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Clonal plants' traits and responses following fire disturbance in *Pinus ponderosa* Lawson & C. Lawson ecosystems in the Colorado Front Range[1]

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Abstract. Mountain ecosystems face increasing disturbance impacts (e.g., wildfire) due to climate change, leading to significant changes in vegetation composition and landscape dynamics. Clonal plants, characterized by their vegetative reproduction strategies, offer a range of ecologically important traits to cope with disturbances. However, clonality is often excluded in postfire vegetation studies in mountain ecosystems, and our knowledge of the ability of clonal plants to respond to differing disturbance regimes is limited. We studied the response of understory vegetation, based on composition and clonal traits, in burned and unburned *Pinus ponderosa* Lawson & C. Lawson (ponderosa pine) stands in the Colorado Front Range. Data from 40 total burned (n = 20) and unburned plots (n = 20) (10 m × 10 m) included relative plant cover and five environmental variables. Burned plots had greater overall clonal plant cover and diversity compared to unburned plots. Although there were statistically distinct differences in species composition between burned and unburned plots, these differences may not be ecologically meaningful. A fourth-corner analysis showed relationships between elevation and slope and type of clonal growth organs, suggesting that elevation, slope, and fire history interact significantly in shaping vegetation community structure. Combined responses of lateral spread and ramet length of *Arctostaphylos uva-ursi* L. (kinnikinnick) differed significantly in areas impacted by wildfire to those unburned, whereas that of *Antennaria parvifolia* Nutt. (small-leaf pussytoes) showed no differences, suggesting a species-specific response of clonal traits following fire. Our findings indicate that clonal plants dominate the understory in burned *P. ponderosa* stands. We suggest managers and modelers account for plant clonal traits for a comprehensive understanding of postfire forest recovery.

Key words: community response, mountain ecosystems, plant clonality, vegetation dynamics, wildfire

Mountain ecosystems face various disturbances due to climate change, with wildfires being significant contributors (Hansen *et al.* 2001; IPCC 2023). Wildfires shape forest ecosystems, altering ecological processes, landscape dynamics, and vegetation structures (Johnston *et al.* 2016; Stevens-Rumann and Morgan 2019). Mixed-intensity fires can boost understory vegetation diversity by reducing fire-sensitive species and altering growing conditions (Keyser *et al.* 2008), and postfire tree mortality frees up resources and reduces competition for resilient understory vegetation, including clonal plants (Tubbesing *et al.* 2020). Although much research examines the response of vegetation to fire, few studies focus on clonal plant response, even though we know clonal plants behave differently than nonclonal plants (Franklin *et al.* 2021). Knowing that clonal plants make up most species (Klimešová *et al.* 2021), we attempt to tease out the different response of clonal and nonclonal understory plants in Colorado's *Pinus ponderosa* Lawson & C. Lawson (ponderosa pine) forests.

Clonal plants, perennials that reproduce vegetatively through ramets, are initially dependent on the parent but subsequently develop their own root and shoot systems, forming genetically identical interconnected individuals (Franklin *et al.* 2020; Klimešová *et al.* 2021). These highly modular plants excel in rapid colonization, stress tolerance, and efficient resource sharing (Stuefer 1996), giving them an edge over nonclonal plants in some disturbed environments.

Clonal traits, such as clonal growth organs (CGOs) (e.g., epigeogenous and hypogeogenous rhizomes, bulbs, horizontal aboveground stems, and root splitters) support clonal plants' recovery postdisturbance. Clonal growth organs are structures that enable a plant to reproduce asexually and spread by producing new genetically identical individuals. Lateral spread and connection persistence

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are other clonal traits that also aid in recovery (Klimeš *et al.* 1997; Klimešová *et al.* 2019). After disturbances alter soil nutrients, rhizomes and stolons explore nutrient-rich patches, colonizing bare ground through horizontal growth (Klimeš *et al.* 1997). This lateral spread helps clonal plants compete for resources postdisturbance (Pausas *et al.* 2018). Herben *et al.* (2012) highlighted a trade-off between vegetative and seed reproduction, with varying reproduction methods benefiting clonal plants based on environmental conditions, but in general, clonal plants do well in heterogenous conditions (Louâpre *et al.* 2012; Liu *et al.* 2016) typical of postfire environments (Schoennagel *et al.* 2008; Das Gupta *et al.* 2019).

Wildfires shape vegetation patterns, making understanding plant responses vital, especially clonality. Exploring vegetation recovery trajectories helps predict resilience in disturbed mountain ecosystems (Viana-Soto *et al.* 2020; Seidl and Turner 2022), guiding effective forest management and conservation efforts (Hart and Chen 2006). Although studies have explored understory responses to wildfires in *P. ponderosa* forests, few focus on clonality's role in postfire recovery. Our goal was to fill this gap by studying postfire responses and clonal plant traits in burned and unburned *P. ponderosa* plots. Our objectives were to (a) compare clonal plant cover and diversity in burned *versus* unburned plots; (b) examine plant species composition changes in these plots, considering clonal *versus* nonclonal contributions; and (c) examine clonal traits (lateral spread, ramet length) of *Arctostaphylos uva-ursi* L. (kinnikinnick) and *Antennaria parvifolia* Nutt. (small-leaf pussytoes) across burned and unburned plots.

We hypothesized that burned plots would show greater clonal plant percent cover and diversity due to their adaptability in disturbed conditions and rapid recolonization ability. Thus, we anticipated significant community composition differences. Clonal plants' unique vegetative spread and recovery mechanisms should be more evident postfire. Clonal traits like lateral spread and ramet length in *A. uva-ursi* and *A. parvifolia* can indicate how these plants respond to disturbances (Klimešová *et al.* 2019). Lateral spread shows horizontal expansion and resource acquisition, whereas ramet length reflects vertical growth, highlighting clonal plant fitness and growth strategies (Klimešová and Klimeš 2008). We also hypothesized significant differences in these clonal traits between burned and unburned plots, suggesting plastic responses to the postfire environment.

Methods. STUDY AREA. This study was conducted in *P. ponderosa* forests of the Arapaho and Roosevelt National Forests (ARNF) in the Colorado Front Range after the 2020 Cameron Peak Fire, which is considered one of the largest wildfires in the history of Colorado (NPS 2021) (Fig. 1). The ARNF covers about 1.5 million acres and is primarily coniferous. *Pinus ponderosa* dominates at elevations between 1,800 and 2,500 m, accompanied by understory species such as graminoids, forbs, and shrubs (Fryer 2018). Other conifers like *Pinus contorta* Douglas ex Loudon (lodgepole pine), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Pinus flexilis* James (limber pine), and *Juniperus scopulorum* Sarg. (Rocky Mountain juniper) appear at mid-high elevations (2000–2500 m). Plots receive an average annual precipitation of 38.3 cm, with temperatures varying from 2 °C in January to 32 °C in June (data from 1991 to 2020; Western Regional Climate Center 2007).

FIELD AND UNDERSTORY VEGETATION MEASUREMENTS. Sampling area was delineated and informed based upon the combination of historical fire data in the Colorado Front Range and on-site inspection. Prior to onfield visit, we reviewed historical data on the Cameron Peak wildfire to provide guidance on sampling locations and understand the spatial extent and severity of the fire (ArcGIS 2023). We then systematically drove through *P. ponderosa* stands within the potential sampling area to inspect potential burned and unburned plots. Based upon onfield inspection, the 20 burned plots were sampled by assessing *P. ponderosa* stands that had experienced complete canopy fire consumption during the wildfire event. Similarly, the 20 unburned plots used as controls were sampled plots that had not experienced fire damage in at least the last two decades (Fig. 2). Although sampling techniques relied on visual assessment during field visits, the locations of plots were recorded using GPS devices (Garmin eTrex 32x, Garmin Ltd., Olathe, KS) to ensure accurate locations of plots. Plot sampling was conducted in a systematic manner to minimize bias and ensure representation across the study area. Each of the 40 total burned and unburned plots was 10 m × 10 m, with plots at least 50 m apart. In every

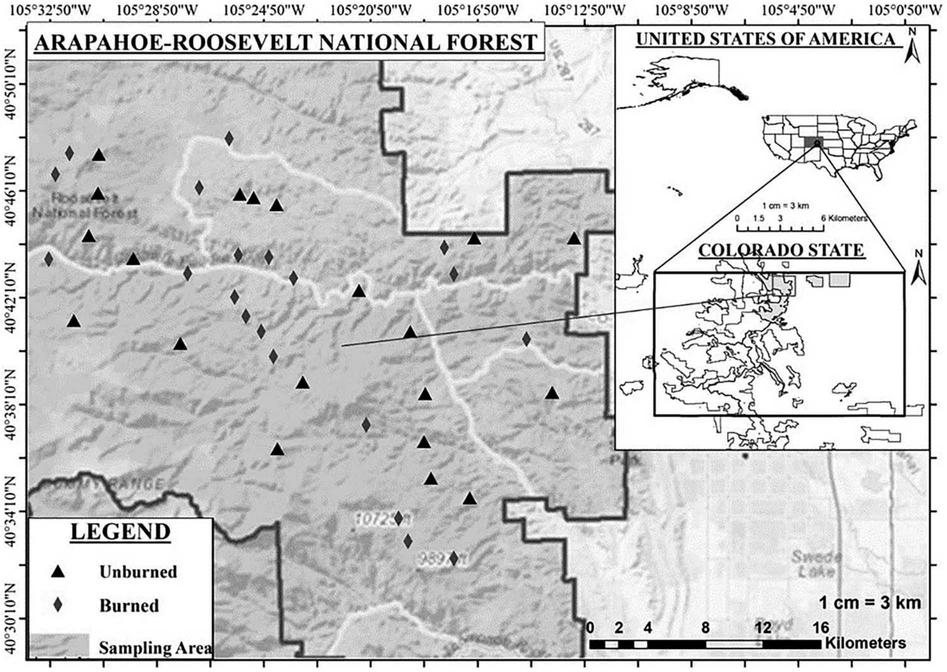

FIG. 1. Map of the 40 plots sampled from understory vegetation distributed within burned (n = 20) and unburned (n = 20) *Pinus ponderosa* stands in the Colorado Front Range.

sampled plot, we took the following environmental data from the plot center: elevation, slope, aspect, longitude, and latitude (Appendix 1).

Past studies assert that using plant cover data effectively characterizes plant communities, describes plant-environment interactions, and monitors plant ecosystems through time (Mueller-Dombois and Ellenberg 1974; Anderson 1986). Visual estimates of relative percent cover were done using the ocular method of estimating percent cover for all plant species in each plot, both clonal and nonclonal (Helm and Mead 2004). We estimated percent

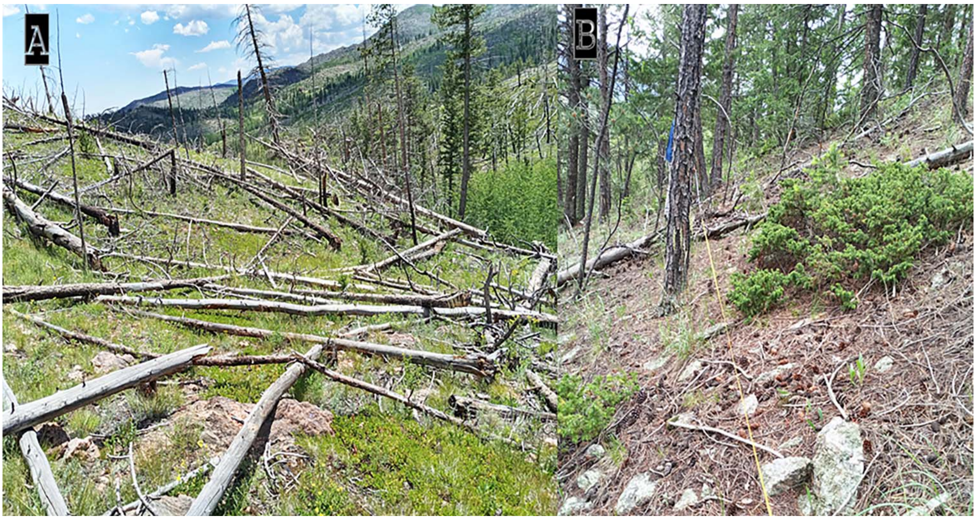

FIG. 2. Photograph of the study area showing burned (A) and unburned (B) *Pinus ponderosa* stands in the Colorado Front Range.

cover of each plant species separately within each plot by pooling plant species abundances before calculating relative percent cover. The choice of percent cover over an ordinal cover scale is supported by a recent study by Dengler and Dembicz (2023). In their study, the authors found that direct percent cover estimation produces lower mean absolute and relative errors compared to the use of ordinal scales, particularly for cover values above 1% (Dengler and Dembicz 2023). If a plant could not be identified, we followed the Assessment Inventory and Monitoring methods (Toevs *et al.* 2011) and initially named that plant as an unknown species. The plant was collected, with detailed descriptions and photos, brought to the University of Northern Colorado herbarium to be keyed and identified, and once identified, reclassified to species in the data set. Taxonomic identification followed Ackerfield (2015). CLO-PLA 3 (Klimeš and Klimešová 1999; Klimešová and Klimeš 2008), and TRY plant trait databases (Kattge *et al.* 2020) were used to label species as clonal or nonclonal based on their dominant CGO such as epigeogenous rhizome, hypogeogenous rhizome, bulb, root splitter, and horizontal aboveground stem. In addition, the USDA PLANTS Database (USDA 2024) was used to provide other ecological traits of species, including life form (forb, shrub or graminoid) and the photosynthetic pathway that each species utilizes (C3, C4, or CAM).

Clonal Traits Measurements. Ten plots each from burned and unburned areas were selected to study clonal traits' responses in *A. uva-ursi* and *A. parvifolia*. These plots were chosen based on their distribution. We aimed to compare lateral spread and ramet length between burned and unburned plots, as these traits indicate clonal reproduction and recovery postdisturbance (Klimeš and Klimešová 2008; Pausas *et al.* 2018). Measurements followed Klimešová *et al.* (2019) protocols, with lateral spread measured between offspring and rooting units, and ramet length from base to tip. Five measurements per plant were used to calculate an average, and five individuals were averaged for each plot.

Data Analyses. We were primarily interested in assessing the relative percent cover (i.e., cover of all species in each plot summed to 100%) and diversity of clonal plants in burned and unburned plots of *P. ponderosa* stands. Diversity variables (i.e., richness and evenness) were calculated using relative cover of full species matrix for 40 total plots with 27 clonal taxa/species in PC-ORD. Since percent cover and diversity data did not meet assumptions of normality and homoscedasticity of variances, unpaired nonparametric Mann-Whitney U-tests were conducted to assess whether each of our response variables—relative percent cover, richness, and evenness—differed between burned *versus* unburned plots for clonal plants. For clonal plant trait measurements, a MANOVA (Multivariate Analysis of Variance) was used to detect the effects of burned *versus* unburned plots on lateral spread and ramet length for each clonal plant *A. uva-ursi* and *A. parvifolia* in a combined model. Although lateral spread and ramet length may respond differently, analyzing them together allowed for a comprehensive assessment of trait responses. All analyses were conducted using R Statistical Software (version 4.3.1; R Core Team 2021, Vienna, Austria).

PC-ORD 7.10 (McCune and Mefford 1999) was used to conduct multivariate analyses to study species composition differences in burned and unburned plots and the roles of clonal and nonclonal plants. We used four multivariate analyses: NMS (nonmetric multidimensional scaling), MRPP (multiresponse permutation procedures), ISA (indicator species analysis), and FCA (fourth-corner analysis) to explore trait-environment relationships.

Nonmetric multidimensional scaling ordinates points (burned and unburned plots in our case) in a reduced-dimensional space, preserving the pairwise dissimilarity among them. This helps to visualize patterns and relationships in ecological communities (McCune and Grace 2002). Nonmetric multidimensional scaling was used because the data did not follow linear, parametric assumptions for normality and homogeneity of variances, which is common with ecological community data (Clarke 1993; McCune and Grace 2002). Autopilot with the "Slow and Thorough" setting using "Sørensen distance" measure was used to run 50 iterations to create a configuration for the ordination including 104 clonal and nonclonal taxa/species in the primary species matrix and 40 total burned and unburned plots (Appendix 2). The second matrix had five environmental variables collected at each plot from the center (elevation, slope, aspect, latitude, and longitude). Multiresponse permutation procedures and ISA were performed to complement and help interpret the NMS ordination.

Multi-response permutation procedures is a nonparametric statistical test that determines whether there are significant differences between groups based on multivariate response variables (Pillar 2013). In this case, we used MRPP to assess the dissimilarity in species composition between burned and unburned plots using the "Sørensen distance" measure. Based on the weighting technique, the analysis can generate the *T* statistic, which measures the difference between groups, with more negative values indicating stronger separation; the *A* statistic, which reflects within-group homogeneity, ranging from –1 (no agreement) to 1 (perfect agreement); and *P*, which is the probability of smaller or equal delta (McCune and Mefford 1999).

Indicator species analysis was used to determine which plants were significantly associated with burned and unburned plots. The analysis helps to determine which species (clonal or nonclonal) are indicators of these specific environmental conditions (Dufrêne and Legendre 1997; McCune and Grace 2002).

The fourth-corner analysis explores species' trait-environment relationships. It is called the "fourth-corner" because it combines three corners of species ecological traits, environment variables, and species cover data, and then leaves the fourth corner to examine the relationship among species, environmental variables, and plant ecological traits (Dray *et al.* 2014). Specifically in this study, FCA was used to determine whether environmental variables had any relationship with species ecological traits and with differences in species composition observed in the NMS ordination.

Results. Relative Percent Cover and Diversity Area of Clonal Plants. We identified 104 understory species (27 clonal and 77 nonclonal) in all 40 burned and unburned plots. Invasive species were rare in all plots. Clonal plants (Table 1) and nonclonal plants were mainly forbs, with a few shrubs and graminoids. Both plot types had an overstory dominated by *P. ponderosa* but included *P. flexilis* and *P. menziesii* to a lesser extent. *Achillea millefolium* L. (common yarrow), *Campanula rotundifolia* L. (bluebell bellflower), and *A. parvifolia* showed the greatest cover among forbs. *Arctostaphylos uva-ursi, Artemisia ludoviciana* Nutt. (white sagebrush), *Artemisia frigida* Willd. (prairie sagewort), *Cercocarpus montanus* Raf. (alderleaf mountain mahogany), and *Purshia tridentata* (Pursh.) D.C. (antelope bitterbrush) were the shrubs with the most cover. In terms of graminoids, *Carex rossii* Boott (Ross' sedge), *Bromus tectorum* L. (cheatgrass), and *Poa bulbosa* L. (bulbous bluegrass) were the species with the greatest cover in our plots.

Clonal plant percent cover differed significantly between burned and unburned plots ($U = 332$; $p < 0.001$), being greater in burned plots (Fig. 3). Burned plots averaged 12 species, whereas unburned had 6, with standard deviations of 1.883 and 1.071, respectively. Clonal plant richness was significantly higher in burned plots ($U = 397$; $p < 0.001$; Fig. 4), but evenness did not differ between plot types ($U = 203.5$; $p = 0.935$; Fig. 5).

Community Structure. Species community composition in burned and unburned plots using NMS ordination yielded a three-dimensional solution explaining 64.3% of the variance ($p = 0.004$). The final stress level was 18.11 with a solution instability of < 0.0001 after 102 iterations. Nonmetric multidimensional scaling axis 1 explained 25.2% of the variance, capturing a significant portion of species composition variation. The positive end of axis 1 correlated with higher *C. rossii*, *Pascopyrum* Á. Löve (wheatgrass), *Helianthus pumilus* Nutt. (little sunflower), *P. bulbosa*, and *Mertensia ciliata* E. James ex. Torr G. Don (tall fringed bluebells). Conversely, the negative end of axis 1 correlated with *Cirsium arvense* (L.) Scop. (Canada thistle), *Geranium* sp. (geranium), and *A. millefolium*. The only environmental variable that was positively correlated with NMS axis 1 was slope, whereas elevation and latitude were negatively correlated. Plots formed distinct burned and unburned groups in ordination space (Fig. 6).

Nonmetric multidimensional scaling axis 2 contributed an additional 23.4% of the variance. Species strongly correlated with the positive end of axis 2 included *Taraxacum officinale* F. H. Wigg. (common dandelion), *Potentilla fissa* Nutt. (bigflower cinquefoil), and *C. rossii*. *Viburnum edule* (Michx.) Raf. (squashberry), *C. rotundifolia*, and *A. millefolium* showed weaker positive correlations with axis 2. Species negatively correlated with this axis included *Erigeron eximius* Greene (sprucefir fleabane), *Sedum lanceolatum* Torr. (spearleaf stonecrop), *P. bulbosa*, and to a lesser extent, *Draba graminea* Greene (Rocky Mountain draba). All environmental variables had weak

Table 1. Clonal plants with dominant clonal growth organs (CGOs) in sampled plots of the *Pinus ponderosa* stands in the Colorado Front Range (from CLO-PLA 3 & TRY databases).

Species	CGO
Achillea millefolium L.	epigeogenous stem (rhizome)[1]
Antennaria parvifolia Nutt.	epigeogenous stem (rhizome)
Arctostaphylos uva-ursi L.	epigeogenous stem (rhizome)
Bromus inermis Leyss.	hypogeogenous stem (rhizome)[2]
Campanula rotundifolia L.	epigeogenous stem (rhizome)
Cerastium arvense L.	root-splitter[3]
Carex rossii Boott	epigeogenous stem (rhizome)
Cirsium arvense (L.) Scop.	roots with adventitious buds[4]
Chenopodium album L.	horizontal aboveground stem[5]
Cystopteris fragilis (L.) Bernh.	epigeogenous stem (rhizome
Draba graminea Greene	root-splitter
Koeleria macrantha (Ledeb.) Schult.	root-splitter
Oxytropis campestris (L.) DC.	bulb[6]
Phleum pratense L.	epigeogenous stem (rhizome)
Pseudocymopterus montanus (A. Gray) J.M. Coult. & Rose	epigeogenous stem (rhizome
Poa bulbosa L.	epigeogenous stem (rhizome)
Poa pratensis L.	hypogeogenous stem (rhizome)
Pulsatilla patens (L.) Mill.	epigeogenous stem (rhizome)
Purshia tridentata (Pursh) DC.	epigeogenous stem (rhizome)
Ribes aureum Pursh	roots with adventitious buds
Rubus idaeus L.	epigeogenous stem (rhizome)
Salix L.	horizontal above-ground stem
Symphoricarpos orbiculatus Moench	epigeogenous stem (rhizome)
Taraxacum officinale F.H. Wigg.	root-splitter
Thalictrum alpinum L.	epigeogenous stem (rhizome)
Tragopogon dubius Scop.	epigeogenous stem (rhizome)
Vicia sativa L.	epigeogenous stem (rhizome)

[1] An organ originating from stems that grows aboveground.

[2] A clonal growth organ formed underground.

[3] A plant whose primary root system splits into buds and ramets without the need for secondary roots.

[4] A plant's main roots, including the hypocotyl and adventitious roots, which can develop on their own or in response to an injury.

[5] A clonal growth organ rooting in the soil and providing connection between offspring plants or formed by a creeping axis of a plant.

[6] A short underground stem surrounded by fleshy leaves or leaf bases, storing nutrients.

correlations with axis 2. However, the unburned plots tended to cluster at the negative end of axis 2, whereas burned plots clustered toward the positive end of this axis.

The third NMS axis accounted for 13.4% of the explained variance. The positive end of axis 3 had strong correlations with *Castilleja puberula* Rydb. (shortflower Indian paintbrush) and *V. edule*. The negative end was strongly correlated with *A. ludoviciana*, *P. tridentata*, *Heterotheca villosa* (Pursh) Shinners (hairy false goldenaster), *H. pumilus*, *Bromus inermis* Leyss. (smooth brome), and *C. montanus*. Slope was strongly negatively correlated, whereas elevation, aspect, longitude, and longitude all had negative correlations.

Multi-response permutation procedures ($T = -9.970$, $A = 0.021$, $p \leq 0.001$) analysis revealed statistically significant differences in vegetation composition between burned versus unburned plots, albeit a low A value questions ecological significance. Indicator species analysis identified 16 indicator species for both burned and unburned plots out of the 104 taxa/species in the species matrix ($p \leq 0.05$) with 63% clonal indicating burned plots and one clonal species indicating unburned plots (Table 2).

Fourth-corner analysis revealed no significant relationships between elevation, slope, latitude, longitude, and life form. Environmental variables had weak correlations with clonality (all $p > 0.05$). However, CGOs were associated with elevation and slope. Specifically, elevation related to horizontal aboveground stems, epigeogenous rhizomes, and root splitters ($p = 0.025$, $p = 0.019$, and $p =$

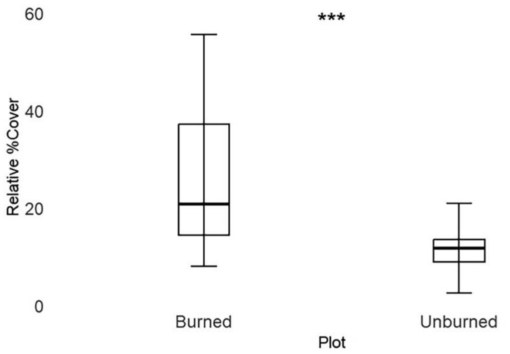

FIG. 3. Relative percent cover of clonal plants from burned versus unburned *Pinus ponderosa* stands in the Colorado Front Range.

0.032, respectively), whereas slope related to epigeogenous rhizomes ($p = 0.023$). Environmental variables did not relate with photosynthetic type (all $p > 0.05$). Overall, elevation, slope, and fire history significantly influenced vegetation structure, consistent with NMS ordination results (Table 3).

CLONAL TRAITS RESPONSE IN BURNED AND UNBURNED PLOTS. MANOVA results suggested that the combined responses of lateral spread (LS) and ramet length (RL) of *A. urva-ursi* were significantly higher in burned plots compared to unburned plots (Pillai Trace F = 0.5624, $p < 0.001$; Fig. 7). Although these traits in *A. urva-ursi* varied in plasticity after fire in burned plots, unburned plots showed less variability. In contrast, *A. parvifolia* showed no significant differences in LS or RL between burned and unburned plots (Pillai Trace F = 0.1042, $p = 0.393$; Fig. 8), with unburned plots also displaying less trait variability.

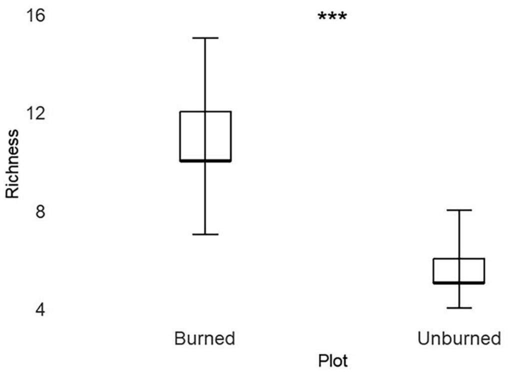

FIG. 4. Richness of clonal plants from burned versus unburned *Pinus ponderosa* stands in the Colorado Front Range.

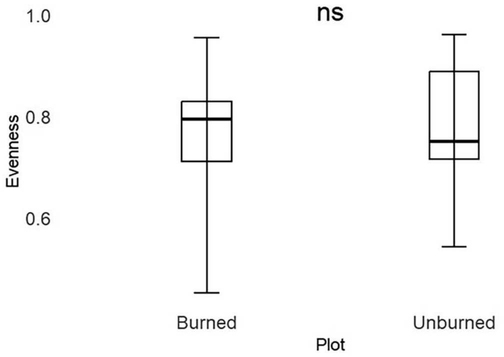

FIG. 5. Evenness of clonal plants from burned versus unburned *Pinus ponderosa* stands in the Colorado Front Range.

Discussion. RELATIVE PERCENT COVER AND DIVERSITY OF CLONAL PLANTS. Our study focused on the response of understory clonal plants in *P. ponderosa* stands in the Colorado Front Range following fire. We expected burned plots to show greater clonal plant cover and diversity than unburned plots. We also predicted that the different responses of clonal and nonclonal plants would result in significant changes in overall species composition between burned and unburned plots. In addition, we hypothesized that clonal traits of *A. uva-ursi* and *A. parvifolia* would differ

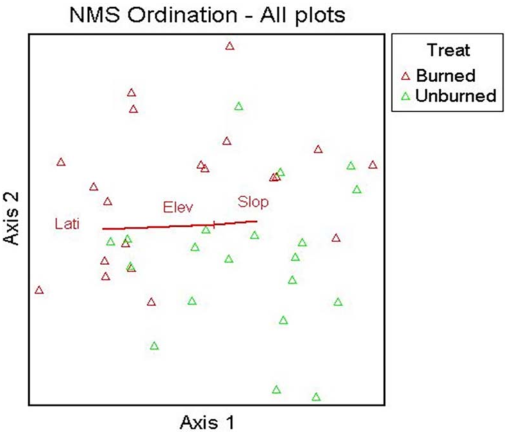

FIG. 6. NMS ordination of the understory species composition for all 40 burned and unburned plots of *Pinus ponderosa* stands in the Colorado Front Range. A three-dimensional solution was recommended, but only two dimensions are shown here. Burned plots are marked by red triangles, whereas unburned plots are marked by light green triangles with five environmental variables (elevation, slope, aspect, latitude, and longitude).

Table 2. Indicator species analysis (ISA) results for species across study plots from *Pinus ponderosa* stands in the Colorado Front Range.

Species	Plant type	Plot indicated	Observed indicator value	P-value
Achillea millefolium L.	Clonal	Burned	80.0	0.0002
Campanula rotundifolia L.	Clonal	Burned	67.0	0.0004
Purshia tridentata (Pursh) DC	Clonal	Burned	55.0	< 0.001
Oxytropis campestris (L.) DC	Clonal	Burned	45.0	0.002
Taraxacum officinale F.H. Wigg.	Clonal	Burned	37.3	0.041
Cirsium arvense (L.) Scop.	Clonal	Burned	35.0	0.009
Poa pratensis L.	Clonal	Burned	35.0	0.007
Rubus idaeus L.	Clonal	Burned	25.0	0.023
Thalictrum alpinum L.	Clonal	Burned	25.0	0.045
Mertensia ciliata (James ex Torr.) G. Don	Nonclonal	Burned	25.0	0.043
Potentilla fissa Nutt.	Nonclonal	Burned	66.8	0.001
Artemisia ludoviciana Nutt.	Nonclonal	Burned	48.6	0.046
Festuca saximontana Rydb.	Nonclonal	Burned	40.0	0.002
Bromus madritensis L.	Nonclonal	Burned	30.0	0.020
Verbascum thapsus L.	Nonclonal	Burned	45.0	0.001
Cystopteris fragilis (L.) Bernh.	Clonal	Unburned	25.0	0.048

in their clonal traits' responses between burned and unburned plots. Overall, the findings partially supported our hypotheses. Although burned plots did show increased clonal plant cover and diversity as predicted, the changes in species composition may not be ecologically significant. Additionally, the clonal traits responses of the two studied plants did not differ much between burned and unburned plots.

Several studies indicate that plant clonality plays a key role in ecosystem recovery and community restoration after disturbances (e.g., Fahrig *et al.* 1994; Oborny *et al.* 2000; Van Mantgem *et al.* 2020). Here, we found greater clonal plant cover in burned plots, attributing this to their resilience, colonization ability, and vegetative reproduction from strong bud banks and CGOs like rhizomes and stolons (Klimešová and Martínková 2022). In addition, postfire environments often exhibit increased heterogeneity, affecting soil, microclimate, and vegetation at broader scales (Schoennagel *et al.* 2008). Although our study focused on community-level effects, clonal plants thrive in these varied postfire landscapes, benefiting from quick regrowth and

Table 3. Results of fourth-corner analysis (FCA) examining the relationship of environmental variables with species ecological traits from *Pinus ponderosa* stands in the Front Range of Colorado.

Environmental variable	Species ecological trait	F value	P value
Elevation	clonality	0.745	0.837
	life form	7.734	0.632
	CGOs	35.401	0.002
	photosynthetic type	5.812	0.319
Slope	clonality	0.71	0.822
	life form	5.174	0.698
	CGOs	23.21	0.028
	photosynthetic type	2.633	0.433
Aspect	clonality	4.994	0.380
	life form	4.499	0.436
	CGOs	5.384	0.601
	photosynthetic type	2.182	0.437
Latitude	clonality	1.544	0.753
	life form	9.643	0.372
	CGOs	11.218	0.272
	photosynthetic type	3.712	0.465
Longitude	clonality	4.676	0.395
	life form	8.676	0.127
	CGOs	4.281	0.724
	photosynthetic type	3.647	0.330

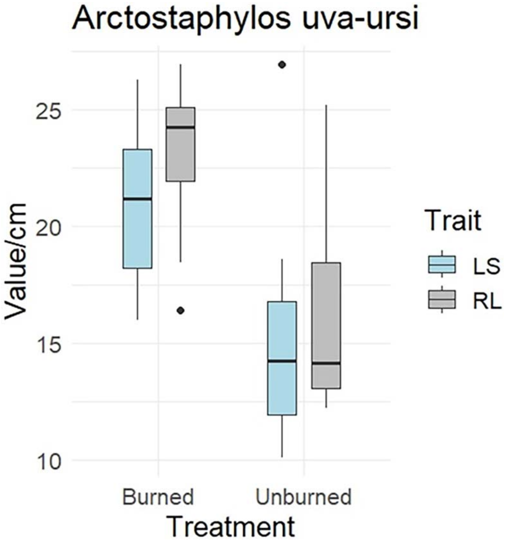

Fig. 7. Response of lateral spread and ramet size of *Arctostaphylos uva-ursi* for burned versus unburned *Pinus ponderosa* stands in the Colorado Front Range.

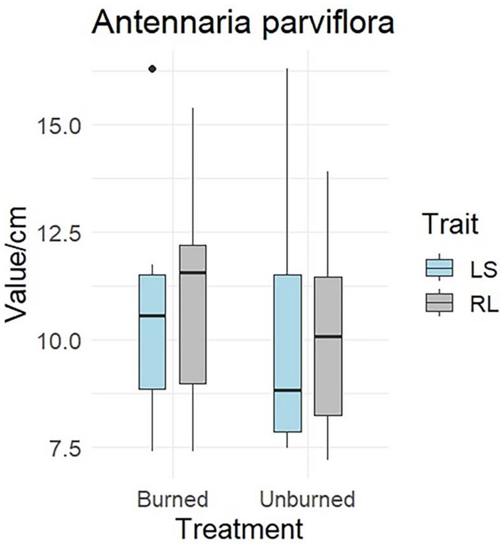

FIG. 8. Response of lateral spread and ramet size of *Antennaria parvifolia* for burned versus unburned *Pinus ponderosa* stands in the Colorado Front Range.

resource exploitation (Svensson *et al.* 2013). This increased cover is also linked to traits like physiological integration and resource allocation, crucial for clonal plant dominance in disturbed ecosystems (Liu *et al.* 2016).

Our data suggest that clonal plant species richness increases postfire. Clonal plants had more species in burned plots compared to unburned ones, consistent with other studies (e.g., McMahon *et al.* 2017; Pausas *et al.* 2018). However, clonal plant evenness did not differ between burned and unburned plots. Similar evenness suggests fire does not change the relative abundance of clonal species. This evenness could influence community stability and resilience postfire, affecting recovery ability (Sasaki and Lauenroth 2011; Battisti *et al.* 2016).

COMMUNITY STRUCTURE. Nonmetric multidimensional scaling ordination axis 1 primarily represents elevation gradient in vegetation community structure, likely influenced by topography, especially in unburned ponderosa pine plots. On the positive end of axis 1, species such as *C. rossii*, *Pascopyrum* sp., *H. pumilus*, *P. bulbosa,* and *M. ciliata* were associated at higher elevations, indicating cooler conditions. These species likely thrive in cooler conditions typical of higher elevations in the unburned ponderosa communities. The negative end of axis 1 was correlated with *C. arvense*, *Geranium* sp., and *A. millefolium* linked to lower elevations, possibly due to the dense *P. ponderosa* canopy cover. Although elevation emerges as the main driver of species along axis 1, particularly in unburned plots, there might be an interaction between elevation and fire history in shaping vegetation community structure.

Nonmetric multidimensional scaling axis 2 represents a postfire disturbance and species-specific response gradient. Burned plots mainly cluster at the positive end, including species such as *T. officinale, C. rossii*, and *P. fissa*, which can thrive postfire due to clonality or wind-dispersed seeds (Toth 1991). These species benefit from postfire microhabitats and establish quickly. On the negative end of axis 2, species like *E. eximius*, *S. lanceolatum*, *P. bulbosa*, and *D. graminea* apparently preferred less disturbed habitats. Further, unburned plots mostly clustered at the negative end of this axis and we believe fire regimes in the Colorado Front Range likely influenced these patterns. It should be noted that “unburned” really implies burned less recently, as all plots have burned at some time in this *P. ponderosa* ecosystem.

Nonmetric multidimensional scaling axis 3 corresponds to variation in species cover related to postfire vegetation structure. The positive end had only *C. puberula* and *V. edule*, which are not indicative of postfire environments in the literature. However, at the negative end, we saw species with greater cover commonly found in postfire environments. These species included *A. ludoviciana*, *P. tridentata*, *H. villosa*, *B. inermis*, and *C. montanus.* Species cover along this axis also correlated negatively with slope, indicating slope’s role in shaping species distribution. Steeper slopes might experience different fire behavior, affecting postfire community structure (Bassett *et al.* 2015).

The data suggests that there are slight compositional differences between burned and unburned plots, but we interpret these cautiously. Indicator species analysis identified 16 significant indicator species, but only three had values above 60. This low indicator value is likely due to many species being widespread across plots. Clonal plants like *A. millefolium, C. rotundifolia, C. arvense, Oxytropis campestris* (L.) DC. (field locoweed), *P. tridentata, T. officinale,* and *Poa pratensis* L. (Kentucky bluegrass) were significant indicators in burned plots, aligning with our expectation that clonal plants respond more directly to fire disturbance. This supports the idea that clonal plants enhance postfire ecosystem resilience (Falk *et al.* 2019).

We found no relationships between clonality, life form, photosynthetic type, and environmental variables like elevation, slope, aspect, longitude, and latitude. This aligns with our prediction that these traits are relatively stable across species regardless of environmental variations. However, responses within these traits can vary; for example, clonal plants may exhibit diverse strategies postdisturbance.

Significantly, elevation and slope were related to certain CGOs, like horizontal aboveground stems and rhizomes. This suggests clonal plants allocate resources to these CGOs more at higher elevations or steeper slopes, possibly enhancing their ability to spread and access resources postdisturbance (Štõastná *et al.* 2012). Elevation also strongly correlated with NMS axis 1 and was related to CGOs in the FCA. This indicates that elevation and fire history interact to shape vegetation in these Colorado Front Range ecosystems, suggesting a nuanced response to environmental conditions (Klimešová *et al.* 2012).

Clonal Traits Response in Burned and Unburned Plots. The responses of clonal plant species *A. uva-ursi* and *A. parvifolia* to fire varied, highlighting the importance of understanding each species' unique postdisturbance behavior (Franklin *et al.* 2020; Bell *et al.* 2023). Specifically, *A. uva-ursi* exhibited increased lateral spread and ramet length in burned plots, potentially aiding its recovery and growth postfire. Although few studies focus on these species' responses to fire, Hutchings and de Kroon (1994) found that clonal traits like lateral spread can vary based on environmental conditions and genetics. This trait plasticity in response to disturbance is vital for resource competition and foraging (Dong and de Kroon 1994; Hutchings and de Kroon 1994; Dietz and Steinlein 2001). Such variability has practical implications for ecosystem management, especially in fire-prone areas. It underscores the need for tailored management plans that account for each species' specific needs postfire.

In summary, this study highlights that elevation, slope, and fire history collectively influence the understory vegetation of *P. ponderosa* stands in the Colorado Front Range. Three years after the fire, burned plots showed increased relative cover and diversity of clonal plants, displaying their resilience and adaptability to disturbances. Our findings are important for foresters, managers, and modelers to understand clonal plant performance and response to changing fire regimes. Given the importance of clonal plants in postdisturbance recovery, future research should delve into the mechanisms behind their success. Long-term monitoring of postfire ecosystems will further elucidate the sustainability of clonal plants and their traits.

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Appendix 1

Elevation, slope, aspect, and GPS coordinates of plot locations in study area.

Plot number	Plot type	Elevation	Slope	Aspect	Latitude	Longitude
1	Burned	1927	30	50	40.7927	−105.54
2	Burned	1918	30	49	40.7797	−105.54
3	Burned	1910	33	49.5	40.7713	−105.45
4	Burned	1901	34	52	40.7339	−105.30
5	Burned	1908	36	40	40.7267	−105.55
6[*]	Burned	2458	32	190	40.7178	−105.46
7[*]	Burned	2416	35	180	40.6660	−105.41
8[*]	Burned	2428	30	230	40.7530	−105.39
9[*]	Burned	2425	15	290	40.5650	−105.33
10[*]	Burned	2416	25	270	40.6769	−105.25
11	Burned	2420	25	50	40.7173	−105.29
12	Burned	2434	20	170	40.7280	−105.41
13	Burned	2409	35	242	40.6233	−105.35
14	Burned	2391	25	190	40.5401	−105.29
15[*]	Burned	2487	10	110	40.5508	−105.32
16[*]	Burned	2490	25	110	40.6816	−105.42
17	Burned	2484	20	50	40.7030	−105.43
18[*]	Burned	2488	17	60	40.7149	−105.39
19[*]	Burned	2472	8	110	40.6912	−105.43
20[*]	Burned	2477	28	286	40.7292	−105.43
21[*]	Unburned	2103	30	326	40.7922	−105.52
22[*]	Unburned	2187	29	290	40.7679	−105.52
23	Unburned	2230	31	310	40.7672	−105.43
24	Unburned	2313	33	299	40.7651	−105.42
25[*]	Unburned	2352	36	302	40.7608	−105.41
26	Unburned	2012	10	76	40.7415	−105.52
27	Unburned	1995	25	25	40.7272	−105.50
28	Unburned	1986	30	90	40.6501	−105.39
29	Unburned	1953	34	84	40.7401	−105.28
30	Unburned	1881	35	10	40.7073	−105.36
31[*]	Unburned	2486	15	28	40.5780	−105.29
32	Unburned	2475	4	72	40.5902	−105.31
33[*]	Unburned	2473	10	254	40.6087	−105.40
34[*]	Unburned	2471	12	340	40.6887	−105.53
35[*]	Unburned	2477	10	104	40.6744	−105.47
36	Unburned	2473	5	210	40.7401	−105.22
37	Unburned	2471	4	300	40.6437	−105.23
38[*]	Unburned	2466	2	280	40.6816	−105.32
39[*]	Unburned	2464	2	128	40.6430	−105.31
40[*]	Unburned	2461	8	170	40.6130	−105.31

* Plots chosen for clonal traits responses.

Appendix 2

Species list indicated by plot type (burned, unburned or both) and plant type (clonal or nonclonal) in study area.

Species	Plot Type	Plant Type
Achillea millefolium L.	Both	Clonal
Allium sp. L.	Burned	Nonclonal
Antennaria parvifolia Nutt.	Both	Clonal
Arctostaphylos uva-ursi L.	Both	Clonal
Arnica cordifolia Hook.	Unburned	Nonclonal
Artemisia frigida Willd.	Both	Nonclonal
Artemisia ludoviciana Nutt.	Both	Nonclonal
Artemisia tridentata Nutt.	Both	Nonclonal
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Burned	Nonclonal
Bromus ciliatus L.	Unburned	Nonclonal
Bromus inermis Leyss.	Burned	Clonal
Bromus madritensis L.	Burned	Nonclonal
Bromus marginatus Nees ex Steud.	Unburned	Nonclonal
Bromus tectorum L.	Both	Nonclonal
Cactaceae Juss.	Unburned	Nonclonal
Calamagrostis rubescens Buckley	Unburned	Nonclonal
Campanula rotundifolia L.	Both	Clonal
Carex rossii Boott	Both	Clonal
Carex scopulorum T. Holm.	Both	Nonclonal
Carex sp. L.	Unburned	Nonclonal
Castilleja puberula Rydb.	Both	Nonclonal
Centaurea montana L.	Burned	Nonclonal
Cerastium arvense L.	Both	Clonal
Cercocarpus montanus Raf.	Both	Nonclonal
Chamaenerion angustifolium (L.) Holub ssp. *angustifolium*	Burned	Nonclonal
Chenopodium album L.	Both	Clonal
Chrysothamnus sp. Nutt.	Both	Nonclonal
Cirsium arvense (L.) Scop.	Both	Clonal
Cystopteris fragilis (L.) Bernh.	Unburned	Clonal
Draba graminea Greene	Unburned	Clonal
Echinocereus sp. Engelm.	Unburned	Nonclonal
Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird	Burned	Nonclonal
Erigeron annuus (L.) Pers.	Both	Nonclonal
Erigeron eximius Greene	Both	Nonclonal
Eriogonum umbellatum Torr.	Both	Nonclonal
Erysimum capitatum (Douglas ex Hook.) Greene	Both	Nonclonal
Euonymus sp. L.	Both	Nonclonal
Euphorbia brachycera Engelm.	Burned	Nonclonal
Festuca arizonica Vasey	Burned	Nonclonal
Festuca saximontana Rydb.	Burned	Nonclonal
Gaillardia aristata Pursh	Burned	Nonclonal
Galium boreale L.	Unburned	Nonclonal
Galium triflorum Michx.	Unburned	Nonclonal
Geranium sp. L.	Both	Nonclonal
Helianthus pumilus Nutt.	Both	Nonclonal
Heracleum maximum W. Bartram	Unburned	Nonclonal
Hesperostipa comata (Trin. & Rupr.) Barkworth	Both	Nonclonal
Heterotheca villosa (Pursh) Shinners	Both	Nonclonal
Heuchera bracteata (Torr.) Ser.	Both	Nonclonal
Heuchera parviflora Bartlett	Both	Nonclonal
Juniperus communis L.	Both	Nonclonal
Juniperus scopulorum Sarg.	Unburned	Nonclonal
Koeleria macrantha (Ledeb.) Schult.	Both	Clonal

Continued.

Species	Plot Type	Plant Type
Lupinus angustifolius L.	Both	Nonclonal
Lupinus argenteus Pursh	Both	Nonclonal
Luzula parviflora (Ehrh.) Desv.	Burned	Nonclonal
Mertensia ciliata E. (James ex. Torr) G. Don	Unburned	Nonclonal
Oxalis albicans Kunth	Unburned	Nonclonal
Oxytropis campestris (L.) DC.	Both	Clonal
Packera multilobata (Torr. & A. Gray ex A. Gray) W.A.Weber & Á. Löve	Both	Nonclonal
Pascopyrum smithii (Rydb.) Á. Löve	Unburned	Nonclonal
Pascopyrum sp. Á. Löve	Both	Nonclonal
Penstemon sp. Schmidel	Both	Nonclonal
Penstemon strictus Benth.	Both	Nonclonal
Penstemon whippleanus A. Gray	Burned	Nonclonal
Phleum pratense L.	Both	Clonal
Physaria acutifolia Rydb.	Burned	Nonclonal
Pinus contorta Douglas ex Loudon	Unburned	Nonclonal
Pinus flexilis James	Both	Nonclonal
Pinus ponderosa Lawson & C. Lawson	Both	Nonclonal
Poa bulbosa L.	Both	Clonal
Poa nervosa (Hook.) Vasey	Unburned	Nonclonal
Poa pratensis L.	Burned	Clonal
Polemonium sp. L.	Burned	Nonclonal
Populus tremuloides Michx.	Burned	Clonal
Pseudocymopterus montanus (A. Gray) J.M. Coult & Rose	Both	Clonal
Pseudotsuga menziesii (Mirb.) Franco	Both	Nonclonal
Pulsatilla patens (L.) Mill.	Both	Clonal
Purshia tridentata (Pursh) DC.	Both	Clonal
Ranunculus adoneus A. Gray	Unburned	Nonclonal
Ribes aureum Pursh	Both	Clonal
Ribes sp. L.	Both	Nonclonal
Rosa sp. L.	Burned	Nonclonal
Rosa woodsii Lindl.	Burned	Nonclonal
Rubus idaeus L.	Both	Clonal
Salix sp. L.	Burned	Clonal
Sedum lanceolatum Torr.	Both	Nonclonal
Solidago multiradiata Aiton	Both	Nonclonal
Solidago simplex Kunth	Both	Nonclonal
Sporobolus cryptandrus (Torr.) A. Gray	Burned	Nonclonal
Symphoricarpos albus (L.) S.F. Blake	Burned	Nonclonal
Symphoricarpos orbiculatus Moench	Burned	Clonal
Taraxacum officinale F.H. Wigg.	Both	Clonal
Thalictrum alpinum L.	Burned	Clonal
Tradescantia occidentalis (Britton) Smyth	Burned	Nonclonal
Tradescantia sp. L.	Burned	Nonclonal
Tragopogon dubius Scop.	Both	Clonal
Trifolium pratense L.	Both	Nonclonal
Trisetum spicatum (L.) K. Richt.	Burned	Nonclonal
Verbascum thapsus L.	Both	Nonclonal
Viburnum edule (Michx.) Raf.	Unburned	Nonclonal
Vicia sativa L.	Burned	Clonal
Vulpia octoflora (Walter) Rydb. var. *octoflora*	Burned	Nonclonal