

Response of a Rare Endemic, *Penstemon clutei*, to Burning and Reduced Belowground Competition

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Abstract: *Penstemon clutei*, a rare perennial beardtongue endemic to the ponderosa pine forest of the Sunset Crater volcanic field of northern Arizona, presents an opportunity to test the hypothesis that restoration of historic ecosystem conditions may enhance the sustainability of a rare species. We tested prescribed burning and root trenching treatments as proxies for the surface fires and reduced tree densities characteristic of historic ponderosa pine ecosystems in a study area at O'Leary Peak, part of the Sunset Crater volcanic field (Coconino National Forest, AZ). Prescribed burning killed many mature *P. clutei* plants and negatively affected density for at least 3 years post-burn. In contrast, trenching to cut root competition of overstory trees led to a 1200 percent increase in *P. clutei* plants. Precipitation influenced the response. Seed germination experiments showed that *P. clutei* does not have innate dormancy. Germination rates in the lab ranged from 5 to 70 percent under a range of environmental and fire-related conditions (i.e., cold stratification, light, exposure to ash, NH₄), but these factors were not statistically significant. Tested seedling establishment rates in situ were very low (0.4%). These experiments suggest that the observed *P. clutei* population increase following severe wildfires (1973 Burnt fire, 1996 Hochderffer fire) may have been due primarily to the removal of tree competition rather than to direct fire effects. Further experimentation is suggested to develop ecological information for thoughtful integration of ecosystem restoration with the habitat needs of rare plants.

Rare plant species present fundamental challenges for the management of forest ecosystems. Conservation of native biological diversity is central to management of public resources, as mandated by the Endangered Species Act and other legislation, but often little is known about the ecology of rare species (National Plant Conservation Initiative, 1995). The very fact of rarity limits our ability to adequately sample or experimentally study species to obtain the types of ecological information needed to support management decisions (Palmer 1987, Owen and Rosentreter 1992). In the absence of information, the conservative position is to minimize management action in the hopes of avoiding habitat degradation. This approach may be the best we can do in many settings, but it may be useless or even counterproductive in others. Many ecosystems are currently in conditions far removed from the structural and disturbance patterns characteristic of the environment in which native species evolved. These altered conditions may be an underlying reason for the present rarity of some species and perpetuation of these conditions through "no-action" management may unintentionally contribute to further loss of habitat.

Penstemon clutei, a rare perennial beardtongue endemic to the ponderosa pine (*Pinus ponderosa*)

forest of the Sunset Crater volcanic field of northern Arizona, presents an opportunity to test the hypothesis that restoration of historic ecosystem conditions may enhance the sustainability of a rare species. Changes in ponderosa pine ecosystems have been well documented (Weaver 1951, Cooper 1960, Covington and Moore 1994, Arno et al. 1995, Swetnam and Baisan 1996, Fulé et al. 1997, Moore et al. 1999). Briefly, the historic regime of frequent low-intensity fires was disrupted by livestock grazing and fire suppression beginning around 1870–1880. Extensive timber harvesting and snag cutting removed a major fraction of the old-growth trees, but dense stands of young trees form continuous fuels across landscapes and vertically within stands. Heavy tree competition causes reduced productivity and increased mortality of old-growth trees (Biondi 1996, Stone et al. 1999, Mast et al. 1999) and reduced understory plant productivity (Riegel et al. 1995, Covington et al. 1997), and affects a host of ecosystem attributes including nutrient cycling and wildlife habitat (Covington et al. 1997). Wildfire size, intensity (crownfires), and severity (overstory and understory mortality) have increased throughout the ponderosa pine range (Swetnam and Betancourt 1998). As a result, the restoration of historic eco-

system characteristics, especially though thinning and burning, is a management strategy receiving great attention (U.S. General Accounting Office 1998).

Although ecosystem restoration may be an appropriate "coarse-filter" strategy for ponderosa forest management (Kaufmann et al. 1994), it is challenging to integrate large-scale treatments with the "fine-filter" approach usually adopted for biological conservation of rare species. The ponderosa pine–*Penstemon clutei* forest provides a good test system for several reasons: (1) The species receives special management consideration, but it is not a federally listed threatened species. (2) Penstemons and many other taxa in the Scrophulariaceae are early successional species, logically adapted to frequent disturbance. (3) The Coconino National Forest, which encompasses almost all of the *P. clutei* range, must deal with management issues in *P. clutei* habitat on a continuing basis, including pipeline and road expansion, recreational site development, off-road vehicle use, timber and mineral resource extraction, and fire management.

The Burnt Fire in November of 1973 burned a portion of the *Penstemon clutei* habitat west of Sunset Crater National Monument. Goodwin (1979) reported that *P. clutei* plants proliferated in the burned area with vigorous growth and abundant reproduction. He concluded that *P. clutei* was a pioneering species requiring periodic disturbance by fire. Vigorous plants and prolific regeneration were also observed after the intense Hochderffer fire in 1996 in the northwestern portion of the *P. clutei* range (P. Z. Fulé, personal observation, 1997 and 1998). Disturbance created by an unusual tornado and subsequent timber salvage (1992–1994) was also associated with increased *P. clutei* abundance (Crisp 1996). After Goodwin's (1979) observations, two prescribed burning studies were carried out by the Forest Service. The first study, in 1982, was conducted under wet conditions and gave inconclusive results (Nagiller 1992). The second study, in 1991, was hampered by a lack of replication and also gave preliminary results of an inconclusive mix of mortality and regeneration (Nagiller 1992).

Beginning in 1992, we initiated studies to quantify *P. clutei* response to prescribed burning and to understand seed germination requirements. Germination response to a range of treatments has been studied extensively in a variety of western penstemons (e.g., Kitchen and Meyer 1991, Raeber and Lee 1991). In commercial production of *P. clutei*, moist chilling for 90 days results in 70–80

percent germination (Plants of the Southwest, Santa Fe, New Mexico, personal communication 1992). Studies on the closely related *Penstemon palmeri* have demonstrated that it is a relatively nondormant species in comparison to other penstemons, but dormancy and requirements for moist chilling and light are variable (Kitchen and Meyer 1991, 1992). Moist chilling at winter temperatures induced secondary dormancy in approximately half of a sample of *P. palmeri* seeds (Meyer and Kitchen 1992). The secondary dormancy was removed by warm summer temperature treatment, suggesting that *P. palmeri* has a strategy of cyclic seed dormancy, dividing seeds into spring and autumn germination groups (Meyer and Kitchen 1992). Seed collected from a recently burned site exhibited primary dormancy an order of magnitude higher than seed from other collections (Meyer and Kitchen 1992). *Penstemon* species from cold, high-elevation habitats required more extensive moist chilling to remove primary dormancy (Kitchen and Meyer 1992, Meyer 1992). The low-elevation species *P. parryi* exhibits little response to moist chilling (Raeber and Lee 1991). Viability of *P. palmeri* seeds in storage remains 83 percent after 2 years and reduces to 50 percent after 15 years (Stevens et al. 1981). Given its ecological characteristics intermediate between *P. parryi* and *P. palmeri*, *P. clutei* might be expected to have an intermediate moist chilling requirement and long seed viability.

Plant regeneration following fire is not necessarily through seed germination and establishment. *Penstemon haydenii* in Nebraska was found to reproduce primarily vegetatively (Flessner and Stubbendieck 1992). A study of disturbance effects by fire and pocket gophers on *Penstemon grandiflorus* in Minnesota showed that plants that survived fire resprouted and displayed no increased reproductive output (Davis et al. 1991a). Even though fire appeared to have a negative impact on individual *P. grandiflorus* plants, the population as a whole was dependent on fire and gopher disturbance to maintain a suitable, open habitat (Davis et al. 1991b). *Ipomopsis aggregata*, a species associated with *Penstemon clutei* that displays a similar growth form, resprouted following fire in northern Arizona, although growth and vigor were reduced in burned plants (Paige 1992). Seedling establishment of *I. aggregata*, however, increased 116-fold over controls (Paige 1992). Vose and White (1987) found that reproduction of several understory species, including *Penstemon virgatus*, following fire in northern Arizona occurred

from residual seed or seed rain from surviving plants, rather than from buried seed populations. In an investigation of the regeneration of several understory species following fire in California chaparral, Keeley et al. (1985) distinguished several reproductive strategies. Herbaceous perennials tended to resprout, whereas annuals divided into an opportunistic class with varying germination requirements and a fire-dependent class that displayed strong germination response to heat or the presence of charred wood (Keeley et al. 1985).

In 1997, after evaluating negative results from the prescribed burning experiment described below, we investigated the hypothesis that the vigorous *P. clutei* responses seen after the Burnt and Hochderffer fires and the 1992 tornado were due to the mortality of overstory trees, thereby removing root competition. Competition with overstory vegetation may affect understory plants either through light interception or through the relatively greater ability of trees to extract water and nutrients from the soil. Southwestern ponderosa pine forests have relatively open canopies (40–65% canopy cover by vertical projection at sites across northern Arizona, Fulé et al. 1997 and unpublished data). Riegel et al. (1995) tested the effects of light versus root competition on understory species composition and cover in an Oregon ponderosa pine forest. Both factors were significant, but trenching to remove tree root competition increased the cover and density of 60 percent more understory species than in the canopy-reduction treatment (Riegel et al. 1995).

From 1992 to 2000, we conducted the following studies on *P. clutei*: (1) We measured germination response to a variety of environmental factors in lab and field settings. (2) We tested the hypothesis that prescribed fire would increase *P. clutei* density by removing litter and competing vegetation. (3) We tested the hypothesis that cutting root competition through trenching would increase *P. clutei* density.

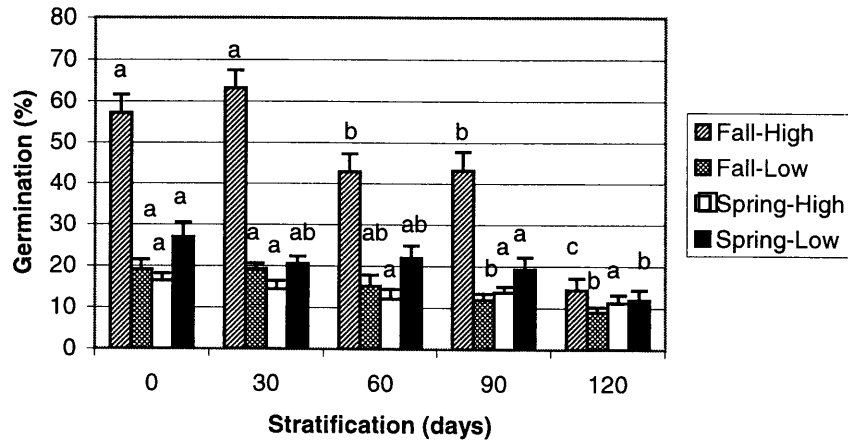
Methods

P. clutei was described by Nelson (1927) and named after the original collector, Willard N. Clute. The plant was classified as a subspecies of *Penstemon pseudospectabilis* by Keck (1937), then reclassified as an independent species by Clokey and Keck (1939) who considered it intermediate between *P. pseudospectabilis* ssp. *connatifolius* and *P. palmeri*. *Penstemon clutei* falls between these species in size and appearance, attaining heights of more

than 1 m with pink to purple flowers (Goodwin 1979, specimens at Deaver Herbarium, Northern Arizona University, Flagstaff). Goodwin (1979) and Phillips et al. (1980) described the habitat of *P. clutei* as limited to about 65 sq km in the cinder hills around Sunset Crater on soils covered with up to 25 cm of raw volcanic cinders of alkaline olivine basalt formed in the most recent volcanic eruption (A.D. 1046). An apparently disjunct population is located in cinder hills around Indian Flat, about 20 km northwest of Sunset Crater. *Penstemon clutei* is distributed in patches, with the greatest occurrence in areas of sparse herbaceous vegetation, past logging disturbance (stumps, skid trails), and recently killed snags (Phillips et al. 1992, Crisp 1996). The dominant vegetation is ponderosa pine, with scattered *Pinus edulis* and *Juniperus osteosperma*. Understory species commonly associated with *P. clutei* include *Chrysothamnus nauseosus*, *Fallugia paradoxa*, *Penstemon barbatus*, and *Verbascum thapsus*. An intensive survey of the southern habitat region by Phillips et al. (1992) also found *Rhus trilobata* occurring frequently with *P. clutei*, although no associated species were reliable *P. clutei* indicators. Because the age of the oldest *P. clutei* plants was estimated at 5 to 10 years, maintenance of a soil seed bank could be important for the regeneration of such short-lived plants (Phillips et al. 1992). The presence of a root-boring insect larva that could reduce the life span of the plants was also noted (Phillips et al. 1992). Pollination by both hummingbirds and bees has been observed in *P. clutei* (Phillips et al. 1980) and the closely related *P. pseudospectabilis* (Reid et al. 1988, Lange and Scott 1999). Phillips et al. (1992) summarized the legal protection history and status of *P. clutei*; it is currently considered a sensitive species with the USDA Forest Service (Arizona Game and Fish Department 1997).

The experimental studies described here were conducted on Coconino National Forest lands at O'Leary Peak, adjacent to Sunset Crater National Monument (Figure 1). The elevation of the study area is approximately 2100 m. Soils are cindery and deep, well-drained Vitrandic Ustochrepts and Typic Ustorthents (USDA Forest Service 1995). Weather records from Sunset Crater National Monument, 1 km south of the study area, show a bimodal precipitation pattern typical of southwestern forests. Annual precipitation averages 43.9 cm (1969–1993), occurring in winter and during the summer monsoon (July–September), but precipitation has varied widely in recent decades from 23.6

(a)



(b)

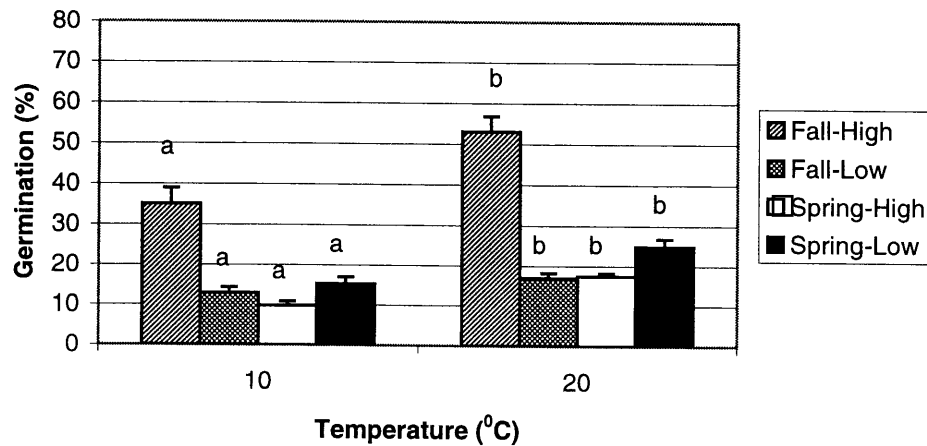


Figure 1. (a) Germination percentages of four *P. clutei* seed lots (fall/spring seasons, high/low elevations) stratified for different periods. Different superscript letters indicate significant differences between stratification periods within seed lots. Standard error bars shown. (b) Germination percentages of four *P. clutei* seed lots at two temperatures (all stratification periods combined). Different superscript letters indicate significant differences between temperatures within seed lots.

cm in 1989 to 66 cm in 1992. The average minimum temperature in January is -11°C and the average maximum temperature in July is 29°C .

Seed Germination Studies

Seed lots were collected from *P. clutei* plants on May 18 and October 18 in 1993. The May collection (spring) was from seed capsules that matured in 1992, and the October collection (fall) was from 1993 seed. Seeds were collected below and above 2,290 m elevation (low and high elevation, in the vicinity of O'Leary Peak, Coconino National Forest). A seed predatory insect was encountered in 70 percent of seed collections from 20 separate plants in May of 1996. The insect was identified by the USDA Systematic Entomology Laboratory as *Kleidocerys ovalis* Barber (Hemiptera: Lygaeidae), a seed bug. Subsequent informal examinations of *P. clutei* seed capsules have shown the bugs to be present every year but at lower rates of infestation than that observed in 1993.

Two lab germination experiments and a field seeding trial were conducted. The first lab study followed a fractional factorial experimental design for an exploratory test of multiple factors that were associated with triggering germination in other fire-adapted plant species. The defining relation for the 28-2V design was $I = ABCDG = ABEFH = CDEFGH$. The alias of any effect can be found by multiplying the effect by the words in the defining relation (Montgomery 1984:342), so the alias structure of C, for example, was $C = ABDG = ABCEH = DEFGH$. Study factors at high/low or presence/absence levels were (a) heat pulse, 70°C for 5 minutes which mimics low seed-bank temperature average from California chaparral (Keeley et al. 1985, Keeley 1987) and New Jersey grass studies (Cheplick and Quinn 1988); (b) ammonium-nitrogen, 77 ppm, based on post-fire NH_4^+ concentration in ponderosa pine (Covington and Sackett 1992); (c) charred litter (Keeley et al. 1985, Keeley 1987); (d) collection elevation, which is related to genetic diversity; (e) charred *P. clutei* litter; (f) nitrate-nitrogen, 40 ppm, based on post-fire NO_3^- concentration in ponderosa pine (Covington and Sackett 1992); (g) light, 12-hour photoperiod presence/absence (Meyer and Kitchen 1992); and (h) collection date, which is related to primary dormancy. Groups of 25 *P. clutei* seeds were placed on moistened filter papers in covered (not sealed) pyrex petri dishes and allowed to germinate in a Percival growth chamber at 15°C and 60 percent relative humidity. Germinated seeds were counted and removed weekly for 5

weeks, beginning January 21, 1994. Analysis of the design was done with Yates' algorithm (Montgomery 1984:337). The alpha level for all analyses was 0.05.

The second lab germination study tested *P. clutei* seeds from the four seed lots collected in 1993. Seeds were stored in paper bags at approximately 20°C until germination tests were conducted in 1997. Germination tests were conducted in climate-controlled incubators (Percival model I37-LL). Five cold stratification periods (0, 30, 60, 90, and 120 days) and two germination temperatures (10°C and 70°C) were tested. For cold stratification treatments, seeds were soaked in deionized water for 24 h, drained, placed in plastic bags, and stored in the dark at $3-4^{\circ}\text{C}$ for the length of the treatment period. At the end of the stratification period, 20-50 seeds were placed in petri dishes on moistened filter paper. Five dishes were used per treatment combination (seed lot X stratification X temperature). Two germination chambers were used and conditions were set at 30 percent relative humidity, 10 h of light exposure, and a constant temperature of either 10°C or 20°C .

Seeds were counted every 3 days and the number of germinated seeds was recorded until germination was complete (i.e., no additional seeds germinated between successive counts). Seeds were considered to have germinated when emerging radicals reached at least 2 mm in length. Germination (%) was calculated as the maximum number of seeds counted per dish divided by the total number of seeds present. Factorial analysis of variance (ANOVA) was used to test for main effects due to stratification period and growth chamber temperature. Analyses were conducted separately for individual seed lots. Data were square root transformed when necessary to meet analytical assumptions (normal distribution and similar variance). Main effects were tested at an alpha level of 0.05.

A field seeding trial was conducted as part of a mitigation effort for a natural gas pipeline project. The factors were disturbance and seeding at two levels each (presence/absence), applied in a split-plot design implemented on April 27, 1993, with 10 blocks consisting of two quadrats of 1 sq m each in the disturbed right-of-way and two in the adjacent undisturbed forest. Seeding with 50 stratified seeds was assigned randomly to one quadrat in each of the disturbed and undisturbed sites. The blocks were distributed at approximately 900 m intervals along the 11 km transect where the pipeline passed through *P. clutei* habitat. No

seedlings were found on quadrat inventories in June and September, so the experiment was repeated on October 2, 1993, using unstratified seeds from a September, 1993, seed collection along the pipeline. One hundred seeds per sq m were placed in new quadrats adjacent to the original locations. Quadrats were inventoried in June and August of 1994.

To minimize mortality to the species, the role of vegetative propagation in *P. clutei* was not assessed directly. Several dead *P. clutei* were excavated and found to have long rhizome-like roots. However, the small "seedling" *P. clutei* plants observed on the plots each summer appeared to be actual seedlings starting with cotyledons.

Prescribed Burning

An experiment on the effects of prescribed burning on the *P. clutei* community was established in 1994. Forty *P. clutei* plant-centered plots were established between July 29 and August 1 of 1994 at the same sites described for seed collection in the first germination studies. Because the sample plots were centered on existing plants, a technique often used in rare-plant studies (Travis and Sutter 1986), all data were calculated in terms of plants per plot and the actual absolute density of *P. clutei* and other species (plants per ha) in the study sites was unknown. Each plot was a 2.5 m radius circle (area = 19.6 sq m) centered 0.3 m northwest of an existing *P. clutei* plant. All species were tallied within each plot. *P. clutei* was tallied in four categories: seedling, second-year plant, mature plant, and dead. Field experience indicated that the distinctions between the living plant categories were approximate. Fuels were measured on two perpendicular planar transects established SE-NW and SW-NE on each plot following the methods of Brown (1974) and Sackett (1980). Plots were randomly selected for burn or control treatments. Burning was conducted on September 26, 1994, between 9:30 AM and 2:30 PM. Temperatures ranged from 21.1 to 23.9° C, winds averaged 8.5 km per hour (max 13.6 km/h), and relative humidity decreased from 26 to 20 percent during the burning period. Flame lengths averaged 29.1 cm, corresponding to an average fireline intensity of 17.7 kW per m (Agee 1993). Burn season effects were tested on a second experimental site immediately north of the lower elevation fall burning site. Forty new plots were established April 6–7 of 1995. Twenty randomly selected plots were burned on April 27, 1995, between 9:30 and 11:30 AM. Temperatures ranged from 12.8 to 16.1° C,

winds averaged 8.5 km per hour (max 17 km/h), and relative humidity decreased slightly from 28 to 27 percent during the burning period. Flame lengths averaged 34.7 cm, corresponding to an average fireline intensity of 25.9 kW per m (Agee 1993). The fall burn plots were remeasured on July 10–11, 1995. All 120 plots, including spring and fall burns, were remeasured August 28–September 4, 1996, August 5–7, 1997, and August 20–25, 1998.

Changes in *P. clutei* density, species richness, and fuels were analyzed with repeated measures analysis of variance (Systat 8.0, SPSS Science, Chicago). Data were square-root transformed to meet ANOVA assumptions. Community data were assessed with nonmetric multidimensional scaling, a nonparametric ordination procedure (PC-Ord 4.0, MjM Software, Gleneden Beach, Oregon). Indicator values were calculated for individual species based on relative abundance and relative frequency. A Monte Carlo procedure with 1000 iterations was used to assess the probability of encountering indicator values by chance.

Belowground Competition

In 1997 (October 1–10) we established eight new experimental plots within the low-elevation burning study area, each paired with a nearby control plot from the original burn experiment. The belowground effects of tree removal were simulated by digging a narrow trench approximately 1 m deep around each plot. Trenches were located 50 cm outside the plot boundary to avoid physical disturbance within the measured area and were lined with plastic sheeting to minimize tree root regrowth (Milne 1979). Trenches were backfilled immediately after lining. Plots were remeasured on August 25, 1998, September 1, 1999, and August 15, 2000. *P. clutei* density, species richness, fuels, and community data were analyzed as described for the prescribed burning study above.

Results

Seed germination in the fractional factorial experiment ranged from 8 to 80 percent. Analysis of variance for main effects and two-way interactions indicated that only the pre-existing elevation and collection date factors were statistically significant, with fall seeds and high-elevation seeds germinating best. Tests of statistical significance in the fractional factorial design rely on the assumption that higher-order interactions may be considered as error, in the absence of a pure error term, so the ANOVA *p* values should be treated with caution. Because the collections were not

replicated, the identification of "elevation" and "season" as causal factors of differences between seed lots is tenuous.

The second germination experiment showed that cold stratification significantly affected *P. clutei* germination for three of the four seed lots (Figure 1). In all cases, mean germination decreased as cold-stratification period increased from 0 to 120 days. Decreases were most dramatic for the fall high-elevation collection, which had consistently higher germination than the other seed lots under all treatment conditions. Germination for this lot decreased almost 50 percent as the stratification period was increased from 0 to 120 days. Although during stratification seeds were kept in the dark and at temperatures just above freezing (3–4° C), germinated seeds were observed in the stratification bags at 120 days. Temperature significantly affected germination of all seed lots (Figure 2). On average, germination was increased by 9.7 percent when germination temperature was kept at 20° C compared with a constant 10° C. Similar to cold-stratification tests, the difference in germination between the two temperature regimes was most dramatic for the fall high-elevation seed lot compared with the other collections.

The field seeding trial resulted in extremely low seedling establishment. No seedlings were established following the April 1993 seeding. Seedlings established on only three seeded quadrats and no unseeded quadrats following the October 1993 seeding. The total establishment rate was 0.6

percent on the disturbed pipeline quadrats and 0.1 percent on the undisturbed quadrats. These values were considered too low for meaningful statistical analysis.

Prescribed Burning

Contrary to expectations, burning caused a significant decline in *P. clutei* density, dropping from an average of 6.5 plants per plot before burning to 1.6 plants per plot at the end of the first growing season after the fire, a 75 percent reduction (Table 1). Season of burning (fall/spring) and site elevation (low/high) were not significant factors. *P. clutei* densities also declined over the study period in two of the three control sites. The low-elevation fall control declined by 53 percent and the low-elevation spring control declined by 75 percent between 1994-95 and 1998. Only the high-elevation fall control maintained a nearly constant *P. clutei* density (2% decline). Coupled with a recovery of *P. clutei* densities in the burned plots, *P. clutei* densities in burned and control plots differed by less than 1 plant per plot by 1998, averaging 2.1 and 3.0 plants, respectively. Litter (total of freshly fallen as well as decomposing material) declined significantly in the burned plots, with an average reduction of 2.0 cm, and the litter depth remained constant through 1998. Species richness was not significantly affected by the burning treatment. Plant community ordinations indicated minor shifts between treatments and years. Burn treatment plots tended to group together by year, whereas control plots were generally clustered.

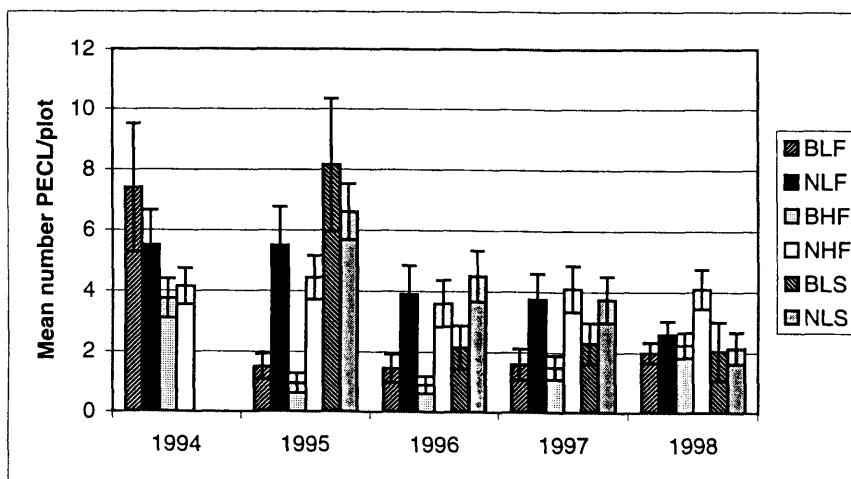


Figure 2. Changes in burn and control plots from 1994 through 1998. B = burn, N = no-burn (control), L = low elevation, H = high elevation, F = fall burning season (September 1994), S = spring burning season (April 1995). Standard error bars shown.

Table 1. Density of *P. clutei* (PECL, number per 19.6 sq m plot), species richness, litter depth, and woody fuel. N = 20 in each category, N/A = not available. Data shown are mean, (standard error), and min-max. The pretreatment year (Year 1) was 1994 for the fall burn and 1995 for the spring burn, so the fall burn sites have 5 years of data (1994–1998) whereas the spring burn sites have 4 years of data (1995–1998).

	Pretreatment (Year 1)	Year 2	Year 3	Year 4	Year 5
Low-Elevation Fall Burn					
PECL density	7.4 (2.1) 1-34	1.5 (0.4) 0-6	1.5 (0.5) 0-8	1.6 (0.5) 0-8	2.0 (0.3) 0-5
Spp. richness	6.1 (0.4) 3-10	4.6 (0.5) 2-9	8.0 (0.8) 3-14	7.5 (0.7) 3-14	6.4 (0.5) 2-10
Litter (cm)	2.6 (0.4) .6-6.2	0.9 (0.1) .1-2.0	0.9 (0.2) 0-3.2	0.6 (0.1) 0-2.1	1.0 (0.2) .1-2.7
Low-Elevation Fall Control					
PECL density	5.5 (1.2) 1-22	5.5 (1.3) 0-18	3.9 (1.0) 0-14	3.8 (0.8) 0-13	2.6 (0.4) 0-7
Spp. richness	6.2 (0.4) 2-9	4.9 (0.3) 1-8	7.7 (0.8) 3-12	7.7 (0.8) 0-13	6.7 (0.5) 2-10
Litter (cm)	2.9 (0.3) .8-6.4	2.6 (0.3) .7-5.8	2.5 (0.4) .5-5.8	1.9 (0.3) .2-5.1	2.0 (0.3) .3-5.6
High-Elevation Fall Burn					
PECL density	3.8 (0.7) 1-12	1.0 (0.3) 0-6	0.9 (0.3) 0-5	1.5 (0.4) 0-7	2.3 (0.4) 0-7
Spp. richness	7.0 (0.5) 3-11	4.6 (0.4) 0-7	8.5 (0.8) 0-15	8.8 (0.7) 1-13	7.8 (0.7) 0-11
Litter (cm)	2.6 (0.5) .4-8.2	0.6 (0.1) .1-1.6	0.6 (0.1) .1-1.5	0.5 (0.1) .2-1.2	0.4 (0.1) 0-1.7
High-Elevation Fall Control					
PECL density	4.2 (0.6) 1-11	4.5 (0.7) 1-12	3.6 (0.8) 0-14	4.1 (0.8) 0-13	4.1 (0.6) 0-9
Spp. richness	7.6 (0.4) 5-12	6.2 (0.3) 4-8	9.3 (0.8) 4-16	9.1 (0.9) 4-15	7.8 (0.5) 3-12
Litter (cm)	3.2 (0.4) .4-6.7	2.6 (0.3) .8-6.7	3.4 (0.6) .6-8.8	2.6 (0.4) .7-6.1	2.2 (0.4) .2-5.4
Low-Elevation Spring Burn					
PECL density	8.2 (2.2) 1-36	2.2 (0.7) 0-13	2.3 (0.7) 0-11	2.1 (1.0) 0-15	N/A
Spp. richness	N/A	7.7 (0.7) 2-15	7.4 (0.6) 4-14	5.8 (0.5) 2-10	
Litter (cm)	2.3 (0.4) .2-6.3	0.6 (0.1) 0-1.7	0.6 (0.1) 0-1.5	0.5 (0.1) 0-1.7	
High-Elevation Spring Control					
PECL density	6.6 (0.9) 1-14	4.5 (0.8) 1-16	3.8 (0.8) 0-14	2.2 (0.5) 0-8	N/A
Spp. richness	N/A	6.3 (0.6) 1-11	6.5 (0.6) 2-11	4.8 (0.5) 1-8	
Litter (cm)	2.6 (0.4) .5-6.8	2.0 (0.3) .6-5.5	1.7 (0.3) .4-5.7	1.9 (0.4) .2-7.4	

Removing annual species from the analysis eliminated differences in treatment patterns, suggesting that the shifts were related to annual climatic variation (Table 2). Indicator species for the burn and control treatments are identified in Table 3.

Belowground Competition

P. clutei density in the eight trenched plots (average 7.9 plants per plot) was higher than that of the eight nearest control plots (3.4 plants per plot) even prior to treatment in 1997, but the difference was not statistically significant (Figure 3). By 1998, the trenched *P. clutei* density averaged 8 plants but the control density dropped to 2.5 plants, a significant difference. In 1999, *P. clutei* densities increased sharply in both trenched and

control plots, but the rise was much steeper in the treated plots (104.9 plants) than the controls (14.0 plants). The monsoon season in 1999 was the wettest of the 1992–2000 study period, with 37.2 cm of precipitation from June through September (Table 2). The 1999 monsoon also comprised the highest proportion (78%) of annual precipitation during the study period. In 2000, a dry year, *P. clutei* densities declined to an average of 30.6 plants in the trenched plots and only 1.5 plants in the controls. No notable *P. clutei* increase occurred on the disturbed trench areas outside the plots. Community ordination indicated a minor separation between the trenched and control plots, but with considerable overlap. Indicator species for trenched plots are shown in Table 1.

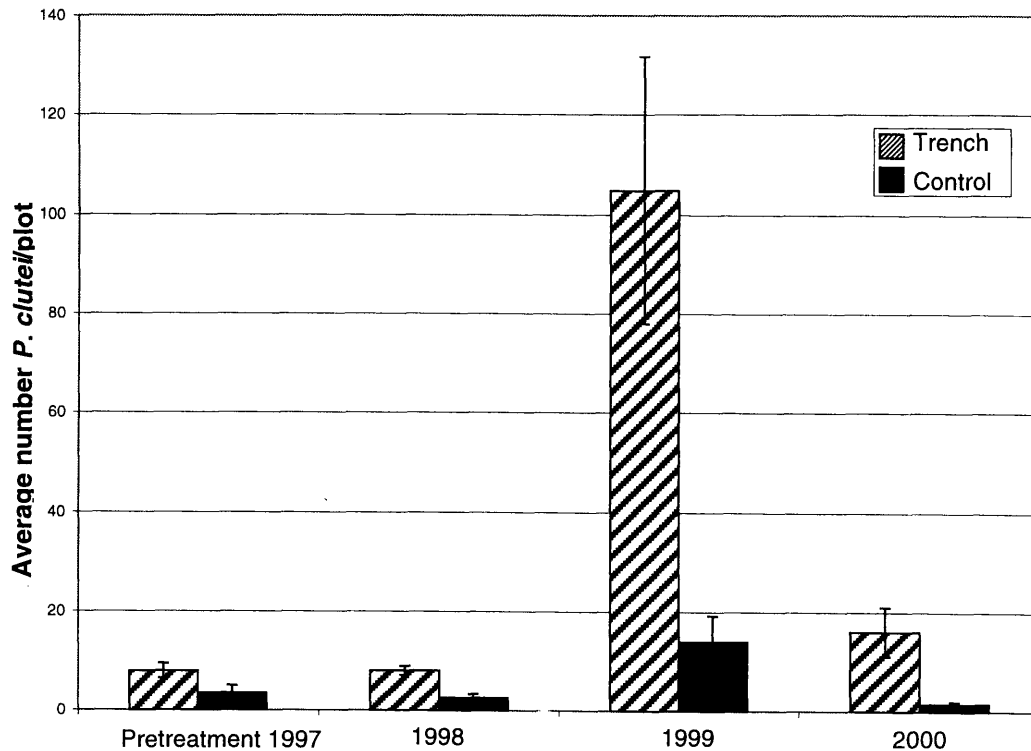


Figure 3. *P. clutei* density increased substantially in 1999—a year with excellent growing season moisture—in both trenched and control plots, but the increase in the trenched plots was eight times greater than in the controls. *P. clutei* densities declined sharply in 2000, a dry year, but trenched densities remained significantly higher than controls.

Discussion

The reasons why *P. clutei* is sparsely distributed in nature were not completely clarified by this set of studies. *P. clutei* germinated readily with moisture under lab conditions with little or no innate dormancy necessary. Increasing periods of stratification, in fact, decreased germination, contrary to the experience of Plants of the Southwest (Santa Fe, New Mexico). These germination characteristics are adaptive in light of the fact that warm, moist soils are typically present during the monsoon season (late June through September) in the Sunset Crater area and that we have observed most seedling regeneration to occur in the monsoon season, rather than the spring. However, in contrast to the high lab germination rates, field establishment of the species on seeded quadrats was dismal (0.4%). The long-term demographic

data (1993–2000) from the burning and trenching control plots also show a general decline in *P. clutei* numbers over time, and no counteracting increase in *P. clutei* density was observed outside the permanent plots. Variability in germination among seed lots collected at different dates and elevations suggests that genetic or environmental factors may influence germination.

Trenching was the only experimental treatment that resulted in highly significant increases in *P. clutei* density, but our approach had many limitations due to the small scale of the experiment ($N = 16$). The control plots started out with a lower average density than the trenched plots and we did not quantify differences in soil moisture, physiological processes, plant vigor, biomass, flowering, pollination, seed production, viability, predation, soil seed bank, or plant herbivory.

Table 2. Annual and monsoonal (June–September) precipitation at Sunset Crater National Monument from 1992 through 1999. Data from National Climatic Data Center, Asheville, NC.

	1992	1993	1994	1995	1996	1997	1998	1999
Annual (cm)	66.0	47.0	41.1	29.5	32.3	51.8	47.3	47.4
June–Sept (cm)	18.2	12.8	23.1	11.6	21.6	26.7	25.2	37.2

Table 3. Species found in burning and trenching experiments. Species found on burn plots only are shown with *, species found on trench plots only are shown with **. Species identified as strong and significant treatment indicators, based on relative abundance and relative frequency, are shown with the indicator value (maximum 100) and p value.

Family	Species	Indicator burn	Indicator control	Indicator trench
Burn	Indicator			
Control	Indicator trench			
Amaranthaceae	<i>Amaranthus albus</i>			
Asclepiadaceae	<i>Asclepias subverticillata</i>			
Asteraceae	<i>Agoseris</i> sp.**			
	<i>Artemisia dracunculus</i> *			
	<i>Bahia dissecta</i>			
	<i>Brickellia chlorolepis</i>			
	<i>Brickellia grandiflora</i>			
	<i>Chrysothamnus nauseosus</i>			
	<i>Cirsium wheeleri</i> *			
	<i>Conyza schiedeana</i>			
	<i>Erigeron</i> sp.			
	<i>Helianthus petiolaris</i> **			
	<i>Heterosperma pinnata</i> *			
	<i>Hieracium fendleri</i>			
	<i>Lactuca serriola</i>			
	<i>Machaeranthera canescens</i> **			
	<i>Senecio spartioides</i> *			
	<i>Solidago</i> sp.**			
	<i>Tragopogon dubius</i>			
Berberidaceae	<i>Berberis fremontii</i> *			
Brassicaceae	<i>Arabis fendleri</i>			
	<i>Physaria newberryi</i>			
	<i>Schoenocrambe linearifolia</i>		30.0 / .02	
Cactaceae	<i>Opuntia</i> sp.*			
Caryophyllaceae	<i>Drymaria leptophylla</i> **			
Chenopodiaceae	<i>Chenopodium album</i> *			
	<i>Chenopodium desiccatum</i> *			
	<i>Chenopodium graveolens</i>			
Commelinaceae	<i>Commelina dianthifolia</i>			
Euphorbiaceae	<i>Chamaesyce revoluta</i>			
	<i>Chamaesyce serpyllifolia</i>			
	<i>Euphorbia albomarginata</i>			
	<i>Euphorbia lurida</i>			
Fabaceae	<i>Phaseolus angustissimus</i>			
Fumariaceae	<i>Corydalis aurea</i> **			
Geraniaceae	<i>Geranium caespitosum</i>			54.3 / .006
Grossulariaceae	<i>Ribes cereum</i>			
Hydrophyllaceae	<i>Nama dichotomum</i>			
	<i>Phacelia crenulata</i>			
Lamiaceae	<i>Monardella odoratissima</i>			
Loasaceae	<i>Mentzelia collomiae</i>			
Molluginaceae	<i>Molluga cerviana</i>			
Nyctaginaceae	<i>Mirabilis decipiens</i>	29.3 / .004		
	<i>Mirabilis linearis</i>			

Table 3 (continued)

Family	Species	Indicator burn	Indicator control	Indicator trench
Onagraceae	<i>Oenothera caespitosum</i>			
Pinaceae	<i>Pinus edulis</i> **			
	<i>Pinus ponderosa</i>			
Poaceae	<i>Aristida arizonica</i> *			
	<i>Bouteloua gracilis</i> *			
	<i>Elymus elymoides</i>			
	<i>Muhlenbergia minutissima</i>			
	<i>Muhlenbergia montana</i>			
	<i>Poa fendleriana</i> *			
	<i>Stipa comata</i>			
Polemoniaceae	<i>Ipomopsis arizonica</i> *			
Rosaceae	<i>Fallugia paradoxa</i>			
Rubiaceae	<i>Galium wrightii</i> *			
Scrophulariaceae	<i>Linaria dalmatica</i>			
	<i>Verbascum thapsus</i>			
	<i>Penstemon barbatus</i>			
	<i>Penstemon clutei</i>		57.6 / .001	85.7 / .001
Solanaceae	<i>Physalis hederifolia</i>			

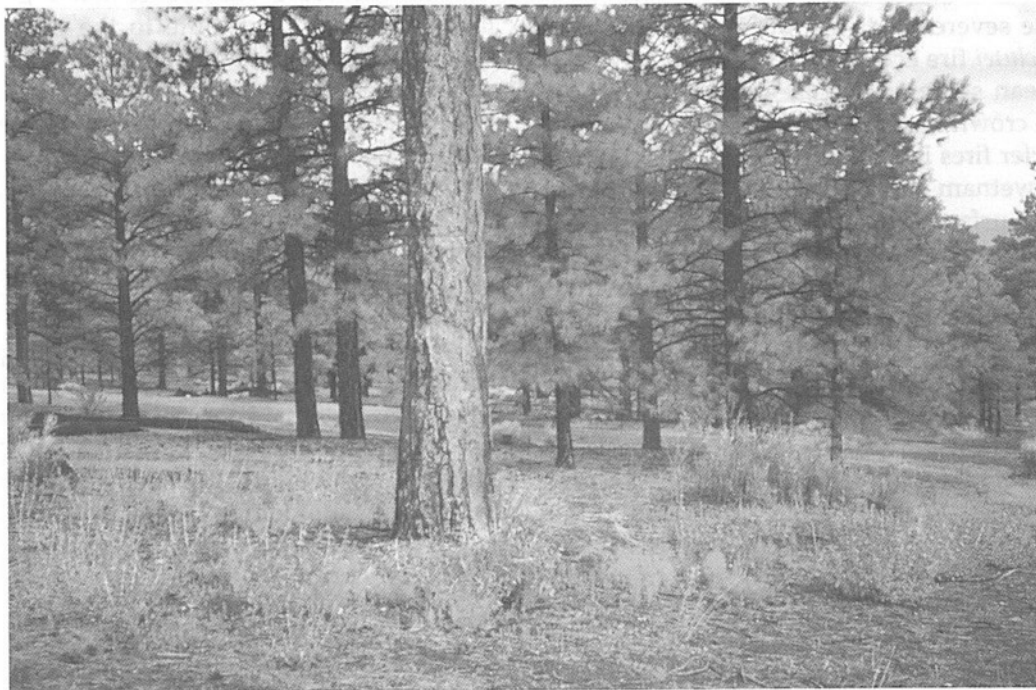


Figure 4. Vigorous *P. clutei* plants growing around the base of a mature ponderosa pine tree that died around 1997–1998 in the lower elevation study area (photo Oct. 1999). This example of *P. clutei* response to the removal of tree competition may be a natural analog to the effects of the trenching experiment.

Therefore the mechanisms underlying the increase remain uncertain and further research will be useful. The trenching process itself and the plastic liner may have affected plot hydrology apart from simply cutting root competition, but the effect may have been just as likely to keep water out as to keep it in. Three preliminary conclusions were drawn from the trenching study: (a) cutting root competition has a significant positive effect on *P. clutei* reproduction, (b) the trenching effect was more pronounced in a year with favorable climate (1999) but was also evident in a less-favorable year (1998) and was sustained into a dry year (2000), and (c) root competition appears to be much more important for *P. clutei* response than light competition, consistent with the results reported by Riegel et al. (1995). We did not manipulate the light environment, but still had a highly significant population increase.

Although prescribed burning decreased *P. clutei* density, contrary to the initial research hypothesis, the historic role of fire in the ponderosa pine ecosystem may not have been adequately simulated in our experiment. The prescribed fires were of low intensity and did not kill any trees, unlike the severe wildfires that led to questions about *P. clutei* fire ecology in the first place. Prior to European settlement there is no evidence for extensive crown fires at the scale of the Burnt and Hochderrfer fires in southwestern ponderosa pine forests (Swetnam and Baisan 1996). But naturally occurring surface fires in relatively undisrupted ponderosa and related forests do create patchy tree mortality at scales ranging from individual trees to a few hectares (Fulé and Covington 1997, Fulé et al., unpublished data). These patches of fire-caused mortality and other tree deaths from windthrow, insects, pathogens, or lightning may have comprised important disturbance patterns that facilitated *P. clutei* regeneration. Figure 4 shows vigorous *P. clutei* regeneration around the base of a recently deceased mature ponderosa pine tree, possibly a natural analog to the trenching experiment.

Management Recommendations

The high year-to-year variability in *P. clutei* densities and the general trend in the control plots toward declining *P. clutei* density are issues of concern for sustaining this rare species. Results from this study and others (Goodwin 1979, Phillips et al. 1992, Crisp 1996) support a positive relationship between *P. clutei* abundance and dis-

turbance, within certain parameters.

Low-intensity surface fire alone appears unlikely to benefit *P. clutei*, although there are other valuable reasons for burning in the forest environment. However, more intense prescribed fires that kill some trees or a combination of thinning trees and burning may be promising treatments that could facilitate *P. clutei* regeneration and simultaneously meet other ecosystem management goals, such as restoring historic forest structure and fire disturbance regimes. Other methods of simply killing overstory trees, such as snag creation through cutting cambium or inducing insect attack, may also benefit *P. clutei* regeneration.

Even severe ground disturbance may create environments that benefit *P. clutei* vigor and reproduction. Many *P. clutei* plants observed on the Transwestern pipeline and on roadcuts were among the most vigorous in the region. However, repeated physical impacts that destroy established plants, such as off-road vehicle use in the Cinder Hills, appear to reduce *P. clutei* populations.

The management of a rare species that is adapted to disturbance is difficult because "protection" by excluding disturbance that might damage the plants may contribute to the decline of the species. The Coconino National Forest has had a proactive management policy of encouraging experimentation and monitoring of the species. Further management-level experiments focusing on restoration of historic disturbance patterns and understanding the mechanisms of *P. clutei* response would be valuable.

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