ORIGINAL RESEARCH

Survival of the rare *Packera layneae* (Asteraceae), under chaparral and after fire

DEBRA R. AYRES^{1*}, VIRGINIA MEYER², MELANIE GOGOL-PROKURAT³, AND LAUREN FETY⁴

¹California Native Plant Society, El Dorado Chapter, www.eldoradocnps.org

² Sacramento City College, 3835 Freeport Blvd, Sacramento, CA 95582, USA

³ California Department of Fish and Wildlife, 1700 9th Street, Sacramento, CA 95811, USA

⁴ The Conservation Fund, 215 West Standley St, Suite 11, Ukiah, CA 95482, USA

*Corresponding Author: drayres@ucdavis.edu

Conservation of rare plants requires an understanding of how the species responds to natural and artificial disturbance dynamics. For chaparral species this includes the natural disturbances of fire and shrub canopy closure during the interfire period, and the effect of shrub clearing for fuel reduction. Packera layneae is a federally listed rare herbaceous perennial subject to all these disturbances; its center of distribution is upon the gabbro soils surrounding Pine Hill in western El Dorado County, CA an area known as a hotspot of botanical diversity. Combining genetic data with mapping following a 2007 wildfire in Shingle Springs, we found that the species survives fire and chaparral overgrowth due to underground rhizomes and caudices that resprout after fire and enable its persistence under dense chaparral canopies; as well, seed recruitment of new genetic individuals occurred within discrete patches. Seedlings were not found the spring following the 2007 fire, suggesting fire killed the soft-walled seeds. Surveys across the Pine Hill area from 2005-2007 found populations flowering and producing seed in recently burned and cleared areas as well as under mature chaparral; however, the proportion of plants flowering decreased as shrub density increased. From our 2019 surveys of a new 4.25 km fuel break around the perimeter of Pine Hill in Rescue, CA (0.983 km²) we found the species resprouted from plants growing under the dense chaparral canopy on the southern, eastern, and western aspects but did not occur on the northern exposure or under dense oak canopy. As the seedling regeneration niche is unknown, preservation of established populations is vital to the long-term persistence of the species.

Key words: El Dorado County, fire ecology, gabbro soil, Packera layneae, Pine Hill

Packera layneae (Greene) W.A. Weber & A. Love (Asteraceae), Layne's ragwort, is a federally listed threatened and state listed rare plant that occurs in the Sierra Nevada foothills of central California. It is a perennial herb that dies back in the winter and emerges from the soil in mid-March. It reportedly resprouts from a tap-rooted caudex, grows 4-7+ dm tall, and flowers from April to June (Trock, 2012). The center of its distribution is upon the gabbro-derived soil intrusion around Pine Hill in western El Dorado County (see Klip et al. 2020, this issue for additional description) where the species is found flowering in openings within and adjacent to chaparral. It also has limited occurrence on serpentine soils in Tuolumne and gabbro and serpentine soils in Yuba County (Williams 2014). The species is primarily outcrossing, and has the ability to disperse its seeds on the wind (Marsh and Ayres 2002); however, Williams (2014) found most seeds dispersed within 1 m of the maternal plant. Genetic analyses revealed pronounced genetic differences among the populations in the three geographically distant counties, and between two El Dorado County populations separated by 5.5 km (Marsh and Ayres 2002).

Chaparral is a shrub-dominated community that periodically burns and re-establishes after fire. Species adapted to these dynamics must survive fire by re-sprouting or arising from seeds in the soil, and survive the subsequent closure of the shrub canopy lasting several decades. Early reports (Baad and Hanna 1987) speculated that *P. layneae* was an early successional species occupying temporary openings in the chaparral that was eliminated as the chaparral regrew after fire. On the other hand, from 2005 to 2007, we found *P. layneae* in both undisturbed, mature chaparral, as well as in previously burned or mechanically cleared areas, suggesting it can persist under varying disturbance regimes. The questions of whether and how the species survives fire, clearing, and a long interfire period (90+ years) under a dense chaparral canopy are questions addressed in this paper.

METHODS

We evaluated population size, flowering, and seed output in plots representing varying levels of disturbance from 2005–2007. Plant survival and occurrence were evaluated following a 2007 wildfire in Shingle Springs, CA and 2017–2019 shrub clearing to create a fuel break around the perimeter of Pine Hill, Rescue, CA; the two sites are separated by approximately 8 km (Figure 1).

Disturbance study

We collected data at 33 plots where *P. layneae* was present from 2005–2007, including burned, mechanically cleared, and undisturbed mature chaparral. Data collected at each plot included shrub cover estimates, number of *P. layneae* plants, metrics of plant size and flowering, and seed output. For a full description of methods, see Gogol-Prokurat (2009).

Post-fire study

On 7 June 2007, the 12 ha (30 acre) Palmer wildfire broke out on the Ponderosa 50 parcel of the Pine Hill Preserve in Shingle Springs, a 20 ha preserve, due north of Highway 50 and 400 m west of Ponderosa Road (hereafter Pondo), a site dominated by *Arctostaphylos viscida /Adenstoma facsicularis* chaparral. Tree ring counts of a *Quercus kelloggii* individual

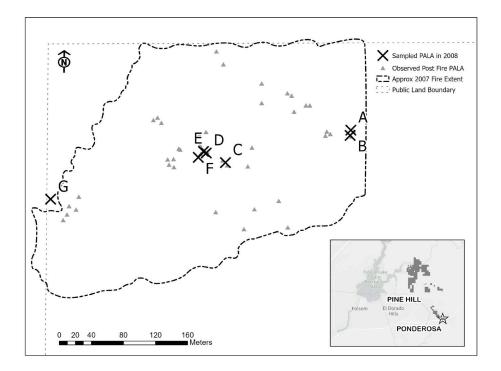


Figure 1. Map of *Packera layneae* within the Ponderosa-Palmer Fire in Shingle Springs, CA. Inset locality map shows the Pondo and Pine Hill study sites; the dark multi-square areas are the units of the Pine Hill Preserve on the gabbro soil intrusion.

killed in the fire indicated the tree was over 90 years old at time of death, suggesting the chaparral had last burned in 1917 or earlier. We surveyed the burned area 14 April 2008. *Packera layneae* rosettes were aggregated into 42 discrete patches, that were mapped, scattered throughout the burned area (Figure 1). The number of rosettes was counted in 16 patches. Seven patches were chosen for genetic analysis, 6 of which were within the burned area (patches A-F); patch G was outside the fire's perimeter and was densely flowering; the number of flower heads on 10 flowering stems, haphazardly chosen, were counted; heads per stem ranged from 2 to 13 (average = 5). None of the rosettes in the burned area flowered. The *P. layneae* rosettes were clearly resprouts, not seedlings, as the rosettes were robust, with many leaves, and lacked cotyledons.

Genetic analyses

In May 2008, we collected newly emerged leaves, one per rosette, from the 7 mapped patches, sampling 4–10 rosettes per patch (n = 39) for genetic fingerprinting. The burned patches were haphazardly chosen along a line through the center of the population (Figure 1). We sampled rosettes at the north-south and east-west limits of each chosen patch, as well as in the patch center, and counted the rosettes included in the patch. Each sample's location was determined and documented by GPS. Samples were placed on ice and taken to the lab at UC Davis. DNA extraction and PCR reactions were performed according to the protocols of Marsh and Ayres (2002). Due to limited funding, PCR was performed using only 2 ISSR

primers, 807 and 823 that had each produced 3 polymorphic bands in previous work (6 bands total) (Marsh and Ayres 2002). We ran reactions twice to verify band reproducibility.

To facilitate identification of genets (genetic individuals) and ramets (multiple rosettes from a single genet), we analyzed the presence/absence (1/0) matrix of the 6 polymorphic bands for genetic distance using the Euclidean distance coefficient and the resulting distance matrix was then used to construct a dendrogram using NTSYS-pc, version 2.01d (Rohlf 1993). Those rosettes within a patch that had identical or different genetic fingerprints were readily identified.

Mapping distribution on Pine Hill

From 2016 to 2019, the El Dorado Chapter of the California Native Plant Society (CNPS) collaborated with the California Department of Fish and Wildlife (CDFW) and the California Department of Forestry and Fire Protection (CalFire) to establish a 21-m firebreak along the 4.25 km perimeter (area surveyed = 8.9 ha) of Pine Hill to prevent fire from moving onto the Pine Hill Preserve from private land and vice versa (see Figure 1, Klip et al. 2020, this issue). The fire break was created by hand crews with chainsaws who cut down all shrubs taller than 30 cm followed by pile burning of the debris. The CNPS's goal was to survey for rare plants, map their distribution along the perimeter (see Klip et al. 2020, this issue) and locate areas free of rare plants to place the burn piles. There is no record of when the perimeter last burned in a wildfire, although there is some evidence for fuel break burning in 1975 and 1983 (Mario Klip, CDFW, personal communication).

We conducted botanical surveys in 2017 along created pathways before general clearing and after clearing was completed in 2019. The CNPS waited to begin the surveys until leaves of *Wyethia reticulata* and *P. layneae* emerged in the spring and became identifiable; this occurred in mid-March. A cadre of volunteers was formed, team leaders were trained by experienced botanists, and 12 survey days were held from 16 March through 11 April 2017. After the perimeter had been cleared, botanists from the El Dorado Chapter of the CNPS returned and completely surveyed and mapped the perimeter for all rare plant species in spring 2019.

RESULTS

Disturbance study

P. layneae populations were identified in areas with a history of recent burning and clearing as well as in undisturbed chaparral. There was no significant difference in the number of plants found in populations regardless of disturbance history (Table1; Gogol-Prokurat 2009); however, the proportion of plants flowering decreased as shrub density increased (Figure 2).

Post-fire study

In 2008, small rosettes of *P. layneae* were found in 42 discrete patches; the total area occupied by patches (0.02 ha) was 0.17% of the total burned area of 12 ha. Each rosette in a patch was separated by 0.5–4 m (Figure 1). The number of rosettes per patch ranged from 8 to 173, with an average of 42.4 small rosettes/patch, for a total of 1,782 rosettes. Rosette

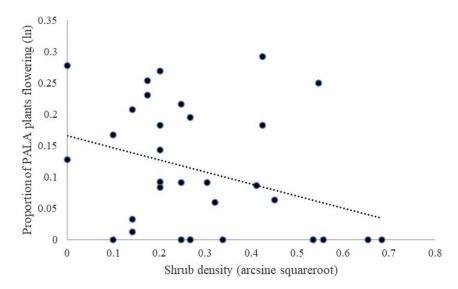


Figure 2. Relationship between chaparral shrub density and the proportion of *P. layneae* plants flowering per population, 2005–2007 surveys of populations throughout the gabbro soil, El Dorado County, CA.

Disturbance type	# of Plots	Average (SE) % shrub cover	Range of shrub cover	Average (SE) number of plants/m ²	Range of plants/m ²	% of plants flowering	Average (SE) plant height (cm)	Seed output (SE) per plant
Undisturbed	10	22 (3.6)	7–42	0.15 (0.05)	0.005 - 0.52	17	54 (2.5)	520 (59)
Cleared	15	12 (2.4)	2–29	0.49 (0.21)	0.03-2.46	21	48 (3.8)	600 (90)
Burned	8	6 (0.7)	2-8	0.32 (0.16)	0.04-1.25	16	50 (2.0)	580 (65)

Table 1. Summary of plant density and flowering in 33 occupied plots, 2005–2007 surveys of populations throughoutthe gabbro soil, El Dorado County, CA.

density over the entire burned area was 0.015 rosettes/m² while density within patches was 14 rosettes/m². The six patches chosen for genetic analysis had an average of 63 rosettes/ patch, within an average area of 4.6 m² (Table 2). No seedlings were found in the spring immediately following fire. None of the rosettes in the burned area flowered in the year following fire; 2 years after fire flowering was abundant (personal observation).

Genetic analyses

Plants arising from a single sexually produced seed are genetic individuals that are termed "genets." If the plant expands clonally, then the clonal offshoots from a genet will have the identical genotype and are termed "ramets." We indentified 19 unique genotypes in 39 samples. Twenty-nine samples with either a unique genotype or that occurred in different patches were considered to be genets that arose from separate seed establishment events

			•			
Patch	Patch size (m ²) burned plots	# of Samples per Plot	# of genets per plot	Max distance between ramets (m)	# of rosettes/ m ² burned patches	# of Genets/ m ² burned patches
A	5.70	5	1	3.3	4.6	4.56
В	5.84	5	4	2	4.1	3.29
С	7.74	6	6	No ramets	22.3	22.34
D	1.00	4	3	0.36	20.9	15.67
Е	1.75	5	5	No ramets	12.0	12.03
F	5.61	5	2	1.8	20.5	10.26
G (unburned)	N/A	10	8	N/A	N/A	N/A
Average (SE) for burned patches	4.61 (1.08)	5.00 (0.26)	4.14 (0.76)	1.86 (0.60)	14.10 (3.42)	11.36 (3.26)

 Table 2. Summary of 2008 genetic analyses, mapping, and rosette densities of 7 Packera layneae patches at Ponderosa Preserve, Shingle Springs, CA following a 2017 wildfire.

(Table 2). All samples in patches C and E were genetically different and therefore were genets. Genetically identical samples from within a patch could have resulted by chance or due to clonal expansion of a single genet, i.e. ramets. The odds of obtaining 2 genetically identical samples by chance, as in patches B, D, and G were 0.23 (19/39)*(18/38); the odds of 4 identical samples as in patch F were 0.047 (19/39)*(18/38)*(17/37)*(16/36); and the odds of 5 identical samples as in patch A were 0.020. The distances separating presumed ramets were 2m to 3.3m in patch A and 0.80m to 2m for patch F. As 74% (29/39) of the samples were genets the population size is estimated to be 1,324 genets (0.74*1,782).

Mapping distribution on Pine Hill

Packera layneae was found resprouting along the cleared perimeter on the sunnier exposures, South-, East-, and West-facing slopes previously covered by dense chaparral; there were no occurrences on the shady northern perimeter or in the oak woodland on the eastern exposure. In 2019, two years after clearing, seedlings were observed in the cleared SE corner (pers. obs.). As we did not record the presence of seedlings in the 2017 survey, it is unknown yet whether the species recruits by seed under the dense chaparral canopy.

DISCUSSION

Packera layneae survives both fire and clearing due to underground structures protected by the insulation of 3 to several cm of soil. Clonal expanse up to 3 m, based on genetically identical ramets occurring in the same patch, indicates that the species is capable of rhizomatous growth. However, clonal growth within patches does not explain the extremely patchy distribution we found after wildfire as we also found genetic evidence of multiple recruitment events by seed within patches (Table 1). Local seed dispersal of <1 m was found by Williams (2014) perhaps explaining the patchy distribution. Rhizomes and caudices likely allow the plants to survive long periods of canopy closure between fires, perhaps longer than 90 years. Clearly, *P. layneae* is not a successional species that dies out under chaparral as once posited. However, conclusions on clonal spread based on only 6 markers should be regarded as preliminary awaiting robust genetic studies using more markers and samples as the 6 genetic markers were not adequate to resolve all samples. The species either does not have a seed bank, or seeds are killed by fire. Williams (2014) found seeds germinated 3 weeks following cold-moist stratification without a longer dormancy period.

In extensive surveying throughout the gabbro soil intrusion the species was found to occur more or less equally in undisturbed, cleared, and previously burned sites; the effect of disturbance was to increase plant density 2- to 3-fold, but not plant occupancy (Gogol-Prokurat 2009). The higher abundance in disturbed sites suggests vegetative growth or recruitment by seedlings was favored once the site was cleared or burned; however, the time when the disturbance occurred was not known. Across all surveys, there s great variation in rosette density, which may be influenced by both plot placement and disturbance history. Intriguingly, while the Pondo plants did not flower the first spring following fire, our broader disturbance surveys found that *P. layneae* flowered under all conditions. However, the disturbance surveys found the proportion of plants flowering was lower in recently burned plots, possibly also reflecting a delay in flowering after burn events (Table 2).

We found that the proportion of plants flowering declined as total shrub cover increased (Figure 2); therefore, as chaparral matures and shrub cover increases, the proportion of *P. layneae* plants flowering declines. Gogol-Prokurat (2009; Figure 3.1) found a strong correlation between *P. layneae* flower density per population and overall seed output; therefore, as chaparral matures and shrub density increases, the density of flowering *P. layneae* and in turn the overall reproductive output may be expected to decline until the next disturbance event. Plants in undisturbed plots were also taller than those in disturbed areas (Table 2), and it is possible that the increased resource use to compete for light could explain the depressed reproductive output.

Estimating population size in clonal plant species is particularly difficult without the insight provided by genetic analysis. Even so, our estimate of a population size of 1,324 genets exceeds what has been previously reported for this species; population size records for the species vary from 10 to over 1,000 individuals (California Natural Diversity Data Base 1998 reported in USFWS 2002). The distinction between ramets and genets is critical for the conservation of rare clonal plants as genets are the evolutionarily important units while ramets are genetic replicates (Tepedino 2012) that in self-incompatible species, such as *P. layneae*, cannot effect pollination. Tepedino (2012) suggests the population size of clonal plants be estimated downward at least 25% - an estimate in accord with our genetic study.

An important consideration of long-term plant species survival is the nature of the regeneration niche (Grubb 1977). This concept posits if environmental conditions only favor adult plant growth and survival, but not seed production, dispersal, germination, and/ or seedling establishment, then the species cannot endure over evolutionary time intervals. Many chaparral species are killed by fire and only persist by seedling establishment following fire-stimulated germination of seed in the soil seed bank. Therefore, for obligate seeder species such as *Ceanothus roderickii*, fire is an integral component of the regeneration niche. We do not know the dimensions of the seedling regeneration niche for re-sprouting *P. layneae*; seedlings do not appear in the year after fire, and flowering is delayed until the second spring after fire. Flowering did occur in 70% of undisturbed sites, a frequency comparable to the disturbed sites, with equally high seed output per plant (520–600 seeds/ plant) under all conditions (Table 2). Whether seed output resulted in seedling establishment is not known.

On the other hand, Keeley (1991) points out that germination and seedling establishment of resprouting species do not necessarily require fire; rather they regenerate under the shaded and mesic conditions found under the canopy of existing shrubs. As seedling occurrence has not been studied, this aspect of the regeneration niche is unknown. However, we found genetic evidence that multiple local recruitment events occurred to form patches at the Pondo fire site; data and our observations suggest seedling appearance and establishment in naturally open rocky areas, and proximate to an established plant following hand clearing. Further study focusing on the location and survivorship of seedlings is needed to describe the regeneration niche of *P. layneae* to identify the key components for long-term species persistence and to aid in human augmentation and/or introductions of *P. layneae* populations.

Wilson et al. (2009) analyzed the distribution of plant species on the gabbro intrusion in western El Dorado County and determined that there were two variants of the chaparral community, termed mesic resprouting and xeric seeding, based on degree of insolation and plant regeneration strategies. Packera layneae was associated with mesic chaparral with resprouting shrubs Toyon (Heteromeles arbutifolia), Coffeeberry (Frangula californica ssp. tomentella), and Redbud (Cercis occidentalis), resprouting perennial Wyethia reticulata, and chaparral sedge Carex xerophila, and the species was not associated with the most xeric chaparral on the southern exposures or oak woodland on the northern exposures. This is consistent with our surveys on Pine Hill and observations at the Pondo site; P. layneae was mostly absent on the north side and under the canopy of oaks on the east side, but was present under the chaparral on the east, south and west sides. These species associations were supported by Gogol-Prokurat (2009, 2014); in addition, proximity to disturbance such as roads or clearing was a strong predictor of P. layneae occurrence (Gogol-Prokurat 2009). Also of note, Wilson et al. (2009) found the complete absence of any of the rare species on exotic-grass dominated grassland suggesting that naturally occurring grasslands are not suitable habitat for the rare species and/or frequent disturbance that results in conversion of chaparral to grassland will eliminate both rare and common chaparral species.

Conservation implications

Plants survive, persist, and spread under chaparral disturbance dynamics by underground rhizomes up to 3.3 m in length in addition to individual caudices.

Estimates of population size should be reduced by at least 25% to take into account rhizomatous spread by ramets.

There is pronounced genetic structure (Marsh and Ayres 2002) meaning that many populations should be preserved and linked through corridors to allow gene flow.

Evidence indicates that both sexual and asexual reproduction are reduced as chaparral matures and total shrub cover increases. Although the species is adapted to survive and persist through these intervals between disturbance events, a regular disturbance regime is important to ensure the continued reproduction and persistence of this species.

Preservation of suitable habitat, using shrub dominants as indicator species, may be the correct approach to the conservation of this and the other listed species (Gogal-Prokurat 2014). These indicator species may also signal where artificial seeding may be most successful. As local scale genetic structure was also found (March and Ayres 2002) only local seed sources should be used in artificial seeding efforts.

Investigations into the regeneration niche are needed to determine whether clearing by hand is as effective as fire in species regeneration. This knowledge can be used to aid in population growth and augmentation by human-seeding efforts.

ACKNOWLEDGMENTS

We wish to thank the Bureau of Land Management, and especially Pine Hill preserve manager Graciela Hinshaw for their support of this and other research, and botanist Al Franklin who aided in the collection of leaf material under Federal Permit TE-062125-1. Volunteers from the El Dorado Chapter of the California Native Plant Society made the botanical surveys of Pine Hill possible. Laboratory resources were provided by the University of California at Davis. This manuscript was improved greatly by the comments of 6 anonymous reviewers.

Author Contributions

Conceived and designed the study: All authors Collected the data: All authors Performed analyses of the data: DA,VM, MG-P Authored the manuscript: DA Provided critical revision of the manuscript: VM, MG-P

LITERATURE CITED

- Baad, M. F., and G. D. Hanna. 1987. Pine Hill Ecological Reserve operations and maintenance schedule. Prepared for the California Department of Fish and Game, Sacramento, CA, USA.
- Gogol-Prokurat, M. 2009. Ecology and demography of four rare endemic plants on gabbro soils: implications for habitat suitability modeling and conservation. Dissertation, University of California, Davis, CA, USA.
- Gogol-Prokurat, M. 2014. Characterizing habitat suitability for disturbance-dependent rare plants of gabbro soils. California Fish and Game 100:19–33.
- Grubb, P. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107–145.
- Keeley, J. 1991. Seed germination and life history syndromes in the California chaparral. The Botanical Review 57:81–116.
- Klip, M. J., Caldwell, M. R., Ayres, D. R., and V. Meyer. 2020. Effects of a firebreak on plants and wildlife at the Pine Hill Ecological Reserve, a biodiversity hotspot. California Fish and Wildlife Journal. This issue.
- Marsh, G., and D. R. Ayres. 2002. Genetic structure of Layne's Butterweed (Senecio layneae E. L Greene, Asteraceae) using RAPD and ISSR markers. Madroño 49:150– 157.
- Rohlf, F. J. 1993. Numerical Taxonomy and Multivariate Analysis System NTSys-PC Version 1.80 Exeter Software. New York, NY, USA.
- Tepedino, V. J. 2012. Overestimating population sizes of rare clonal plants. Conservation Biology 5:945–947.
- Trock, D. 2012. *Packera layneae*. In Jepson Flora Project, Jepson eFlora. Available from: display.php?tid=77389 (Accessed 4 February 2020)
- United States Fish and Wildlife Service (USFWS). 2002. Recovery plan for gabbro soils plants of the central Sierra Nevada foothills. U.S. Fish and Wildlife Service, Portland, OR, USA.
- Williams, M. 2014. The ecology and distribution patterns of a rare serpentine endemic,

Packera layneae. Thesis, California State University, Chico, CA, USA.
Wilson, J. L., D. R. Ayres, S. Steinmaus, and M. Baad. 2009. Vegetation and flora of a biodiversity hotspot: Pine Hill, El Dorado County, California. Madroño 56:246–278.

Submitted 31 March 2020 Accepted 28 April 2020 Associate Editor was S. Jacks