-stemmed plants remained as multiple-stemmed plants. No plant deaths were observed within the control plots ( $X^2 = 46$ ,  $df = 3$ ,  $p < .0001$  for comparisons between ultimate growth forms of rosettes that were burned and unburned rosettes;  $X^2 = 73.44$ ,  $df = 3$ ,  $p < .0001$  for comparisons between ultimate growth forms of single-stemmed plants that were burned and unburned single-stemmed plants;  $X^2 = 41.15$ ,  $df = 2$ ,  $p < .0001$  for comparisons between ultimate growth forms of multiple-stemmed plants that were burned and unburned multiple-stemmed plants).

### *Effects of fire on plant reproduction*

Fire had no effect on the reproductive success of those individuals that survived. Burn treatment plants that flowered in the year of the burn produced as many flowers, fruits and seeds as plants that were not burned with no delays (personal observation) in the timing of flowering. Furthermore, there was no effect of the burn treatment on the reproductive success of scarlet gilia in the years following (Table 2, Fig. 1A–C). There was, however, a nonsignificant trend toward lower flower production in burn treatment plants that were subsequently browsed by insects or ungulate herbivores in both 1989 and 1990 (Fig. 1A). Browsing by insect and ungulate herbivores on average resulted in an increase in flower and fruit production as previously reported (see Paige and Whitham 1987a; Paige 1992; Table 2, Fig. 1A and B).

Plant height was, however, significantly reduced by the burn treatment in 1989 ( $p < 0.05$ ; Table 2, Fig. 1D). Nonetheless, there was no effect detected on any of the

**Table 2.** Analyses of Covariance for the effects of fire and herbivory through time on *Ipomopsis aggregata*

Source of variation	df	Mean squares and P values			
		Flowers <sup>a</sup>	Fruits	Height	Seeds/fruit
Main effects	4/2 <sup>c</sup>	.358***	1.045***	.0762***	.0103
Burn	1	.0003	.0001	.0573*	.0205
Browsing	1	1.305***	1.495*	.0160	.0000
Burn × browsing	1	.0001	1.05	.0017	.0034
Stem diameter <sup>b</sup>	1	3.073***	1.794**	.2849***	
Year	2	.0737	1.242**	.1262***	
Error	95/16 <sup>c</sup>	.0375	.1866	.0062	.0231

<sup>a</sup> Alpha levels reflect Bonferroni adjustment. Tests were run on log-transformed or log (Y + 1)-transformed data to equalize variance

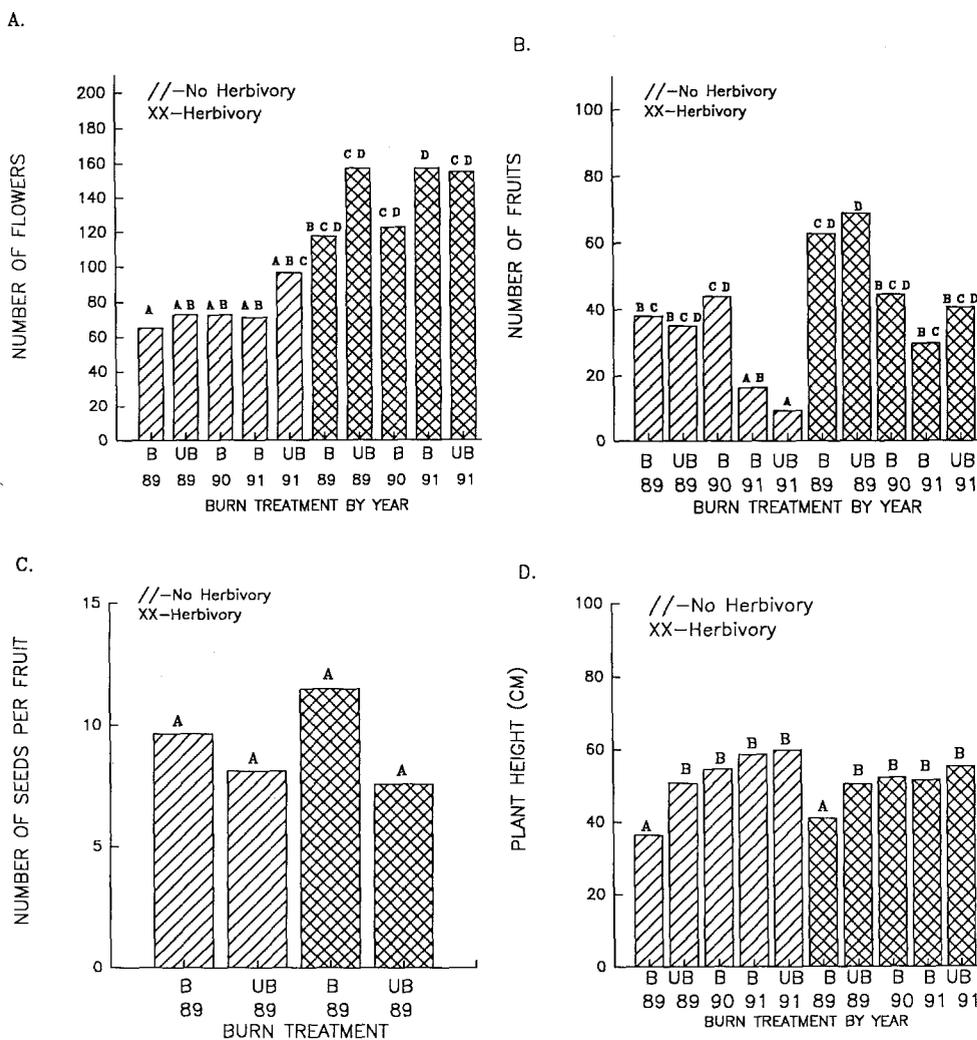
<sup>b</sup> Covariate

<sup>c</sup> For flowers, fruits, height/seeds

\* P < 0.05

\*\* P < 0.01

\*\*\* P < 0.001



**Fig. 1A–D.** Comparisons of relative fitness measures for the effects of fire and herbivory through time on scarlet gilia, *Ipomopsis aggregata*. Fitness measures include: **A.** Number of flowers per plant produced, **B.** Number of fruits per plant produced, **C.** Number of seeds per fruit, and **D.** Plant height. Burn treatments were conducted only in 1989. The effects of the burn treatments were assessed in 1990 and again in 1991. Unburned controls served as controls (unburned plots were not collected in 1990). Burned plots are designated *B* and unburned plots *UB*. Means with the same letters show no significant differences at the .05 level, Least Significant Difference Multiple Range Test. Tests were run on log-transformed or log(Y + 1)-transformed data to equalize variance. Alpha levels reflect Bonferroni adjustment. Sample size for measures on the number of flowers, fruits and height for plants that were not browsed from 1989–1991 was 50 (10 plants per treatment) and 53 for browsed plants (10 plants per treatment for 1989 *UB* and 1991 *B* and *UB*, 12 plants for 1989 *B* treatment, and 11 plants for 1990 *B* treatment). Plant sample size for number of seeds per fruit in 1989 was 20 (5 plants per treatment)

fitness components measured among those plants that flowered. In addition, in an effort to see if average plant size was affected by the previous year's burn, stem diameters were measured on 50 plants from each of the two treatment sites; no significant differences were found (mean stem diameter from the burn sites:  $4.88 \pm 0.27$  mm, unburned sites:  $5.48 \pm 0.31$  mm;  $t = 1.46$ ,  $df = 98$ ,  $p = 0.147$ ).

Although fire had no effect on the reproductive success of individuals that flowered in the year of the burn, there was a significant decline in the number of plants reaching reproductive maturity. In the burn treatment plots only 11% of all plants flowered, 35% died, and 54% formed new rosettes whereas, in the unburned control plots 76% of all plants flowered, 0% died, and 24% remained as

rosettes ( $X^2 = 91.90$ ,  $df = 2$ ,  $p < 0.001$ ). Thus, there was a significant delay in the number of plants reaching reproductive maturity in the year of the burn, with the majority of plants in the burn treatment producing new rosettes. These rosettes will then flower in some subsequent year (personal observation, data herein).

Fire also had a significant effect on the overwintering survivorship of rosettes that were produced following the burn treatment. Only 31% ( $N = 39$ ) of rosettes from the burn treatment survived to the following season, whereas, 83% ( $N = 77$ ) of rosettes from the unburned treatment survived to the following season ( $X^2 = 7.48$ ,  $df = 1$ ,  $p = 0.007$ ).

Fire also triggered seed germination. Burned plots produced 116 times more germinating seed than unburned plots (burn plots: 104.4 seedlings/0.3 m<sup>2</sup>, unburned control plots: 0.9 seedlings/0.3 m<sup>2</sup> in August 1989;  $t = 3.31$ ,  $df = 18$ ,  $p < 0.004$ ). Differences were still significant the second year, but the burned plots suffered from higher winter seedling mortality (burn plots: 3.2 seedlings (rosettes)/0.3 m<sup>2</sup>, unburned control plots: 0.5 seedlings (rosettes)/0.3 m<sup>2</sup> in July 1990;  $t = 2.46$ ,  $df = 18$ ,  $p = 0.024$ ).

#### *Effects of fire intensity*

Fire intensity did not differentially affect the survival and regrowth response of scarlet gilia. Thirty-two percent of all plants ( $N = 31$ ) growing under pine, where fire intensity was greater died, 10% produced multiple inflorescences and 58% produced new rosettes. Of the plants growing in sparse vegetation where fire intensity was not as great 23% of all plants ( $N = 70$ ) died, 11% produced multiple inflorescences, and 66% produced new rosettes ( $X^2 = 0.99$ ,  $df = 2$ ,  $p = 0.63$ ). Furthermore, those plants that produced rosettes showed no significant differences in the number of basal rosettes produced ( $2.88 \pm 0.24$  versus  $3.18 \pm 0.34$  rosettes per plant for high versus low intensity fires, respectively;  $t = -0.78$ ,  $df = 32$ ,  $p = 0.44$ ).

#### *Additional alternatives: Freeze damage and ungulate trampling*

Experimental and observational results suggest that neither freeze damage nor ungulate trampling were important selective agents involved in shaping scarlet gilia's compensatory response. Among plants that were caged over the course of the winter, only 3% ( $N = 65$ ) produced multiple inflorescences. These were probably the result of freeze damage in which the apical meristem of the rosette was destroyed prior to bolting. Although it is difficult to attribute apical release directly to frost damage, direct observation gave all appearances that freeze damage resulted in the death of the apical meristem. Of the 1,952 plants surveyed for breakage by mule deer and elk, as a result of trampling, only 4 (0.2%) plants produced multiple inflorescences. None of the plants from which apical dominance was removed by either freeze damage or ungulate trampling resulted in the production of new rosettes.

## Discussion

### *Fire: An alternative selection pressure to herbivory?*

Burn treatment results suggest that fire was not an important selective agent involved in shaping scarlet gilia's compensatory response. Only 7% of all rosettes and 12% of all single-stemmed plants responded in a fashion similar to that generated by ungulate herbivores, producing multiple inflorescences in response to fire. In contrast, 77% of all plants typically lose their apical meristems to ungulate or insect herbivores in any given year and respond by producing multiple inflorescences (Paige and Whitham 1987a; Whitham et al. 1991; Paige 1992). Furthermore, the timing and level of herbivory is highly predictable from year to year. Ninety-five percent of all ungulate herbivory occurs early in the flowering season during the period of stem elongation prior to flowering. Fire, however, is less predictable from year to year. Thus, herbivory is likely of greater importance as a selective agent involved in shaping scarlet gilia's compensatory response, assuming over-compensation is an evolutionary response to some ecological factor, like herbivory, and not merely a developmental or physiological constraint released through herbivory (see Whitham et al. 1991).

### *Growth response to fire*

Although burn treatment results suggest that fire was not an important selective agent involved in shaping scarlet gilia's compensatory response, scarlet gilia does have the capability of lessening the potential detrimental effects of fire. In response to the burn treatments, 83% of all surviving plants (or 54% of all plants including those that were directly killed by the fire) produced one or more clonally derived rosettes, giving scarlet gilia a second chance at flowering in some subsequent year. This was an unexpected result due to the fact that, in the absence of fire, scarlet gilia rarely produces clonal offspring (2% or less of all plants) at this site (see Paige and Whitham 1987b, data herein). Phenotypic plasticity has been observed in numerous plant species in response to factors such as herbivory (Hendrix 1979; Lubchenco and Cubit 1980; Paige and Whitham 1987a), competition (Turkington 1983), and, of particular interest here, fire (James 1984; Moreno and Oechel 1991). These examples also support the notion that plastic responses can be adaptive. Phenotypic plasticity, or the ability of an organism to alter its physiology/morphology, is particularly important in plants due to their sessile life-styles and their need to cope with ever-changing environmental conditions (Schlichting 1986). However, whether scarlet gilia's clonal response represents an evolutionary adaptation to fire is difficult to assess, and may even be unlikely, particularly in light of the fact that 35% of all plants died as a direct result of the burn. In addition, for those plants that produced new rosettes following the fire there was a significant decrease in overwinter survivorship. Alternatively, there is the possibility that the total removal of aboveground biomass by herbivores could result in clone production. However, total above-

ground herbivory and subsequent clone production has not been observed or experimentally assessed.

Overall, the question is, why does scarlet gilia produce one or more rosettes instead of multiple inflorescences in response to fire? One likely reason is that fire destroys the dormant lateral buds responsible for producing multiple inflorescences in addition to destroying the apical meristem. In response, resources are shunted to the production of clonally derived rosettes from the roots of the plant, the remaining living tissue. Furthermore, since the timing of fire is less predictable than ungulate herbivory (see Paige 1992) the best strategy for scarlet gilia should be rosette formation, which occurs rapidly and allows this monocarpic species a second chance to flower in some subsequent year at a more appropriate time. If plants responded by immediately producing new inflorescences, the time frame for flowering could end up being exceptionally narrow if the burn occurred late in the flowering season, placing plants at a selective disadvantage.

Although one might assume that fire intensity would alter this response, results suggest that this is not the case. Comparisons of plants growing in dense litter, where fire intensity was high, versus those growing in sparsely vegetated areas with negligible amounts of litter, where fire intensity was low, showed no significant difference in regrowth patterns or levels of mortality. Furthermore, there were no significant differences in the number of rosettes produced per plant (data herein) or delays in the timing of rosette production (personal observation). These results, however, are in contrast to the findings of Rundel et al. (1987) and Moreno and Oechel (1991) for chamise (*Adenostoma fasciculatum*), a chaparral shrub. They found that increasing fire intensity increased plant mortality, reduced the number of resprouts per plant and delayed the time of resprouting. These differences are likely due to the fact that *Adenostoma* resprouts from aboveground woody lignotubers that can survive low intensity fires. Scarlet gilia's herbaceous aboveground biomass, however, is destroyed by both high and low intensity fires. Therefore, scarlet gilia resprouts from belowground root biomass, the only structure protected from both high and low intensity fires. Of course one can easily argue that there are other differences between the two habitats, such as nutrient status or water, that could mitigate the effects of fire intensity. Therefore, these results are potentially open to other interpretations and should be viewed with caution.

#### *Effects of fire on plant reproductive success*

Although there was no immediate effect on the reproductive success of individuals that flowered following the burn, significantly fewer individuals from the burn treatments flowered (11% from the burn plots versus 76% from the unburned control plots) and there was significantly higher immediate mortality (35% of all plants from the burn plots versus 0% from the unburned control plots). In addition, over half (54%) of the individuals produced new rosettes in response to fire, and thus delayed flowering for at least one more year. Furthermore, there was a significant decrease in the survival of overwintering rosettes when comparing burn treatment rosettes to rosettes from

the unburned control plots (only 31% of all burn treatment rosettes survived into the next year as compared to 83% of the rosettes from the unburned control plots;  $X^2 = 7.48$ ,  $df = 1$ ,  $p = 0.007$ ).

In the two years following the burn, no significant differences were found in plant reproduction among burned and unburned plots. These results suggest that nutrients are not limiting at this site (also see Paige 1992). Burning converts plant biomass into ash, which releases nutrients, especially P, Mg, K and Ca, into plant available forms (Raison 1979; Wright and Bailey 1982). Nitrogen may also increase in the upper soil profile (Melgoza et al. 1990). Nonetheless, an influx of nutrients did not translate into an increase in plant growth and reproduction on the burn plots. Perhaps in sites that are nutrient limited one might expect such an increase (e.g., see Maschinski and Whitham 1989). There was, however, a significant effect of year on fruit production. In 1991 fruit set was significantly lower than in previous years on both burned and unburned plots for plants that were not browsed and slightly lower for plants that were browsed (Table 2, Fig. 1B). This result is likely due to the combined effects of two factors. Pollinator abundance was lower in 1991 than in either 1989 or 1990 (personal observation) and the 1991 flowering season was exceptionally dry (potentially limiting nutrient transport over all treatments).

The above findings demonstrate that at the population level, all else being equal, fire results in a 4.5-fold decrease in relative fitness. For example, by combining the most direct measures of plant fitness (i.e., the percentage of surviving plants  $\times$  the percentage of plants flowering  $\times$  the number of seeds per fruit  $\times$  the number of fruits), a cumulative estimate of plant performance of burned and unburned plant populations can be obtained. Using data from Table 1 and Fig. 1, if the burned plot started out with 80 plants, following the fire only 65% of these plants would survive and 17.3% would flower. Plants that flowered would produce an average of 62.75 fruits per plant and an average of 11.49 seeds per fruit. Therefore, at the population level 6,489 seeds would be produced. In a like fashion, if the unburned plot started out with 80 plants, all would survive and 76.3% would flower. Plants that flowered would produce an average of 61.62 fruits per plant and 7.7 seeds per fruit. Therefore, at the population level 28,962 seeds would be produced. This represents a 4.5-fold decrease in immediate plant reproductive success in response to fire at the population level. Thus, it would seem that fire would be detrimental to the population as a whole, basically delaying reproduction and resulting in higher mortality rates.

However, fire triggers the germination of seed from the seed bank, opens up space and removes potential competitors for the rapid establishment of scarlet gilia seedlings. In the year of the burn there was a 116-fold increase in the number of germinating seeds (seed banks should be comparable in terms of numbers of seed since there were comparable numbers of parental plants growing on all plots over the past ten years (personal observation)). By the second year this translated into an approximate 6-fold difference in the number of surviving rosettes (from the previous year's seedlings). Thus, fire-induced seed germination could negate the detrimental effects of

fire on the population dynamics of scarlet gilia. Nonetheless, the ultimate outcome is dependent upon the frequency and timing of fire, and a host of biotic and abiotic factors that were not measured in this study.

#### Alternative selection pressures

Two of the most likely alternative candidates involved in the removal of apical dominance in scarlet gilia are freeze damage and ungulate trampling. Both freeze damage and ungulate trampling can cause the removal of apical dominance and a response similar to that generated by ungulate and insect herbivores. However, they are probably minor factors favoring selection toward growth compensation by scarlet gilia. Experimental results, for example, demonstrate that apical dominance was removed in only 3% of plants exposed to freezing temperatures. In addition, observations revealed that ungulate trampling caused breakage and release of apical dominance in only 0.2% of plants.

Additional pressures potentially involved in the release of apical dominance might include pathogen attack or wind damage. Long term field observations, however, suggest that neither of these factors play any role in the release of apical dominance on these sites. Neither wind breakage or pathogen attack have ever been identified as agents involved in the removal of apical dominance.

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