Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest[1]

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Abstract: Although the majority of fires in the western United States historically occurred during the late summer or early fall when fuels were dry and plants were dormant or nearly so, early-season prescribed burns are often ignited when fuels are still moist and plants are actively growing. The purpose of this study was to determine if burn season influences postfire vegetation recovery. Replicated early-season burn, late-season burn, and unburned control units were established in a mixed conifer forest, and understory vegetation was evaluated before and after treatment. Vegetation generally recovered rapidly after prescribed burning. However, late-season burns resulted in a temporary but significant drop in cover and a decline in species richness at the 1 m^2 scale in the following year. For two of the several taxa that were negatively affected by burning, the reduction in frequency was greater after late-season than early-season burns. Early-season burns may have moderated the effect of fire by consuming less fuel and lessening the amount of soil heating. Our results suggest that, when burned under high fuel loading conditions, many plant species respond more strongly to differences in fire intensity and severity than to timing of the burn relative to stage of plant growth.

Résumé : Bien qu'historiquement la majorité des feux dans l'ouest des États-Unis soient survenus à la fin de l'été ou au début de l'automne alors que les combustibles sont secs et les plantes sont en dormance ou près de l'être, des brûlages dirigés sont souvent effectués en début de saison alors que les combustibles sont encore humides et les plantes sont en pleine croissance. Le but de cette étude était de déterminer si la saison durant laquelle un brûlage est effectué influence le rétablissement subséquent de la végétation. Des parcelles brûlées en début de saison, brûlées en fin de saison et non brûlées ont été établies avec plusieurs répétitions dans une forêt mixte de conifères et la végétation de sous-bois a été inventoriée avant et après le traitement. Le rétablissement de la végétation a été généralement rapide après un brûlage dirigé. Cependant, les brûlages effectués en fin de saison ont produit une baisse temporaire, mais importante, du couvert de végétation et une diminution de la richesse en espèces à l'échelle de placettes de 1 m^2 au cours de l'année qui a suivi le traitement. Pour deux des nombreux taxons qui ont été négativement affectés par le brûlage, la diminution de leur fréquence était plus forte après des brûlages effectués en fin de saison qu'après des brûlages effectués en début de saison. Les brûlages effectués en début de saison peuvent avoir atténué les effets du feu en consommant moins de combustibles et en réduisant le réchauffement du sol. Nos résultats indiquent que lorsqu'elles sont brûlées dans des conditions où les combustibles sont abondants, plusieurs espèces végétales réagissent plus fortement aux différences d'intensité et de sévérité du feu qu'au moment d'application du feu par rapport au stade de croissance des plantes.

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Introduction

Fire historically played a dominant role in shaping many forest plant communities (Agee 1993). In the mixed conifer forests of the western United States, the historical fire regime consisted of mostly low- to moderate-severity surface fires with patches of higher severity (Stephenson et al. 1991), the majority of which burned late in the growing season (Caprio and Swetnam 1995; Skinner and Chang 1996; Taylor 2000; Stephens and Collins 2004). In many areas, prescribed fire is now being used in place of wildfire to reduce hazardous fuel accumulation and to create forest structures more resilient to disturbance. That prescribed fire approximates the disturbance historically produced by wildfire is often assumed. However, because of fuel accumulation, the first prescribed burn after a period of fire exclusion

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has the potential to produce greater fire severity than was historically the norm.

Prescribed burns are also sometimes ignited outside of the main historical fire season. In the Sierra Nevada and much of the western United States, prescribed fire is generally applied in two periods: in the early season shortly after cessation of spring precipitation or in the late season prior to the onset of the rainy season. Because of poor smoke dispersal and a short burning window in the late season of many years, an increasing amount of prescribed burning is being done in the early season. Because early-season burns are conducted prior to the onset of the summer dry period, when fuels are still relatively moist, they generally result in less fuel consumption (Kauffman and Martin 1989; Knapp et al. 2005), which may reduce fire severity. However, early-season burns occur during the peak period of plant growth for many species, and concerns have been raised that fires at this time of year may inhibit vegetation recovery.

Plants can withstand fire through structures such as thick insulating bark that prevents heat from reaching the growing tissue, or by resprouting from underground parts located deep enough in the soil that they are able to survive fire. Some species possess traits allowing populations to persist even when adults are killed by fire, such as serotinous cones or seeds that are stimulated to germinate by fire. Other species avoid fire by growing in less fire-prone microhabitats. These fire survival mechanisms may interact with burning season in several ways. Less heat is necessary to kill plant tissue when the moisture content of that tissue is greater (Wright 1970), as is often the case early in the growing season. In addition, many plant species are thought to be most susceptible to fire when carbohydrate reserves are at their lowest levels (Hough 1968; Garrison 1972; Volland and Dell 1981), which has been shown to occur shortly before to shortly after initiation of seasonal growth (de Groot and Wein 2004). Killing the aboveground portion of perennial plants prior to assimilation of carbohydrates from growing season photosynthesis may reduce resprouting (Jones and Laude 1960; Garrison 1972). Harrington (1985) reported that repeated midsummer burns led to fewer *Quercus gambelii* Nutt. (Gambel oak) resprouts, whereas repeated spring and fall burns did not. These summer burns coincided with the period of lowest total nonstructural carbohydrates in the roots (Harrington 1989). In some cases, growing-season prescribed burns have resulted in greater *Pinus ponderosa* Dougl. ex P. & C. Laws. (ponderosa pine) mortality than dormant-season burns (Swezy and Agee 1991; Harrington 1993). Swezy and Agee (1991) postulated that damage to fine roots that are abundant in the litter and duff layers, particularly during the early-season period of tree growth, may have led to the greater mortality. Growing-season burns have also been shown to cause higher mortality and result in less postfire biomass of grasses and forbs, relative to dormant-season burns (Wright and Klemmedson 1965; Brockway et al. 2002).

The seedbank can be differentially affected by season of fire as well. Seeds of some species may tolerate higher temperatures if the soil is dry (Parker 1987). However, wet heat (hot water), which perhaps simulated heating under moist soil conditions found in the early season, was found to be more effective for scarifying dormant *Ceanothus integerrimus* Hook. & Arn. (deerbrush) seeds than dry heat (hot air) (Kauffman and Martin 1991).

Early-season prescribed burns are often conducted under higher fuel moisture conditions than late-season burns, leading to reduced fuel consumption and fire severity (Kauffman and Martin 1989; Knapp et al. 2005). Reports of less plant mortality from early-season than late-season prescribed burns has been attributed to differences in fuel consumption with burning season (Kauffman and Martin 1990; Thies et al. 2005). Higher fuel moisture conditions typical of early season can also result in more unburned patches (Knapp et al. 2005; Knapp and Keeley 2006) where fire-sensitive species are more likely to persist. The size and abundance of these unburned refugia relative to propagule dispersal distances may play in important role in postfire plant recolonization (Eberhart and Woodard 1987; Lee 2004).

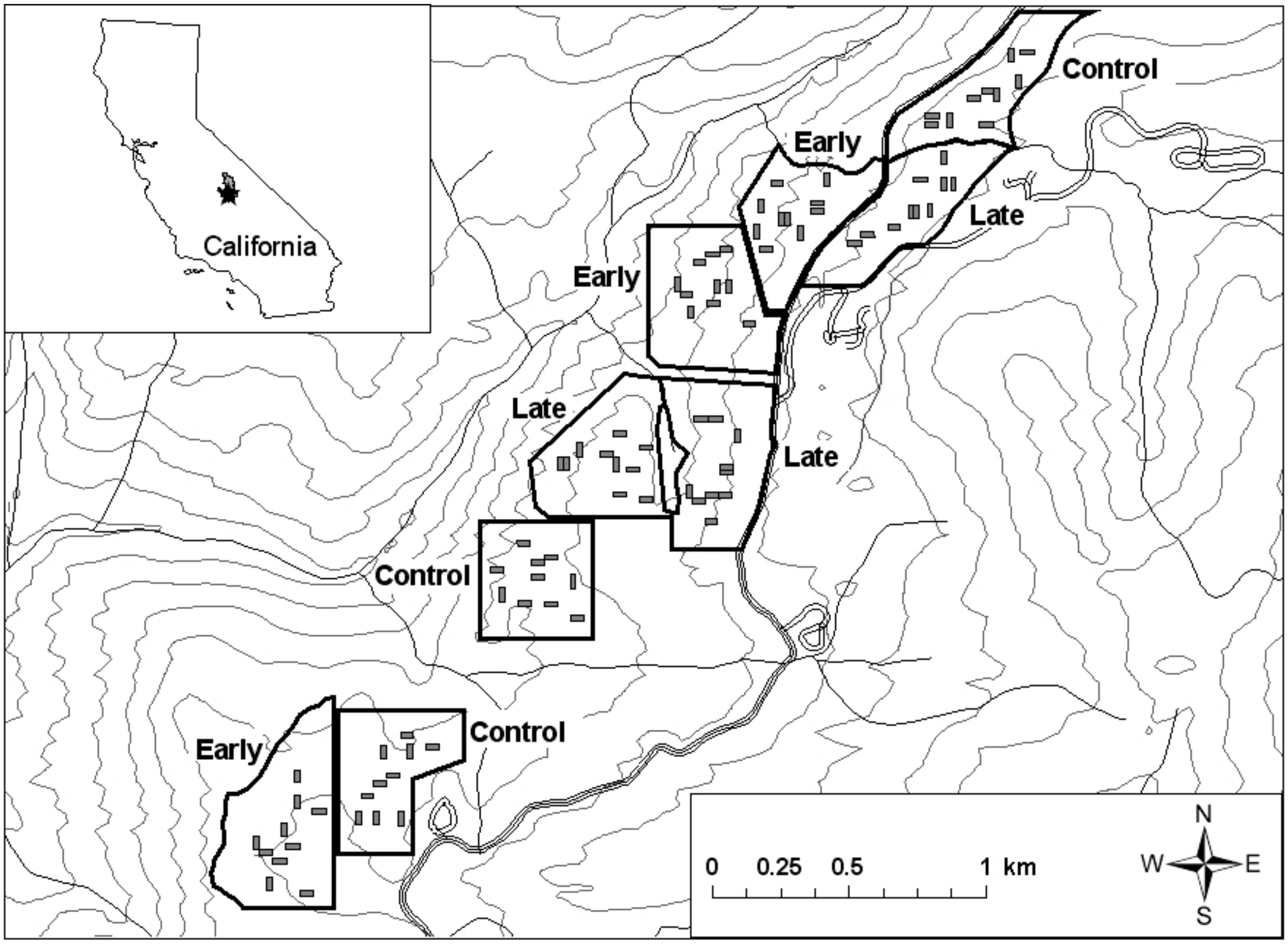
The response of understory vegetation to burning season is complex. Variation in fire-survival strategies among plant species, the season of the burn in relation to the historical fire season, and the amount of fuel consumed all have the potential to influence fire effects (Kauffman and Martin 1990; Sparks et al. 1998; Hiers et al. 2000; Main and Barry 2002). To date, few large-scale replicated studies of the ecological effects of prescribed fire season have been conducted in the western United States, and in some cases, lack of information has hindered the reintroduction of prescribed fire.

The objective of this study was to evaluate the short-term response of nontree understory vegetation associated with mixed-conifer forests of the western United States to early- and late-season prescribed burns. Species were grouped into different growth-form and life-history categories with varying expected responses to fire. Vegetation change from pretreatment levels for plots in early-season burn, late-season burn, and unburned control treatments was determined the season immediately following the burns and several years later to test both the effect of burning and whether response to early-season burns differed significantly from the response to late-season burns. Because alien species invasions are often associated with soil disturbance and the two burning season treatments differed in amount of mineral soil exposed, the effect on presence of alien species was also tested. Lastly, response of many species is related to fire intensity and severity, which varied both between burning season treatments and among plots within burning season treatment; association of measures of fire intensity and severity with vegetation change were tested to shed light on potential mechanisms. It was predicted that fire-sensitive species would be negatively associated with fire intensity or severity measures, whereas fire-promoted species would be positively associated with fire intensity or severity measures.

Materials and methods

Nine experimental units, each 15–20 ha in size, were established in old-growth mixed-conifer forest adjacent to the Giant Forest sequoia grove in Sequoia National Park (36°34′–36°36′N, 118°45′–118°47′W) (Fig. 1). Three replicates each of early-season prescribed burn, late-season prescribed burn, and untreated control were assigned to the units in a completely randomized design. Elevation of the study area ranged from 1900 to 2150 m above sea level, and

Fig. 1. Location of early-season burn, late-season burn, and unburned control units in Sequoia National Park. Vegetation was monitored within ten 20 m × 50 m plots within each unit. The contour interval is 60 m.



tree species, in order of abundance, were *Abies concolor* (Gord. & Glend.) Lindl. (white fir), *Pinus lambertiana* Dougl. (sugar pine), *Calocedrus decurrens* (Torr.) Florin (incense cedar), *Abies magnifica* var. *shastensis* Lemm. (red fir), *Pinus jeffreyi* Grev. & Balf. (Jeffrey pine), *P. ponderosa*, *Cornus nuttallii* Audub. (Pacific dogwood), and *Quercus kelloggii* Newberry (California black oak). Nomenclature for all taxa in this study followed Hickman (1993).

Forests in this area are influenced by a Mediterranean climate, with wet winters (most precipitation falling as snow) and warm dry summers. The presettlement fire return interval in the study area, determined by cross-dating wood sections containing fire scars collected from snags, averaged 27 years, but the last major fire occurred in 1879 (Schwilk et al. 2006). Most fire scars in this area occur within the latewood or at the annual ring boundary, indicating the historical prevalence of late- or dormant-season fire (Caprio and Swetnam 1995; Schwilk et al. 2006). When early-season fires did occur, they were usually associated with dry years (A. Caprio, National Park Service, Sequoia National Park, personal communication, 2004).

Vegetation data collection

Vegetation data were collected within 20 m × 50 m (0.1 ha) modified Whittaker plots (Fig. 1), 10 of which were established per unit. Plots were randomly located in reference to a network of 36 permanent points on a 50 m grid at the center of each unit. The grid point formed one corner of the plot, and placement in one of the four cardinal directions was also random. A list was made of all understory plant species growing in the plot and diameter at breast height (DBH) of all trees with a DBH ≥ 10 cm was measured and species noted. Cover category of understory plant species was visually estimated within twenty 1 m × 1 m subplots systematically located within each plot. Cover categories were based on the following scale: (1) <1%, (2) 1%–10%, (3) 11%–25%, (4) 26%–50%, (5) 51%–75%, and (6) 76%–100%. Units were sampled prior to treatment (2001, all units), 1 year post-treatment (2002, late-season burn units and controls; 2003, early-season burn units and controls), and in the final year of the current phase of the study (2004, all units).

Prescribed burns

Early-season burns were conducted 20 June and 27 June 2002, and late-season burns were conducted 28 September, 17 October, and 28 October 2001. Early-season burns generally occurred close to or during the period of active growth for most understory plant species, whereas late-season burns occurred after most understory plants had ceased seasonal growth and were dormant or nearly so. Ignition was accomplished with drip torches using a strip head fire pattern, with strips approximately 10–15 m apart. The resulting burns were predominantly low- to moderate-intensity surface fires with occasional torching of single small trees. Weather conditions were very similar for burns within the same burning-season treatment. The main difference affecting the way fire burned was that moisture of all woody and forest floor (litter and duff) fuel categories was significantly greater in the early season than in the late season. (Fuel moisture values are given in Table 1 of Knapp et al. (2005).)

Fire intensity and severity measures

Scorch height, an index of fire intensity, was measured on all trees within plots using a laser rangefinder and was calculated as the mean of two measurements: the maximum scorch height and scorch height on the side of the tree opposite to where maximum scorch height occurred. Percentage of ground surface burned, a measure of fire severity, was calculated for each plot by averaging visual estimates of the percentage of each 1 m^2 subplot (to the nearest 10%) that burned.

Statistical analyses

Species cover categories were converted back to percentages (the percentage used was the midpoint of each cover category) for analyses. Cover of broad growth-form (forb, graminoid, and shrub) and life-history (annual or biennial and perennial) groupings were summarized at the plot level (mean of twenty 1 m^2 subplots). Frequency (presence or absence) of the most commonly encountered taxa within subplots was also summarized at the plot level. *Ribes* species (*Ribes roezlii* Regel. (Sierra gooseberry), *Ribes nevadense* Kellogg (Sierra currant), *Ribes viscosissimum* Pursh (sticky currant)) were lumped, as were *Ceanothus* species (*Ceanothus cordulatus* Kellogg (mountain whitethorn), *C. integerrimus*, and *Ceanothus parvifolius* (S. Wats.) Trel. (littleleaf ceanothus)) because of difficulty with identification at the seedling stage. Two *Bromus* species (*Bromus laevipes* Shear (woodland bromegrass) and *Bromus orcuttianus* (Shear) A. Hitchc. (Orcutt's bromegrass)) were lumped because of uncertainty with field identification and growth in similar environments. In addition, more than one *Cryptantha* species may have occurred in the plots, but the seed characteristics necessary for identification were not possible to distinguish in the field.

Measures of diversity are highly dependent on scale, and change over time may be a function of the scale of the disturbance patchiness in relation to the survey area. Therefore, species richness was summarized at both the subplot (1 m^2) and plot (1000 m^2) scales. Change in cover, frequency, and richness in 2002, 2003, and 2004 was calculated as the difference between post-treatment and pre-treatment numbers. Although change in frequency was calculated for the 21 most abundant and widespread taxa (present in at least 5% of subplots in at least one treatment before the burns (2001) and (or) at the end of the experiment (2004); Appendix A), statistical significance of this change was evaluated for only those occurring in greater than 10% of subplots in at least one treatment before the burns (2001) and (or) at the end of the experiment (2004). Limiting statistical analyses to the most abundant species was done to avoid problems of excessive variation associated with low sample size and to reduce the number of individual tests. Significance of treatment on change in cover, frequency, and richness was evaluated with a mixed-model ANOVA, with unit nested within treatment as a random effect and treatment as a fixed effect. Associations between changes in frequency of the most common individual taxa and measures of fire intensity and severity were explored using the same nested mixed-model ANOVA but including scorch height and percentage of area burned as covariates. Cover and frequency data were arcsine square root transformed prior to subtracting post-treatment values from pre-treatment values to improve distributional qualities. Richness data were not transformed. Linear contrasts, set a priori, were used to estimate the effect of burning (burns vs. unburned control), and the effect of season of burning (early vs. late) for the 2004 data.

Results

Prior to the burns, nontree understory cover averaged 16.3% (early-season burn units, 9.6%; late-season burn units, 20.8%; unburned control units, 18.5%). The majority of the understory cover was composed of forbs, including ferns (12.7%), with lesser abundance of graminoids (0.9%) and shrubs (2.7%). Most of the cover was composed of perennials that emerge yearly from underground structures such as rhizomes (96.5%) rather than annuals and biennials (3.5%).

Change in cover with burning treatments

Overall, nontree cover was significantly reduced relative to the unburned control (62%) 1 year after the late-season burns (Table 1). When broken down into growth-form and life-history categories, this initial reduction in cover was evident for both forbs and perennials. Reduction in the cover of graminoids and shrubs approached significance, whereas cover of annuals or biennials did not change. Early-season burns had a much less dramatic effect on understory vegetation, with no change in overall species cover the following growing season (Table 1). Of the major growth-form and life-history categories, only the reduction in graminoids approached significance. By 2004, three growing seasons after the late-season burns and two growing seasons after the early-season burns, all of the herbaceous growth-form categories that were initially reduced in cover by burning had recovered and no longer differed from the unburned control (Table 1). Only shrub cover remained below levels found in the unburned control (Table 1). Cover of annual or biennial species increased over time in the burned plots and in 2004 was significantly greater than in the control. However, no significant differences in cover change were found between early-season and late-season burning treatments for any of the growth-form and life-history categories (Table 1).

Change in richness with burning treatments

At the 1 m^2 scale, overall species richness decreased the first year after late-season burns, largely the result of declines in richness of forbs and graminoids (Table 2). Early-season burns, on the other hand, did not significantly affect richness. This decline in richness with late-season burns was transient, and no change as a result of burning or burning season could be detected at the final field evaluation. Rich-

Table 1. Change in percent cover from pre-treatment levels of all understory species and understory species by growth-form and life-history category.

	2002			2003			2004				
	Unburned	Late	*P*	Unburned	Early	*P*	Unburned	Early	Late	Unburned vs. burned *P*	Early vs. late *P*
All species	0.54 (1.43)	–12.79 (2.66)	0.007	–1.93 (0.91)	–2.61 (0.99)	0.516	0.62 (1.07)	0.78 (1.66)	2.01 (1.86)	0.984	0.377
Forbs	0.70 (1.34)	–9.67 (2.58)	0.014	–1.77 (0.76)	–1.01 (0.94)	0.995	–0.64 (0.99)	1.89 (1.60)	3.73 (1.75)	0.374	0.426
Graminoids	–0.11 (0.08)	–0.60 (0.17)	0.059	0.19 (0.15)	–0.41 (0.11)	0.064	0.35 (0.19)	–0.23 (0.11)	0.32 (0.23)	0.245	0.179
Shrubs	–0.04 (0.28)	–2.52 (0.76)	0.073	–0.35 (0.48)	–1.19 (0.42)	0.340	0.92 (0.32)	–0.88 (0.36)	–2.04 (0.71)	0.018	0.269
Annuals and biennials	1.16 (0.63)	1.67 (0.62)	0.454	0.22 (0.10)	0.95 (0.39)	0.224	0.44 (0.18)	1.65 (0.49)	3.78 (0.88)	0.033	0.153
Perennials	–0.62 (1.20)	–14.46 (2.33)	0.003	–2.15 (0.89)	–3.57 (0.85)	0.357	0.17 (1.07)	–0.88 (1.39)	–1.82 (1.61)	0.263	0.747

Note: Values are means with SEs given in parentheses. Data were arcsine square root transformed prior to statistical analysis. Data collected in 2002 were 1 year after late-season burns, data collected in 2003 were 1 year after early-season burns, and data collected in 2004 were 3 years after late-season burns and 2 years after early-season burns.

ness of annual or biennial species appeared to increase over time with burning. While not initially affected by either burning-season treatment, the increase in numbers of annual or biennial species, relative to the unburned control, approached statistical significance in the final year (Table 2). Perennial species was the only understory plant category differentially affected by burning season, with a greater reduction in richness after late-season than after early-season burns.

At the 1000 m^2 scale, changes in species richness with burning were generally in the positive direction. Overall, species richness was not significantly altered the first year following late-season burns, but increased the first year after early-season burns (Table 2). By the final year of the study, burned plots contained nearly seven more species than unburned plots, a difference that approached statistical significance. However, no difference between early-season and late-season burns could be detected. Many of the growth-form and life-history categories exhibited similar trends. The only exceptions were graminoid species, where numbers did not change with burning in any of the measurement years, and shrub species, which were significantly more numerous after burns in all years. At the end of the experiment, changes in richness at the 1000 m^2 scale did not differ between burning-season treatments for any of the growth-form and life-history categories.

Prior to the burning treatments, no alien species were found within the plots. In 2004, a mean of 0.17 alien species per plot were found within the late-season burn treatment, and a mean of 0.03 alien species per plot were found within the early-season burn treatment. Unburned control plots remained free of alien species. Possibly because of the low numbers of plants found, neither the difference in alien species richness between burning treatments and control nor the difference in alien species richness between early-season and late-season burning treatments was statistically significant (P = 0.184 and P = 0.134, respectively).

Change in frequency of individual taxa with burning treatments

Six of the 12 most common understory taxa were perennial forbs and only one (*Pyrola picta* Smith (white-leaved wintergreen)) showed a significant effect of burning, with a reduced frequency at the end of the experiment (Table 3). The most common perennial graminoid taxa (*Bromus* sp.) also decreased with burning. Conversely, both of the most common annual forb taxa increased with burning (the increase in *Cyptantha* sp. was statistically significant, whereas the increase in *Gayophytum eriospermum* Coville (Coville's groundsmoke) approached significance. Of the three most common shrub species, two (*Galium sparsiflorum* Wight subsp. *sparsiflorum* (Sequoia bedstraw), and *Symphoricarpos mollis* Nutt. (creeping snowberry)) were reduced in frequency by burning (Table 3), and one (*Ceanothus* sp.), which produces seeds that are stimulated to germinate by fire, strongly increased. None of the taxa reduced in frequency by burning was reduced more by the early-season burning treatment than by the late-season burning treatment. In fact, two were significantly more strongly reduced by the late-season burning treatment (Table 3). None of the two common taxa that increased with fire

Table 2. Change in understory species richness from pre-treatment levels.

	2002			2003			2004				
	Unburned	Late	*P*	Unburned	Early	*P*	Unburned	Early	Late	Unburned vs. burned *P*	Early vs. late *P*
1 m^2 scale											
All species	0.20 (0.06)	–0.96 (0.23)	0.008	–0.09 (0.06)	0.19 (0.19)	0.490	0.12 (0.07)	0.34 (0.18)	–0.03 (0.19)	0.887	0.263
Forbs	0.18 (0.06)	–0.95 (0.20)	0.006	–0.13 (0.06)	0.00 (0.14)	0.686	0.05 (0.07)	0.19 (0.14)	–0.08 (0.16)	0.996	0.297
Graminoids	0.01 (0.02)	–0.12 (0.03)	0.063	0.00 (0.02)	–0.06 (0.02)	0.102	0.04 (0.02)	–0.02 (0.02)	0.00 (0.03)	0.184	0.585
Shrubs	0.02 (0.01)	0.10 (0.04)	0.119	0.03 (0.01)	0.25 (0.06)	0.126	0.03 (0.01)	0.17 (0.05)	–0.05 (0.04)	0.248	0.137
Annuals and biennials	0.14 (0.04)	0.18 (0.06)	0.691	0.05 (0.03)	0.26 (0.06)	0.169	0.10 (0.04)	0.35 (0.08)	0.55 (0.09)	0.053	0.275
Perennials	0.06 (0.05)	–1.15 (0.19)	0.003	–0.14 (0.06)	–0.07 (0.16)	0.815	0.01 (0.07)	–0.01 (0.13)	–0.59 (0.14)	0.120	0.026
1000 m^2 scale											
All species	0.4 (0.7)	0.4 (0.9)	0.590	–1.4 (0.7)	4.4 (1.3)	0.016	–0.7 (0.5)	6.0 (1.4)	6.6 (1.4)	0.052	0.855
Forbs	0.3 (0.6)	–0.9 (0.7)	0.369	–1.4 (0.5)	1.9 (0.9)	0.045	–0.9 (0.5)	2.4 (0.9)	2.4 (1.0)	0.172	0.990
Graminoids	0.2 (0.3)	–0.5 (0.2)	0.113	0.1 (0.2)	–0.3 (0.3)	0.284	0.3 (0.1)	0.6 (0.3)	0.5 (0.3)	0.567	0.738
Shrubs	–0.1 (0.2)	1.0 (0.3)	0.035	–0.2 (0.2)	2.8 (0.4)	0.002	–0.1 (0.1)	3.0 (0.4)	3.7 (0.3)	0.002	0.365
Annuals and biennials	0.6 (0.3)	1.5 (0.5)	0.218	0.1 (0.3)	2.9 (0.5)	0.062	1.0 (0.3)	2.9 (0.5)	3.0 (0.4)	0.101	0.933
Perennials	–0.2 (0.5)	–2.0 (0.7)	0.180	–1.6 (0.6)	1.7 (1.0)	0.051	–1.7 (0.4)	3.0 (1.0)	3.1 (0.9)	0.040	0.976

Note: Values are means with SEs given in parentheses. Richness was summarized at both the 1 m^2 and 1000 m^2 scales. Data collected in 2002 were 1 year after late-season burns, data collected in 2003 were 1 year after early-season burns, and data collected in 2004 were 3 years after late-season burns and 2 years after early-season burns.

showed a significant difference between burning season treatments. However, the increase in one (*Cryptantha* sp.) trended towards being greater in the late-season burning treatment (Table 3).

Vegetation change and fire intensity or severity

Changes in frequency of several of the common herbaceous perennial species (*Galium triflorum* Michx., *Hieracium albiflorum* Hook., and *Pyrola picta*) and one of the common woody shrubs that lacked fire-stimulated seed (*Symorphoricarpos mollis*) were significantly negatively associated with scorch height and (or) percentage of area burned (Table 4), indicating that loss of some species from the plots may have been the result of higher fire intensity or fire severity. *Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underwood was the only common herbaceous perennial species where change in frequency was positively associated with a measure of fire intensity or fire severity (Table 4). Change in frequency of the shrub *Ceanothus* sp. was strongly positively associated with increasing scorch height and percentage of area burned (Table 4). For the former variable, a quadratic model was a better fit to the data than the linear model, with the greatest abundance of newly germinated seedlings occurring in areas with intermediate scorch height (Fig. 2).

Discussion

Vegetation change with early- and late-season burns

The mixed-conifer forest understory is generally considered to be very resilient to fire-caused disturbance. This study and others (Harvey et al. 1980; Metlen et al. 2004) demonstrate that most species recover quickly after low- to moderate-intensity prescribed burns. By the time of our final survey of the burned plots, cover of all growth-form and life-history categories except shrubs had returned to or exceeded pre-treatment levels. In addition, no effect of burning season on cover of these categories could be detected. The main difference between burning seasons was the time necessary for recovery. Late-season burns significantly reduced the cover of most life-history categories the first growing season after the fire, while little or no recovery time was necessary after early-season burns.

The overall trend of increasing species richness with prescribed fire (at the 1000 m^2 scale) in this study is similar to findings reported by others (Brockway and Lewis 1997; Sparks et al. 1998; Busse et al. 2000). Early-season burns appeared to initially have a less negative affect on species richness at the 1 m^2 scale, and a more positive affect on species richness at the 1000 m^2 scale. However, for most understory categories, a difference between burning seasons did not persist through the final survey. The greater decline in richness of perennial species (at the 1 m^2 scale) with late-season burns at the end of the study may be due, in part, to differences in the scale of disturbance between seasons. Because some perennial species are favored by the prefire environment and others by the postfire environment, a patchy burn would be expected to result in greater species richness at a scale greater than the patchiness. Unburned patches were found in all 1000 m^2 vegetation plots regardless of season in which they were burned, but small unburned patches

Table 3. Change in percent frequency from pre-treatment levels (2001–2004) of the most common understory taxa (occurring in more than 10% of 1 m^2 subplots in at least one treatment in either of the 2 years), listed from most abundant to least abundant.

Species	Growth form	Life history	Unburned	Early	Late	Unburned vs. burned (*P*)	Early vs. late (*P*)
Hieracium albiflorum	Forb	Perennial	–2.8 (1.3)	–7.8 (2.2)	–17.5 (3.6)	0.102	0.153
Galium sparsiflorum subsp. *sparsiflorum*	(Sub) shrub*	Perennial	0.8 (1.5)	–7.8 (2.7)	–24.5 (4.5)	0.046	0.105
Pteridium aquilinum var. *pubescens*	Forb	Perennial	3.5 (1.6)	1.7 (0.9)	2.3 (1.7)	0.933	0.522
Cryptantha spp.	Forb	Annual	2.8 (1.2)	11.0 (2.5)	25.0 (3.9)	0.006	0.057
Ceanothus spp.	Forb	Perennial	0 (0)	11.8 (3.0)	14.5 (2.8)	0.039	0.696
Draperia systyla	Forb	Perennial	1.2 (0.6)	3.3 (1.8)	4.2 (2.3)	0.314	0.788
Symphoricarpos mollis	(Sub) shrub	Perennial	2.2 (1.0)	–4.8 (1.9)	–13.7 (2.4)	0.010	0.050
Gayophytum eriospermum	Forb	Annual	1.2 (0.8)	7.7 (2.2)	16.2 (3.6)	0.064	0.269
Pyrola picta	Forb	Perennial	–0.8 (1.4)	–1.8 (1.1)	–10.7 (2.1)	0.049	0.008
Galium triflorum	Forb	Perennial	–0.5 (1.0)	–4.5 (2.5)	–3.7 (1.3)	0.473	0.951
Viola purpurea subsp. *purpurea*	Forb	Perennial	–2.8 (1.8)	–1.5 (1.1)	–3.0 (1.1)	0.913	0.335
Bromus spp. (*laevipes* or *orcuttianus*)	Graminoid	Perennial	1.3 (0.8)	–5.8 (1.3)	–2.0 (1.5)	0.020	0.120

Note: Values are means with SEs given in parentheses. Data were arcsine square root transformed prior to statistical analysis.
*(Sub) shrub, small shrub with only the lowest stems woody.

Table 4. Slope coefficients for an index of fire intensity (scorch height) and a measure of fire severity (percentage of ground surface area burned) as covariates in mixed-model analyses of variance on change in arcsine square root transformed frequency (2001–2004) for the 12 most commonly encountered plant taxa.

	Scorch height				Area burned			
Species	ddf	Slope (SE)	*F*	*P*	ddf	Slope (SE)	*F*	*P*
Hieracium albiflorum	45	–0.81 (0.37)	4.63	0.037	45	–0.46 (0.21)	4.81	0.034
Galium sparsiflorum subsp. *sparsiflorum*	43.2	–0.80 (0.50)	2.58	0.116	44.2	–0.30 (0.27)	1.24	0.272
Pteridium aquilinum var. *pubescens*	20.8	0.82 (0.28)	8.63	0.008	25.3	–0.01 (0.20)	0.00	0.946
Cryptantha spp.	47.5	0.09 (0.40)	0.05	0.816	47.7	–0.27 (0.17)	2.44	0.125
Ceanothus spp.	45.1	1.26 (0.39)	10.27	0.002	46.9	0.83 (0.20)	17.36	<0.001
Draperia systyla	37	–0.52 (0.36)	2.08	0.157	37	0.03 (0.28)	0.01	0.904
Symphoricarpos mollis	36	–0.38 (0.47)	0.65	0.425	35.9	–0.71 (0.23)	9.42	0.004
Gayophytum eriospermum	39.8	0.31 (0.53)	0.34	0.564	39.9	–0.17 (0.25)	0.46	0.504
Pyrola picta	35	–0.48 (0.28)	2.90	0.098	35	–0.44 (0.18)	5.57	0.024
Galium triflorum	31.7	–0.88 (0.58)	2.30	0.139	31.9	–0.74 (0.21)	12.10	0.002
Viola purpurea subsp. *purpurea*	14.5	0.51 (1.06)	0.23	0.636	14.6	–0.10 (0.47)	0.05	0.833
Bromus spp. (*laevipes* or *orcuttianus*)	38.6	0.03 (0.43)	0.01	0.935	36.7	0.16 (0.23)	0.49	0.488

Note: Only plots containing the taxa before treatment, after treatment, or both were included in the analyses. Denominator degrees of freedom (ddf) were based on Satterthwaite's approximation.

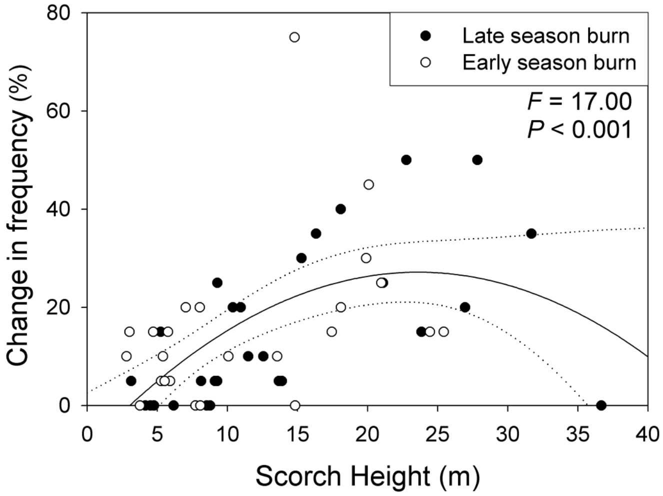
were more numerous after early-season burns than late-season burns (Rocca 2004; Knapp et al. 2005). With late-season burns, most 1 m^2 subplots within 1000 m^2 plots were either completely burned over or not at all (only 4% of 1 m^2 subplots contained both burned and unburned patches), whereas with early-season burns, 37% of 1 m^2 subplots contained both burned and unburned patches (E.E. Knapp, D.W. Schwilk, J.M. Kane, and J.E. Keeley, unpublished data). Thus, fire-sensitive perennial species were more likely to have persisted at the 1 m^2 scale following early-season rather than late-season fire. However, any reduction in richness at the 1 m^2 scale may be of little consequence in the long term, because propagules from unburned islands at the 1000 m^2 scale should readily disperse over these distances.

Change in richness with burning was almost completely the result of increases in native species. Although increases in numbers of alien species were not statistically significant in this study, alien species capitalizing on burn-caused disturbance is a concern (D'Antonio 2000; Keeley et al. 2003), even in this relatively pristine National Park environment. Keeley et al. (2003) found that the abundance of alien species in similar coniferous forests increased with time since fire, and our surveys were possibly not conducted long enough after the burns to detect significant trends.

Response to burning season: the role of microenvironment and plant strategy

Variation in the response of vegetation categories or individual taxa within categories may be attributed, in part, to differences in the growth environment that influence fire severity. In mixed-conifer forests similar to these, North et al. (2005) noted strong associations of understory species with light environment and litter depth. For example, in this study, the most common annual or biennial species (*Cryptantha* spp. and *Gayophytum eriospermum*), which tended to increase with burning, were typically found in open areas with lower tree densities. Patches of bare ground and rock are barriers to fire spread and presence of fewer

Fig. 2. Change in frequency of *Ceanothus* species in prescribed early- and late-season burn plots that experienced variable aboveground fire intensity (as measured by scorch height). The quadratic model was a better fit to the data than the linear model, as determined byAkaike's information criterion. The 95% confidence interval is also shown.



trees suggests that these areas also contained lighter fuel loads. Therefore, the annual or biennial species may have been less likely to experience fire directly. Even when areas containing annual or biennial species burned, fire severity may have been lower on average. Because the frequency of the annual or biennial species group increased over time, it appeared that these species may have benefited as a result of additional favorable bare ground habitat created by fire, more so than the direct impact of fire on seed germination. Late-season burns consumed fuels over a larger percentage of the forest floor than early-season burns (88% vs. 73%) (Knapp et al. 2005) exposing more mineral soil, which would favor annual or biennial species that exploit this habitat. Although the frequency of *Cryptantha* did tend to be higher in the late-season units, such a difference might also be explained by the longer time since fire. Because the final survey in 2004 was completed three growing seasons after the late-season burns and two growing seasons after the early-season burns, all species in the former treatment had an additional year for population expansion.

In contrast to the response of the annual or biennial species of more open habitats, many of the species typically found in shaded areas under the forest canopy (i.e., *Pyrola picta*, *Galium sparsiflorum* subsp. *sparsiflorum*, *Symphoricarpos mollis*, *Hieraceum albiflorum*, and *Chimaphila menziesii* (D. Don) Spreng.; Table 3, Appendix A), where fuel loading, fuel continuity, and therefore, fire severity were likely to be higher, showed the greatest decline with burning. The reduction in all of these species was either significantly greater, or trended towards being greater, with late-season than early-season burns, which is consistent with fuel consumption differences. Late-season burns consumed 88% (158.9 Mg/ha) of the fuels on the forest floor, whereas early-season burns consumed only 67% (121.6 Mg/ha) (Knapp et al. 2005). Therefore, late-season burns may have subjected plants growing in these areas to higher fire intensity. Dry soil at the time of the late-season burns may also have allowed heat to penetrate deeper into the soil, potentially impacting buried buds and rhizomes, from which many perennial species annually emerge. Because water can absorb a considerable amount of heat energy, moisture may buffer against thermal heating of the soil as the fuels at the surface are consumed. Several studies have shown that soil heating below burning fuels is reduced when soils are moist (Frandsen and Ryan 1986; Hartford and Frandsen 1992; Preisler et al. 2000; Busse et al. 2005). Smith et al. (2004) found a greater reduction of fine-root biomass and ectomycorrhizal species richness in the top 10 cm of soil with fall burns conducted under dry conditions than spring burns conducted when fuel and soil moisture levels were higher. It is worth noting that the greater reduction in frequency of some species with late-season burns in this study despite one additional year of recovery time suggests that the difference between burning-season treatments might actually have been underestimated in the results presented here.

Not all species growing in shaded understory environments where high fuel loads are common were negatively affected by burning. Variability in response may be due to differences in the depth of belowground growing buds (Flinn and Wein 1977; Ingersoll and Wilson 1990). For example, frequency of *Pteridium aquilinum* var. *pubescens*, which was not altered by burns in either season, emerges from rhizomes that are more deeply buried than those of many other common understory species (Flinn and Wein 1977) and, thus, less likely to be damaged by a heat pulse from a surface fire.

Seeds of shrub taxa, including *Arctostaphylos*, *Ceanothus*, *Prunus*, and *Ribes*, are often present in large numbers in the duff and soil of mixed-conifer forests (Quick 1956) and readily germinate after fire. Both *Ceanothus*, and *Arctostaphylos* have been reported to germinate after being exposed to heat and (or) chemicals in charred wood (Quick and Quick 1961; Keeley 1987; Kauffman and Martin 1991). Seedlings of *Ceanothus* were particularly numerous in this study and found within both shaded and open microhabitats, suggesting widespread seed dispersal prior to the burns. As expected, seedling abundance was strongly associated with percentage of ground surface burned (Table 4). However, despite a greater proportion of the area within the fire perimeter burned in the late season, no difference in *Ceanothus* species frequency was detected between seasons. As a result of higher severity, the late-season burns could possibly have killed more of the seedbank, canceling out expected gains due to more extensive fire coverage. Given the abundance of shrub seedlings in both early-season and late-season burn units, the decline in shrub cover found with burning in this study is likely transient.

Vegetation change and fire intensity or severity

The response of many species, especially those most strongly affected by the prescribed fire treatments, was associated with fire intensity (scorch height on surrounding trees) and fire severity (percentage of the ground area burned). For most perennial herbaceous species that emerge from underground vegetative structures such as rhizomes, the response appeared to be linear, as predicted in a hypothetical model by Schimmel and Granstrom (1996) — the higher the scorch or percentage of ground area burned, the greater the change in frequency. *Ceanothus* seemingly exhibited a more complex response, with the greatest increase at intermediate fire intensity and lesser increases at low or high fire intensity. The germination response of fire-stimulated seeds depends on the aspect of fire that starts the germination process, whether heat or chemicals in the ash (Kauffman and Martin 1991), but not so much heat that the seeds are killed (Moore and Wein 1977; Harvey et al. 1980; Schimmel and Granstrom 1996; Odion and Davis 2000). Our findings are consistent with Weatherspoon (1988), who noted in forests like those in this study, that high-consumption fires destroyed more of the shrub seedbank than low-consumption fires. Huffman and Moore (2004) reported a similar curvilinear germination response of *C. fendleri* seeds in Arizona, with the maximum germination at intermediate levels of litter and duff consumption. However, greater stimulation of the shrub seed bank with higher fire severity has also been reported (Morgan and Neuenschwander 1988). Comparability of results is difficult, because the response of shrub seeds to fire depends on relative severity of the fires, fuel moisture conditions during the burns, and many other factors that can alter the amount of heat penetration into the soil. It is important to note that scorch height is a measure of aboveground intensity and may not be a good assessment of potential heat transfer into the soil (Alexander 1982). However, because heat transferred upward by flaming combustion (measured as scorch height) and heat transferred downward into the soil by smoldering combustion are generally expected to be greatest in areas with heavy fuel loading, we assumed that they would roughly covary. Although the percentage of ground surface burned may more closely approximate fire severity experienced by underground reproductive structures, fire passing over the surface does not indicate how much duff was removed, which has been shown to be strongly associated with soil heating and plant response (Armour et al. 1984; Schimmel and Granstrom 1996). Therefore, these tests of association with fire-intensity and fire-severity measures should be considered preliminary.

Management implications

Overall, most understory species were not significantly affected by burn season, a finding shared with studies in other forest systems (Sparks et al. 1998). For the few fire-sensitive taxa differentially affected by burning season, the results were counter to our expectations, with a greater reduction in frequency following late-season burns. Despite the lack of evidence for deleterious impacts of early-season burns, we cannot conclude that plant phenology at the time of the burn does not matter. In this experiment, burning season and amount of fuel consumption were confounded. Early-season burns occurred during active plant growth but consumed less fuel, and late-season burns occurred after plant dormancy but consumed more fuel, as is typical for prescribed burns at these times of the year. We can conclude that, for the first prescribed burn following fire suppression, fire's effects on understory vegetation appear to depend more on the amount of fuel consumed and the resulting fire intensity than the plant phenological stage. A negative relationship between fuel consumption and shrub resprouting has previously been reported (Rundel et al. 1981; Kauffman and Martin 1990; de Groot and Wein 2004). However, Kauffman and Martin (1990) noted significantly higher survival of *Q. kelloggii* after early spring burns (before dormancy was broken) than after late-spring burns (during early growth) with similar fuel consumption, suggesting that both fire severity differences and plant phenology may play a role.

With growing urbanization and air-quality conflicts, more prescribed burning will likely continue to be pushed into the early season. It is possible that repeated early season burning might lead to a different outcome than the single prescribed burn reported here, and this warrants investigation. Because of the complex species-specific interactions with burning season, varying the timing of management fires may ultimately promote the greatest diversity of understory vegetation (Hermann et al. 1998; Hiers et al. 2000). It is important to note that the results of this study are specific to high fuel loading conditions following many years of fire exclusion and should not be extrapolated to burns conducted under more normal fuel loading conditions. Once fuels are reduced to historical levels, it is possible that the amount of heat produced and area burned would differ less between early-season and late-season burns, and the influence of plant phenology at the time of the burn might become more apparent. Additional studies conducted under different conditions (fuel loading, timing, weather, and vegetation type) will help fill in gaps in our understanding of burning-season effects and determine how widely the results reported here can be generalized.

Until fuels are reduced to levels similar to those under which fires historically burned, wildfires are likely to cause some adverse ecosystem impacts, and even prescribed fires may burn with unnaturally high severity. Prescribed burns outside of the main historical fire season, when plants are in the midst of early growth, may also not be "natural." However, early-season prescribed burns conducted under relatively moist fuel and soil conditions allow managers to better control the amount of fuel consumed and heat released. With less fuel consumed, more burning cycles may ultimately be required to reduce long-term wildfire hazard, but because the excess fuel is not consumed at once, such early-season prescribed burns may be a valuable tool for moderating the effects on understory vegetation.

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Appendix A

Appendix A appears on the following page.

Table A1. Pre-treatment frequency and change in frequency (2001–2004) of taxa occurring in more than 5% of 1 m^2 subplots in at least one treatment in either of the 2 years, listed from most abundant to least abundant.

	Pre-treatment frequency (%)			Change (2001–2004; %)		
Species	Unburned	Early	Late	Unburned	Early	Late
Hieraceum albiflorum Hook.	24.5	13.7	32.8	–12	–57	–53
Galium sparsiflorum Wight subsp. *sparsiflorum*	9.2	14.0	30.8	9	–56	–79
Pteridium aquilinum (L.) Kuhn var. *pubescens* Underwood	23.8	5.7	25.5	15	29	9
Cryptantha spp.	1.8	0.8	1.7	191	1360	1500
Ceanothus spp.	0.8	0.2	0.3	0	7700	5050
Draperia systyla (A. Gray) Torrey	4.2	9.8	15.8	28	34	26
Symphoricarpos mollis Nutt.	9.0	8.7	18.7	24	–56	–73
Gayophytum eriospermum Covillle	1.7	1.2	0.8	70	657	1940
Pyrola picta Smith	8.8	6.2	14.8	–9	–30	–72
Galium triflorum Michx.	13.0	10.0	8.8	–4	–45	–42
Viola purpurea Kellogg subsp. *purpurea*	11.5	4.5	4.3	–25	–33	–69
Bromus laevipes (Shear) A. Hitchc. or *Bromus orcuttianus* Vasey	3.8	8.2	10.2	39	–71	–18
Adenocaulon bicolor Hook.	7.3	7.5	9.0	–9	–44	–43
Allophyllum integrifolium (Brand) A. & V. Grant	1.2	1.3	0.5	200	550	567
Chimaphila menziesii (D. Don) Spreng.	7.8	3.5	5.7	–26	–95	–100
Osmorhiza chilensis Hook. & Arn.	4.5	3.2	7.7	–70	–68	–85
Ribes spp.	1.3	1.0	1.0	–25	500	417
Achnatherum occidentalis (Thurber) Barkworth subsp. *occidentalis*	4.7	2.2	4.5	11	–15	30
Carex multicaulis Bailey	2.2	2.7	5.3	46	63	–9
Calystegia malacophylla (Greene) Munz subsp. *malacophylla*	0.2	3.3	1.2	0	50	114
Lotus crassifolius (Benth.) Greene var. *crassifolius*	0.0	0.0	0.2	(0.0)*	(5.0)*	700

Note: Two early ephemeral species (*Collinsia torreyi* A. Gray and *Linanthus ciliatui* (Benth.) Greene) were not included because detection depended upon timing of the survey.

*Values are post-treatment frequencies; percent change could not be calculated because the species was not present pre-treatment.