SPECIES REPLACEMENT DURING EARLY SECONDARY SUCCESSION: THE ABRUPT DECLINE OF A WINTER ANNUAL

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Abstract. The factors that contribute to species establishment and decline determine the rate and pattern of successional change. We tested a commonly held assumption that competitive displacement is responsible for the loss of species during succession. Manipulative field experiments were used to examine the effects of interspecific competition on the population dynamics of *Senecio sylvaticus,* a winter annual that briefly dominates post-harvest sites in the western Cascade Range of Oregon. *Senecio* increased in density 400-fold from the first to the second growing season after disturbance but decreased precipitously in year 3 to 10% of the density and 0.5% of the biomass per plot of the previous year. Although interspecific competition reduced the cover and biomass of *Senecio* during its peak year, it had little or no effect on either the population increase or decline; the pattern of change was similar among all treatments. These counterintuitive results underscore the importance of testing, not simply assuming, that interspecific competition is responsible for the replacement of a species during succession.

Key words: allelopathy; annual plants; competition; germination; interspecific competition; intraspecific competition; secondary succession; Senecio sylvaticus; *soil nutrients; winter annual.*

INTRODUCTION

Succession has long been recognized as a fundamental ecological process (Cowles 1899, Clements 1916, Cooper 1926, Gleason 1927, Odum 1969, McIntosh 1981). Although numerous studies have described changes in species composition through time and have sought explanations for these changes, ecologists continue to debate the relative importance of various successional mechanisms and the conditions under which they effect species replacement (Drury and Nisbet 1973, Connell and Slatyer 1977, Miles 1979, Peet and Christensen 1980, Horn 1981, Finegan 1984, Pickett et al. 1987, Tilman 1988, McCook 1994). Increasingly, attention has been focused on the roles of life history characteristics (Egler 1954, Bazzaz 1979, Cattelino et al. 1979, Noble and Slatyer 1980, Pickett 1982, Hobbs et al. 1984, Walker et al. 1986, Halpern 1989) and species interactions (e.g., exploitative competition) (Raynal and Bazzaz 1975, Werner 1976, Van Hulst 1979, Hils and Vankat 1982, Tilman 1985, Armesto and Pickett 1986, Morris and Wood 1989, Bazzaz 1990, Wedin and Tilman 1993) in shaping compositional change. During the early stages of primary and secondary succession, changes in species composition may simply reflect the availability of propagules and the life history traits of species, with inter-

specific interactions only modifying the magnitude or timing of change (e.g., Chapin et al. 1994). However, competition for resources is often assumed to underlie species replacements (Connell and Slatyer 1977, Tilman 1985, Bazzaz 1990). In addition, herbivory (e.g., McBrien et al. 1983, Brown 1985, Edwards and Gillman 1987, Back 1994), disease (e.g., Van der Putten et al. 1993), and allelopathy (e.g., Wilson and Rice 1968, Rice 1974, Raynal and Bazzaz 1975, Jackson and Willemsen 1976) can modify or effect successional change. Because two or more of these factors may operate simultaneously or successively (Hils and Vankat 1982, Finegan 1984, Pickett et al. 1987), elucidating the mechanisms leading to species replacement can be difficult.

The factors that control the increase in abundance of a species during succession may differ dramatically from those that affect its decline. An increase in abundance may be determined largely by life history traits such as seed production, dispersal, and growth rate, although species interactions can facilitate or inhibit the process (Vitousek et al. 1987, Morris and Wood 1989, del Moral and Wood 1993, Chapin et al. 1994). In contrast, the decline of a species is often attributed to competitive effects (Keever 1950, Tilman 1985, 1988), although life history traits such as longevity are also clearly important (e.g., Barclay-Estrup and Gimingham 1969, Marks 1974, Halpern 1989). Explanations for expansion and decline will vary among spe-
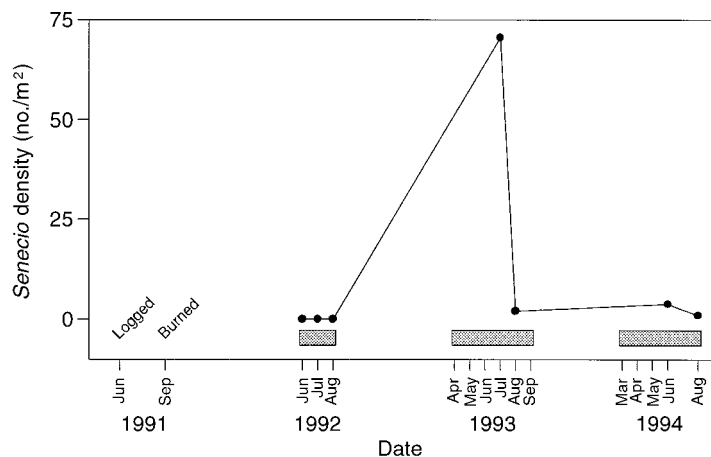
Fig. 1. The timing and magnitude of increase and decline of *Senecio sylvaticus* relative to logging and burning of the Starrbright site. Densities are the means of 25 control plots. *Senecio* was not present prior to harvest (1990) or immediately following logging or burning (1991). Species removal dates (horizontal bars) were: 24–26 June, 24–28 July, and 24–26 August 1992; 2–19 April, 18–25 May, 4–12 July, 21–23 September 1993; 12–17 March, 24–29 April, 24 May–2 June, 30 June–1 July, and 11–15 August 1994. Postharvest sampling dates (indicated by data points) were: 21–23 June, 24–27 July, and 24–26 August 1992; 29 June–9 July and 13–18 August 1993; and 25–30 June and 6–14 August 1994.

cies and successional sequences. Generalizations may emerge from the aggregation of many case studies (see Whittaker and Levin 1977, McIntosh 1981). In this paper, we test the effect of interspecific competition on the rapid expansion and abrupt decline of an exotic winter annual, *Senecio sylvaticus,* during early secondary succession.

Following clear-cut logging and slash burning of forests of the Cascade and Coast Ranges of Oregon, *Senecio sylvaticus* becomes very abundant, often dominant, 2 yr after disturbance, but declines precipitously in abundance in year 3 (West and Chilcote 1968, Dyrness 1973, Halpern 1989, Geyer 1995). The pattern is widespread and highly predictable. Although the rapid increase of *Senecio* reflects the combined effects of a seedbank, an annual life cycle, and copious production of wind-dispersed seed, the dramatic decline is perplexing. Prior to the experiments described here, we hypothesized that loss of *Senecio* resulted from competition with species such as *Epilobium angustifolium,* that dominate later in succession (Halpern 1989). Although implicit in most successional models (e.g., Connell and Slatyer 1977, Tilman 1985), few studies have explicitly tested the assumption that interspecific competition is responsible for the replacement of earlier species by later ones (but see Raynal and Bazzaz 1975, Tilman and Wedin 1991, Wedin and Tilman 1993). In this paper, we demonstrate that competition with other species is not responsible for the decline of *Senecio,* and briefly consider evidence that other factors contribute to its replacement.

METHODS

Study site and species

The study site, the Starrbright timber sale, hosts a set of long-term field experiments that examine the effect of plant species interactions on patterns of early secondary succession in *Pseudotsuga* forests (Halpern et al. 1992). In the nearby Andrews Experimental Forest, postlogging succession has been observed in per-

manent plots for >30 yr (Dyrness 1973, Halpern 1988, 1989, Halpern and Franklin 1990, Halpern and Spies 1995). Experiments at Starrbright have been designed to elucidate mechanisms of species compositional change that have been documented in these earlier descriptive studies.

Starrbright is located on the west side of the Cascade Range, in the deep valley of the South Fork of the McKenzie River (Willamette National Forest, Oregon), ≈25 km south of the Andrews Forest. The 4-ha study site lies at 730 m elevation on a gentle, east-facing slope. The surrounding landscape is a mosaic of mature and old-growth forest, young plantations, and recent clearcuts of varying age. The climate is maritime with mild, wet winters and warm, dry summers. Annual precipitation averages 2300 mm at the nearby Andrews Forest, but only 6% of this falls from June through August (Bierlmaier and McKee 1989). Snowfall is common, but does not persist long at this elevation.

The vegetation and disturbance characteristics of Starrbright were similar to those of the Andrews Forest sites (Rothacher et al. 1967, Dyrness 1973, Halpern 1989). Prior to harvest, Starrbright supported mature to old-growth forest dominated by *Pseudotsuga menziesii,* with *Tsuga heterophylla* and *Thuja plicata* common in the lower canopy. Understories were fairly uniform in composition, dominated by the shrubs, *Rhododendron macrophyllum, Gaultheria shallon,* and *Berberis nervosa. Senecio sylvaticus* was absent from the original forest understory. The forest was clearcut logged in late May and early June 1991 (Fig. 1), although several large trees were left standing for wildlife habitat. The site was broadcast burned on 11 September 1991 (Fig. 1) with a moderate- to high-intensity fire typical of previous slashburns on the Andrews Forest and elsewhere in the region.

Vegetation was sparse the first growing season after burning (6% total plant cover in June 1992), but subsequent changes in composition and cover were rapid, as is common during early succession in these forests.

TABLE 1. Experimental removal treatments used to examine the performance of *Senecio sylvaticus* under altered competitive regimes.

Species removed			
Senecio sylvaticus	*Epilobium angustifolium*	All other species	Response variable(s)
Senecio-response experiment			
Present	Present	Present	*Senecio* frequency, cover, density, biomass/ plot, stem height, and stem diameter
Present	Removed	Present	
Present	Present	Removed	
Present	Removed	Removed	
Senecio-removal experiment			
Removed	Present	Present	*Senecio* germination
Removed	Removed	Present	
Removed	Present	Removed	

The winter annuals, *Senecio sylvaticus* and *Epilobium paniculatum,* dominated the site in year 2 (1993). In year 3 (1994), however, *Senecio sylvaticus* was virtually absent (Fig. 1), and dominance was shared by *Epilobium paniculatum,* invading perennials (*Epilobium angustifolium* and *Gnaphalium microcephalum*), and forest species that survived disturbance (*Berberis nervosa* and *Rubus ursinus*).

Senecio sylvaticus (henceforth *Senecio*) is native to Eurasia, but was introduced into northern California in the 1920s (Robbins et al. 1951 cited in West and Chilcote 1968) and is now common throughout the Coast and Cascade Ranges of western Oregon (West and Chilcote 1968, Morris 1970, Hitchcock and Cronquist 1973). It is most prominent on burned clearcuts (Isaac 1940, Morris 1970, West and Chilcote 1968, Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989), but can also be found on logged, but unburned sites (Gholz et al. 1985) and in other disturbed areas.

Senecio is a winter annual that produces light, wind-dispersed seeds in abundance (West and Chilcote 1968, van Andel and Vera 1977). It is found in the seedbank of older forests (Kellman 1974, Ingersoll and Wilson 1989, Clark 1991, McGee and Feller 1993, Harmon and Franklin 1995), although the longevity of buried seed is unknown. Dormancy is not required for germination (West and Chilcote 1968, Geyer 1995; C. B. Halpern, *unpublished data*). Seeds typically germinate in fall with the first heavy rains and seedlings overwinter as rosettes; germination also occurs in spring (West and Chilcote 1968). Plants bolt in mid-May, flowers are evident by mid- to late June, and seed is dispersed as early as mid-July. Most nutrient uptake occurs before bolting; thereafter nutrients and photosynthate are translocated to stems, then to flowers (van Andel and Vera 1977, van Andel and Jager 1981). The species is reported to have high nutrient requirements, and thus, does well following fires that temporarily increase nutrient availability (West and Chilcote 1968, Kumler 1969). However, others have suggested that *Senecio* does not require unusually high nutrient con-

centrations (van Andel and Vera 1977, van Andel and Nelissen 1979).

Experimental design and sampling procedures

The results described in this paper are drawn from a broader set of long-term studies that examine the effects of species interactions on secondary succession (Halpern et al. 1992). The full experimental design consists of eight species removal treatments and a control that are analyzed as sets of factorial experiments. In this paper we present data from two of these experiments (seven of nine treatments; Table 1). The first experiment examines the responses of *Senecio* to removal of potential competitors (henceforth the *Senecio*-response experiment; Table 1). Both *Epilobium angustifolium* and the set of all other species are removed in a full-factorial design (four treatments): (1) removal of *Epilobium angustifolium,* (2) removal of all species except *E. angustifolium* and *Senecio,* (3) removal of *Epilobium angustifolium* and all other species except *Senecio,* and (4) an unmanipulated control (Table 1). The second experiment provides data on the timing and magnitude of *Senecio* germination. It consists of three treatments from which *Senecio* is removed (henceforth the *Senecio*-removal experiment; Table 1): (1) removal of *Senecio,* (2) removal of *Senecio* and *Epilobium angustifolium,* and (3) removal of *Senecio* and all other plant species except *E. angustifolium.*

Twenty-five replicates of each treatment are arranged in a randomized block design. Within each block, sample plots of 1×1 m are separated by a distance of 2 m. Plots were established in summer 1990, prior to logging, and treatments within each block were assigned randomly after burning.

Cover and density of each vascular plant species were recorded for each of the 175 plots on each sampling date (Fig. 1). We also measured stem heights for all but recumbent species, and stem diameters for all woody and some herbaceous species. These data were used to predict the aboveground biomass of each species (mass per plant and biomass per plot) from re-

gression equations developed on site (Halpern et al. 1996). Because of extremely high densities, *Senecio* was subsampled for height and diameter in 1993, using one-quarter of the 1×1 m plot. Nomenclature follows Hitchcock and Cronquist (1973).

Plant removals were conducted frequently during the growing season (Fig. 1) to minimize competitive effects and soil disturbance associated with weeding. Seedlings were pulled by hand, and sprouts or established stems were clipped at the ground surface. Removals extended into a 0.75-m buffer around each plot (producing a total treated area of 2.5×2.5 m). In treatments where *Senecio* was removed, individuals were tallied as they were pulled.

Data analysis

Analysis of variance (ANOVA) was used to examine the effects of potential competitors on *Senecio* cover, density, aboveground biomass per plot, and germination. A two-way ANOVA was used to examine the effects of removing *Epilobium angustifolium* and the set of all other species on the cover, density, and biomass per plot of *Senecio* (*Senecio*-response experiment). Analyses were performed on data from the first sampling periods in 1993 (July) and 1994 (June), when densities were highest for the year. Plants were too infrequent in 1992 to warrant similar analysis. The total number of germinants removed each year from plots in the *Senecio*-removal experiment was subjected to one-way ANOVA.

We performed two types of analyses to determine whether occupancy of a plot by *Senecio* during the year of peak abundance (1993, year 2) influenced subsequent establishment (1994, year 3). First, we conducted analysis of covariance (ANCOVA) on *Senecio* density data for 1994 (year 3) for all plots in the *Senecio*-response experiment ($n = 100$) using the peak density of *Senecio* in 1993 (year 2) as the covariate. Second, we regressed peak density of *Senecio* in 1994 on peak density in 1993 for the same set of plots.

Model assumptions were subjected to statistical tests: Lilliefors' test (Wilkinson 1990) for normal distribution of residuals and $F_{\max}$ (Sokal and Rohlf 1981) or Levene's test (Sabin and Stafford 1990, Wilkinson 1990) for homogeneity of variances. The assumption of homogeneity of slopes was also tested for ANCOVA (Wilkinson 1990). Data transformations (arcsine square root and logarithmic) were conducted as appropriate (Sabin and Stafford 1990).

RESULTS

Temporal patterns

Abundance of *Senecio* changed dramatically from year to year, but patterns of change were similar among treatments (Fig. 2, Table 2). During the first postdisturbance growing season (1992), frequency of occurrence was low (<25%); it peaked in 1993 (year 2) and

declined slightly in 1994 (year 3) (Fig. 2a). Densities in 1992 (year 1) were <0.2 plants/m² in all treatments (Fig. 2c). By 1993 (year 2), however, densities exceeded 60 plants/m² (Fig. 2c), cover ranged from ≈10–20%, and biomass/plot from ≈40–120 g/m² (Fig. 2b, d), increases of >400-fold in density, >10-fold in cover, and >17-fold in biomass for all treatments (Table 2). In contrast, density, cover, and biomass declined precipitously in 1994 (year 3) in all treatments (Fig. 2b–d, Table 2). Biomass per plot decreased more than other measures of abundance, with mean values in 1994 no more than 0.5% of what they had been the previous year (Table 2).

Mean plant size also changed markedly between years. The few plants present in 1992 (year 1) were extremely large (mean mass of 16.4 g/plant); thereafter average plant mass declined, with plants in 1994 (year 3) weighing 0.01–1.5% of what they had the first year (Table 2). Mean plant height and diameter also decreased annually (June/July dates in Fig. 2e, f). Although mean height and diameter were generally greatest at the last sampling period each year (August), means at that time were based on the few large individuals that survived later into the growing season (note seasonal declines in density, Fig. 2c).

The magnitude and timing of *Senecio* germination differed markedly prior to the summers of peak abundance (1993) and decline (1994) (Fig. 3). In 1993, 2.1–3.3 times as many *Senecio* seedlings were removed from treatments in the *Senecio*-removal experiment as were removed in 1994 (Table 3a). Most germinants appeared before the first weeding in 1993 (April, Fig. 3); seedlings were already abundant the previous fall (November 1992; C. B. Halpern, *personal observation*). In contrast, almost all germinants appeared after the first weeding in 1994 (March, Fig. 3). Thus, either few seeds germinated in fall 1993 or mortality was high prior to March 1994.

Effects of interspecific competition

Removing competitors had no influence on the increase or decline of *Senecio* (Fig. 2, Table 4). Similarly, there were no differences in germination among removal treatments (Fig. 3, Table 3b). However, several measures of within-year growth and survival showed positive responses to removals. In July of the peak year (1993), mean cover and biomass per plot of *Senecio* were significantly higher where other species were removed (Fig. 2b, d, Table 4). At second sampling (August), *Senecio* was alive in a greater number of competitor-removal than nonremoval plots (Fig. 2a), indicating that removals enhanced the summer survival of *Senecio*. Although we did not conduct statistical analyses of plant height and diameter because sample sizes varied greatly among treatments, mean values suggest that competitor removals increased plant size, especially in August of the peak year (Fig. 2e, f). Despite enhanced growth and survival, we could detect
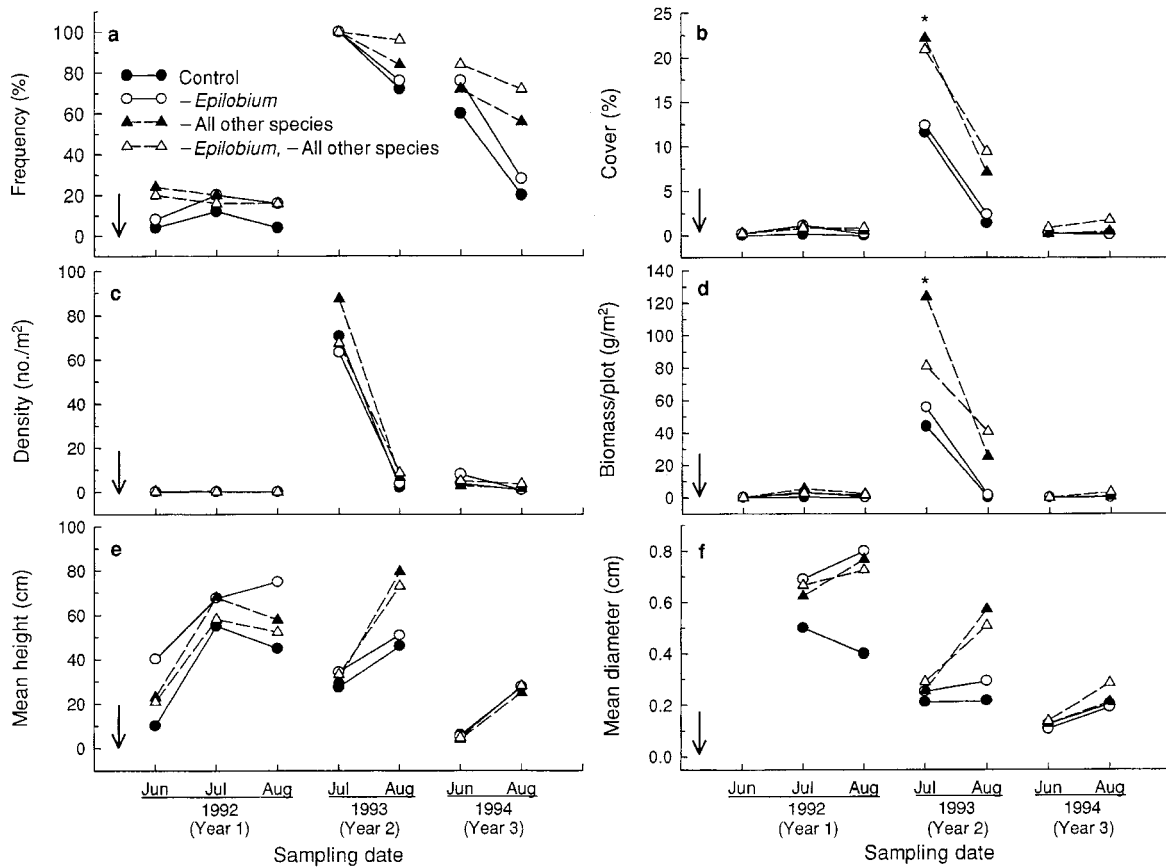
FIG. 2. Temporal changes in (a) frequency, (b) mean cover, (c) mean density, (d) mean aboveground biomass/plot, (e) mean plant height, and (f) mean basal diameter of *Senecio sylvaticus* in the four treatments comprising the *Senecio*-response experiment ($\pm$ *Epilobium angustifolium* and $\pm$ all other species, Table 1). Frequency is the proportion of plots occupied (n = 25) based on plant rooting location. Biomass was predicted from regression equations developed on-site. Because plant growth form changed with time, biomass equations differ by sampling date: June 1992, y = exp[0.084(ht.) $-$ 3.346], R^2 = 0.809; July and August 1992, y = exp[1.846(ln[ht.]) + 1.204(ln[dia.]) $-$ 5.385], R^2 = 0.963; all dates in 1993 and 1994, y = exp[1.378(ln[dia.]) + 1.187(ln[ht.]) $-$ 2.821], R^2 = 0.936; where y = plant mass in grams, and ht. and dia. are height (cm) and basal diameter (cm) of the main stem, respectively. Biomass of individual plants was summed to produce plot-level totals. Asterisks denote sampling dates for which ANOVAs indicated significant main effects (Table 4). ANOVA tests were not performed on height and diameter data because sample sizes varied markedly among treatments (see density values).

no significant effect of removals on *Senecio* density in either year (Fig. 2c, Table 4).

Intraspecific effects on establishment

The abrupt decline in abundance of *Senecio* in 1994 was most pronounced in plots that supported high densities of *Senecio* in 1993. When 1994 density data from the *Senecio*-response experiment (n = 100) were examined using analysis of covariance (ANCOVA), only the covariate, *Senecio* density in July 1993, was significant (Table 5). Thus, the extent of prior occupancy of a plot had a highly significant negative effect on *Senecio* density, even though treatments removing potential competitors had no detectable effect on its abrupt decline. Regression of log density 1994 on log density 1993 for the same set of 100 plots yielded a highly significant negative correlation (Fig. 4), although the total amount of variation explained was relatively small

(R^2 = 0.128). High density in 1993 nearly precluded establishment in 1994. In plots with >50 plants/m² in 1993, densities did not exceed 12 plants/m² in 1994; plots with >150 plants/m² in 1993 had little to no recruitment in 1994 (Fig. 4).

DISCUSSION

The rapid population increase

Senecio sylvaticus increased >400-fold in density and >10-fold in cover, from the first to the second growing season at Starrbright. Similar changes have been reported previously (West and Chilcote 1968, Dyrness 1973, Halpern 1989, Clark 1991). Low densities the first growing season after harvest (1992) reflect consumption of wind-dispersed and buried seed by broadcast burning the previous fall (see also Clark 1991). Thus, the population size in the first year ap-

TABLE 2. Proportional change in mean density, cover, and biomass of *Senecio sylvaticus* for the periods 1992–1993 (years 1–2) and 1993–1994 (years 2–3); and mean plant mass in 1992, 1993, and 1994. Treatments are those in the *Senecio*-response experiment (Table 1).

		Treatment			
Measure of performance	Period†	+ *Senecio*, + *Epilobium*, + all other species	+ *Senecio*, − *Epilobium*, + all other species	+ *Senecio*, + *Epilobium*, − all other species	+ *Senecio*, − *Epilobium*, − all other species
Proportional change in density	1992–1993	1764.00	526.00	437.20	561.33
	1993–1994	0.054	0.127	0.033	0.074
Proportional change in cover	1992–1993	64.56	10.99	20.56	24.33
	1993–1994	0.028	0.028	0.011	0.043
Proportional change in biomass/plot	1992–1993	337.69	17.15	22.58	32.07
	1993–1994	0.005	0.004	0.001	0.002
Mean plant mass (g/plant)‡	1992	3.25	27.00	14.20	21.08
	1993	0.62	0.88	1.42	1.20
	1994	0.05	0.03	0.03	0.04

† Data are from the second sampling period in 1992 and the first sampling periods in 1993 and 1994 (periods of peak cover and biomass).

‡ Mean total plot biomass (g/m²) divided by mean density (no. plants/m²).

peared seed limited; the few plants that established grew extremely well, irrespective of treatments that removed potential competitors. The lack of treatment effects is not surprising given the low total cover of plant species on the site in 1992 (5.8 and 14.9% on control plots in June and July, respectively).

The exceedingly rapid increase in *Senecio* abundance from 1992 to 1993 resulted from a combination of abundant seed produced on site by the few, very large plants present in 1992 and influx of seed from off-site sources in summer and fall 1992 (see also Clark 1991, Clark and Wilson 1994). It is unlikely that a seedbank contributed much to postfire populations (particularly those in years 2 and 3), because *Senecio* seed is lost during burning (Clark 1991), and aerial deposition of seed far exceeds densities in the soil (Kellman 1974).

The rapid buildup of populations is largely attributable to the life history traits of the species: copious, wind-dispersed seed; fall germination; rapid, early growth; and an annual life cycle. Furthermore, results of our competitor removal treatments demonstrate definitively that interspecific competition did not limit the rapid germination or establishment of populations.

The transient removal by disturbance of the original forest vegetation, combined with a flush of nutrients following burning, is pivotal in allowing species with life histories similar to that of *Senecio* to increase rapidly. Although many species are capable of rapidly colonizing forest sites following logging (Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989, Clark 1991), those that attain dominance very early in succession must be capable of rapid population increases.
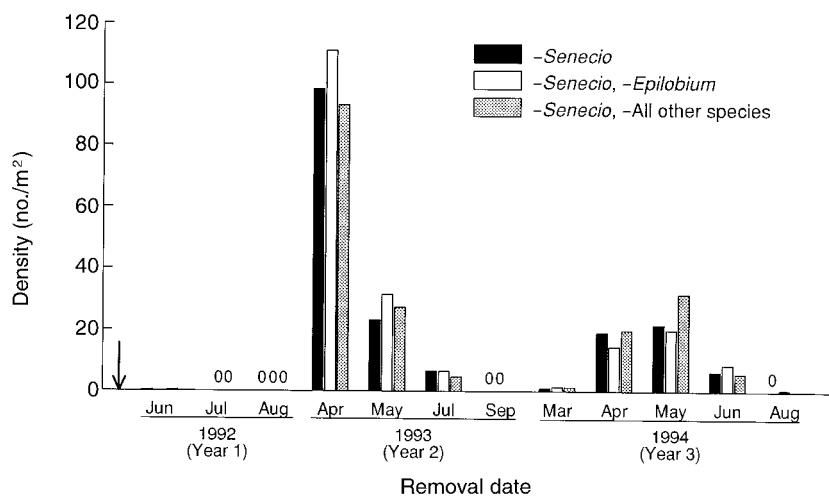

FIG. 3. The number of *Senecio sylvaticus* seedlings removed from the three *Senecio*-removal treatments (Table 1) between June 1992 (year 1) and August 1994 (year 3). The arrow signifies logging and burning in 1991. Zeros for particular treatment-by-removal dates indicate that no seedlings were removed. See Fig. 1 caption for removal dates. Summary statistics and ANOVAs on cumulative numbers of seedlings removed are presented in Table 3.

TABLE 3. Total numbers of *Senecio sylvaticus* germinants removed in years 1 (1992), 2 (1993), and 3 (1994) from plots in the *Senecio*-removal experiment (Table 1). (A) Treatment means ± 1 SE and (B) analysis of variance (ANOVA) results. See also Fig. 3. ANOVA was not performed on 1992 data.

A) Total number of *Senecio* germinants removed per m²

Treatment	1992	1993	1994
− *Senecio*	0.4 ± 0.1	128.5 ± 19.2	48.1 ± 7.5
− *Senecio*, − *Epilobium*	0.1 ± 0.1	149.2 ± 25.1	44.3 ± 6.7
− *Senecio*, − all other species	0.3 ± 0.2	125.3 ± 25.6	58.6 ± 13.9

B) ANOVA results

Source	df	1993† F	1993† P	1994† F	1994† P
Block	24	4.906	0.000***	3.400	0.000***
Treatment	2	1.464	0.242	0.483	0.620
Error	48				
MSE			0.395		0.545
R^2			0.715		0.632

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Transformed as ln(variable + 1).

With the exception of the annual, *Epilobium paniculatum,* few native species in the region are as capable as *Senecio* of rapidly exploiting the ephemeral resources created by this type of intense disturbance.

The abrupt population decline

Although *Senecio* was abundant and produced copious quantities of seed 2 yr after slash burning (C. B. Halpern, *personal observation*), the population declined precipitously in year 3, a pattern observed repeatedly in the western Cascade and Coast Ranges of Oregon (West and Chilcote 1968, Dyrness 1973, Halpern 1989). Competitive displacement is often assumed to be the mechanism for species replacement during succession (Connell and Slatyer 1977, Abul-Fatih and Bazzaz 1979, Tilman 1985, Armesto and Pickett 1986). However, the results of our removal treatments clearly demonstrate that it is not responsible for the loss of *Senecio*: removing competitors did not prevent the population crash. There was little evidence for competition at any point from the dominant perennial colonist, *Epilobium angustifolium,* possibly reflecting differences in the seasonal timing of establishment and growth of the two species (van Andel and Vera 1977, van Andel and

TABLE 4. Analysis of variance (ANOVA) of cover, density, and aboveground biomass/plot of *Senecio sylvaticus* in years 2 (1993) and 3 (1994) from the *Senecio*-response experiment (± *Epilobium angustifolium* and ± all other species, Table 1). See also Fig. 2. Data are from the first sampling period in each year. Treatment codes for pairwise differences: C = control; E = − *Epilobium*; A = − all other species; X = − *Epilobium*, − all other species.

Source	df	Cover† 1993 F	Cover† 1993 P	Cover† 1994§ F	Cover† 1994§ P	Density‡ 1993 F	Density‡ 1993 P	Density‡ 1994 F	Density‡ 1994 P	Biomass‡ 1993 F	Biomass‡ 1993 P	Biomass‡ 1994§ F	Biomass‡ 1994§ P
Block	24	0.816	0.706	1.189	0.281	1.541	0.083	1.327	0.179	1.580	0.071	0.865	0.023*
Removals													
Epilobium angustifolium	1	0.036	0.849	4.290	0.042*	1.495	0.225	3.831	0.054	0.005	0.946	1.829	0.180
All other species	1	19.360	0.000***	3.042	0.085	0.616	0.435	0.062	0.804	6.519	0.013*	0.363	0.549
Two-way interaction	1	0.124	0.726	1.012	0.318	0.082	0.776	0.001	0.979	0.682	0.412	0.040	0.843
Error	72												
MSE		70.582		7.653		0.510		0.963		1.295		0.052	
R^2		0.352		0.339		0.352		0.332		0.385		0.395	
Pairwise differences‖		C E X A		A E C X		E X C A		A C X E		C E X A		A X E C	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Arcsine square-root transformed.

‡ Transformed as ln(variable + 1).

§ ANOVA assumptions were violated for all attempted transformations [ln(x + 1), logit(x), sqrt(x + 1)]. Nonparametric analyses were not attempted because many plots had no plants ($n = 27$), and cover and biomass were uniformly low.

‖ Tukey hsd post hoc test (Wilkinson 1990).

TABLE 5. Analysis of covariance of *Senecio sylvaticus* establishment (density) in year 3 (1994) from the *Senecio*-response experiment (± *Epilobium angustifolium* and ± all other species, Table 1). The covariate is ln(density + 1) of *Senecio* in year 2 (1993). A preliminary model was run to test for homogeneity of slopes of the dependent variable vs. the covariate among treatment combinations (Wilkinson 1990). See Fig. 4 legend for the regression describing the overall relationship between the dependent variable and the covariate.

Source	df	F	P
Block	24	1.158	0.309
Removals			
Epilobium angustifolium	1	2.700	0.105
All other species	1	0.000	0.985
Two-way interaction	1	0.004	0.952
Covariate	1	6.706	0.012*
Error	71		
MSE			0.892
R^2			0.389

  * $P < 0.05$.

Jager 1981; C. B. Halpern, *unpublished data*). Although competition from the seral plant community reduced the size and abundance (cover and biomass per plot) of *Senecio* during the peak year (1993), densities of germinants and established plants were never affected. Any reductions in 1993 were greatly overshadowed by the large decline in all attributes from 1993 to 1994. Thus, our data clearly falsify the hypothesis that interspecific competition causes the abrupt decline of *Senecio*.

Although our field experiments were not designed to test alternative mechanisms for the decline, our observations provide insight into possible causes. The negative correlation between density in year 3 and in year 2 suggests a density-dependent, intraspecific effect manifested between years (e.g., auto-allelopathy). West and Chilcote (1968) originally hypothesized that decline of *Senecio* could be attributed to an autotoxic leachate, but their data were inconclusive. Although often implicated (e.g., Wilson and Rice 1968, Muller 1969, del Moral and Cates 1971, Rice 1974, Jackson and Willemsen 1976), allelopathic effects have rarely

been demonstrated conclusively (Facelli and Pickett 1991). In our regression analysis, the amount of variation in 1994 density explained by 1993 density was small, suggesting that factors other than auto-allelopathy are important in the decline. Moreover, the consistent decline among all experimental treatments (including *Senecio*-removal plots that had never supported the species) strongly suggests that site-wide changes in the physical or biotic environment inhibit *Senecio* establishment.

Availability of seeds or germination sites, predation or disease, or changes in soil nutrient availability all potentially limit establishment of *Senecio*. The very large and vigorous 2nd-yr (1993) population produced ample seed to renew the population in 1994 (probably orders of magnitude more seed than was produced on site in 1992). Because dormancy is not required (West and Chilcote 1968, Geyer 1995; C. B. Halpern, *unpublished data*), it is likely that these seeds germinated. Although we have no data for fall and winter (September 1993–March 1994), others have reported that large numbers of *Senecio* germinate in year 3, but fail to survive beyond the cotyledon stage (West and Chilcote 1968, Geyer 1995).

The decline of *Senecio* does not appear to be associated with changes in the availability or physical characteristics of germination sites. Densities in 1993 and 1994 were not correlated with cover of mineral soil or litter ($R^2 < 0.07$ for all comparisons; C. B. Halpern, *unpublished data*). Moreover, ground surface features changed little between years. Cover of mineral soil averaged 15–36% among treatments in 1993 and 8–29% in 1994; cover of litter averaged 59–82% among treatments in 1993 and 64–89% in 1994 (C. B. Halpern, *unpublished data*). Furthermore, *Senecio* does not appear to require a particular substrate for germination. Although it reaches maximal density on burned, mineral soils (Steen 1966, West and Chilcote 1968, Dyrness 1973, Halpern 1987, 1988), it can also be abundant on logged sites that have not been burned (Gholz et al. 1985). Various surface conditions supported germination at Starrbright: the burned duff layer of the former
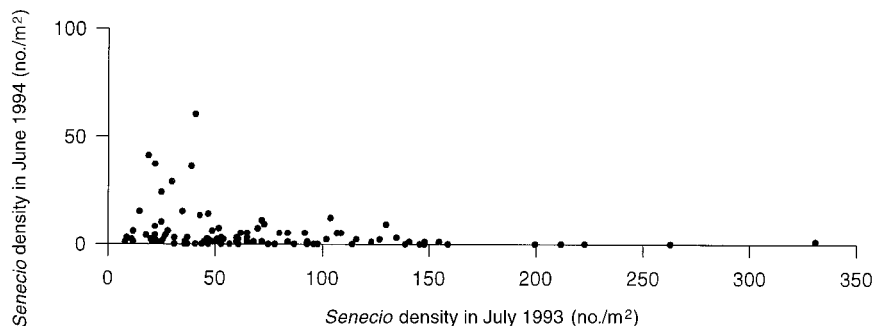

FIG. 4. Density (establishment) of *Senecio sylvaticus* in 1994 vs. density in 1993 for all plots ($n = 100$) in treatments comprising the *Senecio*-response experiment (Table 1). Densities are from the first sampling period of each year. The regression model is ln(density + 1, June 1994) = 3.087 − 0.485[ln(density + 1, July 1993)]; $R^2 = 0.128$, $P = 0.000$.

forest, lightly colored and blackened mineral soil, and subsurface mineral soils exposed by burrowing animals (C. B. Halpern, *unpublished data*). Finally, germination and density did not differ in removal and control plots, providing strong evidence that establishment was not prevented by senescent vegetation or litter on the site.

Predation or disease could be responsible for the recruitment failure of *Senecio* in year 3. Plant-specific, soil-borne diseases contribute to species turnover and succession in other communities (Van der Putten et al. 1993). Although mortality of *Senecio* seedlings induced by fungal infection and aphids has been reported in the greenhouse (Palmblad 1968, West and Chilcote 1968), it has not been observed in the field. We observed no herbivory or disease on plants in either the peak or decline years. However, if damage occurred during fall or winter of 1993, or if it was restricted to belowground structures, it may have gone unnoticed during spring and summer sampling.

In their pioneering work, West and Chilcote (1968) concluded that changes in soil nutrient availability after slash burning contribute to the expansion and decline of *Senecio.* The correlation between population decline and changes in soil nutrient availability is consistent with resource-based models of succession (e.g., Tilman 1985). Soil nitrogen (N) data from our plots indicate an initial flush, followed by a dramatic, site-wide decline in N availability between years 1 and 3 (C. B. Halpern, *unpublished data*). However, we remain cautious about attributing the abrupt decline of *Senecio* to depletion of soil nutrients. Despite their conclusions, the data of West and Chilcote (1968) indicate that addition of N and/or P (phosphorus) did not prevent mortality of *Senecio* germinants on 3rd-yr soils, in greenhouse or field settings. Recent field experiments have also demonstrated that fall fertilization (NPK 22-3-3) of a 3-yr-old site failed to arrest the decline of *Senecio* (Geyer 1995). The availability of soil nutrients other than N or P may be linked directly or indirectly to the decline. An experimental site that supported abundant *Senecio* 2 yr after burning and few plants in year 3 exhibited unusually high densities in year 4 after accidental application of a fertilizer containing fairly high concentrations of potassium (NPK 10-30-10) (Geyer 1995). Thus, changes in nutrient availability may be causally linked to the decline of *Senecio,* but we suspect that nitrogen is not the key element.

Prior to our experiments, we anticipated that interspecific competition was a major causal factor in the commonly observed decline of *Senecio sylvaticus* during postharvest succession. The hypothesis fits well with life history theory that predicts trade-offs between competitive ability and other characteristics (e.g., high fecundity) of ruderal species such as *Senecio* (e.g., Grime 1977, 1979, Grace 1990). Although *Senecio* appears to be a poor competitor, as evident in comparative growth responses in control and competitor-removal treatments, our data demonstrate definitively that interspecific competition does not cause its decline during early succession.

The mechanisms by which early successional species influence establishment of later species has been the focus of most conceptual models of succession (e.g., Clements 1916, Connell and Slatyer 1977) and most experimental tests of those models (e.g., Hils and Vankat 1982, Armesto and Pickett 1986, Morris and Wood 1989, Bertness 1991). In contrast, few studies have examined the influence of later species on earlier ones (cf. Raynal and Bazzaz 1975, Tilman and Wedin 1991, Wedin and Tilman 1993). A rarely tested, but widely held assumption is that competition accounts for species decline. Our experiment falsifies the hypothesis that competition underlies the loss of a dominant winter annual during early secondary succession. This counterintuitive result underscores the importance of testing, and not simply assuming, that competition is responsible for species replacement during succession.

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