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Source: Natural Areas Journal, 42(1) : 4-17

Published By: Natural Areas Association

URL: https://doi.org/10.3375/21-14

Research Article

Post-fire Effects on the Globally Imperiled Chapin Mesa Milkvetch (*Astragalus schmolliae*), 2001–2019

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Associate Editor: Paula Fornwalt

ABSTRACT

Chapin Mesa milkvetch (*Astragalus schmolliae*) is an endemic, obligate piñon-juniper woodland species that occupies approximately 2500 ha in southwest Colorado. In 2002 a crown fire burned 38% of the known distribution in Mesa Verde National Park. Initially, Chapin Mesa milkvetch (CMM) responded positively to the 2002 burn, increasing in density compared to unburned areas. Nine years post-fire (2011), the density in burned areas was nearly twice that of unburned transects. By 2013, the pattern had reversed, and by 2019, the juvenile and adult population in the burned area was reduced to half that of unburned (0.046 plants/m^2 vs. 0.089 plants/m^2). Recruitment of CMM in burned areas in 2019 was near zero: 4 seedlings in 63 burned transects vs. 6079 seedlings in 105 unburned transects. The downward trend in CMM density in the burn is likely associated with intensified competition from the dense grass cover. Prior to the burn, the grass cover in the to-be-burned area was qualitatively similar to that in present day unburned areas, which is 15%, almost exclusively muttongrass (*Poa fendleriana*), a shallow-rooted bunch grass. In 2019, cheatgrass (*Bromus tectorum*) and western wheatgrass (*Pascopyrum smithii*), seeded in 2002, dominated the cover in the burn, averaging 45% cover, collectively. Management practices that assist the recovery of burned piñon-juniper woodland (and therefore CMM), as well as preserving the remaining old-growth piñon-juniper stands, are likely key to CMM long-term survival.

Index terms: cheatgrass; pinyon-juniper; post-fire seeding; succession; wheatgrass

INTRODUCTION

The piñon-juniper ecosystem, covering 48 million acres in Nevada, Utah, Colorado, Arizona, and New Mexico (Miller et al. 2019), is vitally important for biodiversity, and is an important cultural element for Native Americans (Floyd 2003). Nearly 25 bird species depend on this habitat type (Salaz and Wickersham 2016), including piñon jay (*Gymnorhinus cyanocephalus* Wied), gray vireo (*Vireo vicinior* Coues), and juniper titmouse (*Baeolophus ridgwayi,* Richmond)—all piñon-juniper obligates that are declining (Boone et al. 2018). A number of rare plant species occur within this landscape, including Chapin Mesa milkvetch (CMM; *Astragalus schmolliae* C.L. Porter). The outlook for the piñon-juniper system is fraught, as climate change may eliminate or alter current stands, primarily due to a hotter and drier climate and lower available soil moisture, leading to extreme tree mortality, increased fire frequency, and insect outbreaks (Breshears et al. 2005; Adams et al. 2009; Rondeau et al. 2017; Andrews et al. 2018; Friggens et al. 2018). Stand-replacement fire intervals in piñon-juniper habitat at Mesa Verde National Park (NP) were about 400 y prior to 1995 (Erdman 1970; Floyd et al. 2004), after which Floyd et al. (2004) stated that the strong post-1995 uptick in Mesa Verde NP fires was an increase in frequency and size, likely due to a change in climate. Prior to 1996, most fires at Mesa Verde NP were small (<0.1–4 ha). Nearly one-half of the piñon-juniper stands in Mesa Verde NP have burned in the past 30 y, more than three times the total area burned in the previous century (Floyd et al. 2021).

Recovery of a piñon-juniper woodland stand after a large fire is on the order of centuries rather than decades (Erdman 1970; Huffman et al. 2012). Erdman (1970) found that at Mesa Verde NP, several centuries passed before the structure began to resemble an old-growth woodland. Huffman et al. (2012) observed that aggregate structural complexity generally increased as a linear function of time since fire, with the most complex woodlands occurring after 250 y. The seral stages that a site experiences may vary based on pre-fire vegetation as well as establishment of nonnative species (Floyd et al. 2021). Erdman (1970) noted that perennial grasses dominated the early stages of a burned woodland, reaching a peak around 4 y post-fire. Under natural regeneration, these grasses consisted of muttongrass (*Poa fendleriana* (Steud.) Vasey), Indian ricegrass (*Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth), and squirreltail grass (*Elymus elymoides* (Raf.) Swezey), all native bunch grasses that occur in the Park's piñon-juniper stands. After about 25 y, shrubs (e.g., bitterbrush, [*Purshia tridentata* (Pursh) DC.], banana yucca [*Yucca baccata* Torr.], and mountain mahogany [*Cercocarpus montanus* Raf.]) became the dominant vegetation. Concurrently, seedlings of piñon pine (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* (Torr). Little) established, generally in the shade of these nurse-plant shrubs. After several centuries, the trees dominated and the understory was composed of sparse shrubs, grasses, and forbs. Erdman's (1970) mature forest description and persistent woodland conditions, put forth by Huffman (2012), mirrors the old-growth stands that currently exist in Mesa Verde NP. The majority of the CMM population occurs in old-growth piñon-juniper stands, thus the post-fire changes are of interest.

Plant Description

CMM is among the most restricted of Colorado's plant species. The species consists of one population and a few small peripheral subpopulations. It is endemic to Chapin Mesa and Park Mesa, a minor portion of Mesa Verde NP and Ute Mountain Ute tribal land. A recent genetic study indicated that CMM had a high level of interconnectedness through gene flow, likely mediated through pollinator behavior. At the current time, it does not appear to be suffering genetic consequences from its small range size (McCauley and Cortes-Palomec, pers. comm.). The primary population occupies about 2500 ha on Chapin Mesa of which 806 ha is within Mesa Verde NP. It grows primarily in deep red loess soil characterized as a clay to clay loam (NRCS 2017). Although this species is globally rare, it is one of the densest forbs on Chapin Mesa, with an estimated 500,000 plants in the Park portion of the mesa (Anderson 2001). It is currently proposed as threatened by the USFWS (2020) and is given a global conservation status rank of G1 (Globally Critically Imperiled) by Colorado Natural Heritage Program (CNHP 2020). The International Union for the Conservation of Nature gives this species its highest global ranking: Critically Endangered (Contu 2012).

CMM is an herbaceous perennial, estimated to live 2–3 decades or more, based on 100% survival rate of adult plants observed for 6 y in unburned areas and caudices with up to 39 annuli (Rondeau pers. obs.). The taproot of mature plants extends down 35–55 cm before sending out lateral roots (Friedlander 1980; Rondeau pers. obs.), enabling the plant to exploit water resources moderately deep in the soil, which are replenished by winter moisture. Above ground, mature stems reach a height of around 25 cm, arising from a woody caudex that is buried approximately 5–10 cm below the soil surface. The aboveground stems wither away in the fall, and new sprouts arise in the spring. This subterranean caudex is insulated from the heat of fires; thus, CMM individuals routinely survive fires. After severe winter drought years, most plants remain dormant throughout the following growing season, with no visible growth. (Dormancy has also been recorded in other *Astragalus* species, e.g., Gremer 2010.) Therefore, apparent density (number of visible plants per square meter) will reflect true density (live plants/m^2) only in wetter years; in this work "density" records the number of emerged plants (apparent density).

In favorable years, both flowers and fruits are present in late May and fruits expel their seeds in late June. The species is characterized by showy, bee-pollinated white flowers and downward-curving pods. Seed production can be robust in favorable years (Anderson 2004) and seed longevity likely extends over many years (Anderson 2004). Seeds germinate in April and May, and occasionally in June; however, seedlings may be completely absent in dry springs, such as 2001. Seedlings put much of their energy into growing a long taproot, rather than aboveground biomass, and seldom reach more than 7 cm in height. Plants can begin to flower when they are 5 y old (Rondeau pers. obs.). CMM is considered highly vulnerable to climate change due to its restricted range and increased habitat vulnerability (Handwerk et al. 2015).

Post-fire Management

Floyd et al. (2006) documented an invasion of musk thistle (*Carduus nutans* L.) and cheatgrass (*Bromus tectorum* L.) following fires (1989, 1996, and 2000) and concluded that post-fire seeding would reduce musk thistle. Following the 2002 Long Mesa fire, Mesa Verde NP managers seeded part of the burn in 2003 with five species of native bunch grasses: slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), muttongrass, Sandberg bluegrass (*Poa secunda* Presl.), Indian ricegrass, and squirreltail, and one rhizomatous grass, western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve). The seed mix may have had incidental nonnative cheatgrass; however, it most likely colonized the burned areas from the adjacent Chapin 5 fire which burned in 1996 and had a considerable cheatgrass component (Floyd et al. 2006). The seed mix was largely intended to reduce weed invasions and erosion, and restore natural post-fire succession. Western wheatgrass, while native to Mesa Verde NP, does not currently occur in the CMM population within the piñon-juniper old-growth (Kuhn and Anderson 2012; Rondeau pers. obs.). The current post-fire grassland on Chapin Mesa is vastly different from the one Erdman (1970) described, as it is dominated by cheatgrass and western wheatgrass rather than native bunch grasses. The novel invaders are successful competitors for soil moisture, thereby exhibiting increased biomass, both above and below ground (e.g., Weaver 1919; Harris and Wilson 1970; Melgoza et al. 1990). This novel system likely competes with CMM for limited soil moisture and nutrients. It may also retard establishment of shrubs, considered nurse plants for piñon pine seedlings.

Friedlander (1980) concluded that the abundance of CMM was due to lack of fires. He predicted that fires might significantly reduce densities during post-fire successional periods, primarily due to seed mortality from high fire temperatures. However the opposite occurred following the 1996 Chapin 5 fire, which burned old-growth piñon-juniper woodlands. Other species of *Astragalus* have been known to germinate after fires (e.g., Hessl and Spackman 1995; Fotheringham and Keely 1998; Schwegman 1998; Weeks 2004: pp. 47–70). Researchers associated with the BAER (Burned Area Emergency Response) monitoring program detected an enhancement of growth, flowering, and seed set as well as seedling recruitment after fire (Floyd et al. 1999). Infrequent stand replacing fire stimulated a CMM population on Park Mesa, which showed some decline in density in the next 8 y (Funicelli and Floyd-Hanna, pers. comm.). Floyd et al. (1999) and associates suggested that further studies be conducted to assess the impact of possible competition from seeded native perennial grasses.

It is critical that managers have a clear understanding of short- and long-term consequences of fire. In this study, we began monitoring CMM in 2001, one year prior to the Long Mesa Fire. We had five main research questions: (1) Is seasonal precipitation an important variable in annual CMM emergence? (2) How does CMM density change over time in burned vs. unburned areas? (3) How does CMM recruitment change over time in burned vs. unburned areas? (4) How did the herbaceous ground cover, in CMM habitat, change over time, within the burned area? and (5) How does the root structure of plant communities, within CMM habitat, differ between burned and unburned areas? All of these factors are increasingly relevant to researchers and managers faced with increased wildland fires in the piñon-juniper woodlands.

METHODS

We sampled CMM seedlings, juveniles, and adults and collected herbaceous cover data, within burned and unburned transects in years 2001, 2002, 2003, and 2011–2019. We conducted a literature review of root biomass for the dominant species in burned and unburned transects.

Site Description

Chapin Mesa is approximately 14 km long by 1.5 km wide, highest in the north (2290 m) and lowest in the south (2000 m). The highest points on the mesa are generally in the middle of the mesa, sloping slightly to the east and west before reaching cliff edges on both sides. Soils near the center top of the mesa are deep and fine, with few rock fragments and slow water infiltration (Rondeau pers. obs.), whereas soils closer to the cliffs are shallower and coarser with a high percentage of small rock fragments and fast infiltration (Rondeau pers. obs.). Prior to the 2002 Long Mesa Fire, the entire mesa was dominated by old-growth piñon-juniper woodlands (Floyd et al. 2004; Figure 1A). Shrubs occupied a lesser extent than trees, with bitterbrush occurring more often than Utah serviceberry (*Amelanchier utahensis* Koehne) and mountain mahogany. The ground cover was generally sparse (<20% cover), dominated by muttongrass, prickly pear, and CMM. Bare ground was abundant and often covered by biological soil crust. Figure 1 provides photographs that depict old-growth piñon-juniper, 1 y post-fire and 17 y post-fire.

Areas that burned in 2002 (Figure 1B) had standing dead trees 17 y post-fire (Figure 1C). The burned landscape differed from the woodland in that it was dominated by cheatgrass, western wheatgrass, muttongrass, and smooth brome (*Bromus inermis* Leyss.), and possessed little open ground and only a low cover of biological soil crust. By 2019 a sparse shrub component had emerged, occupying approximately 1–3% of the landscape: the most common shrubs were bitterbrush, banana yucca, rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird), and Utah serviceberry.

Cultural History: Chapin Mesa has a long and rich cultural history. From circa 500 to 1300 C.E. this region was home to a group of farming and hunting people (Ancestral Puebloans; Herring et al. 2014). Archeologists documented that they raised corn, beans, and squash on Chapin Mesa and utilized the wild seeds, nuts, roots, and greens of their woodland environments (Flint-Lacey 2003). Piñon and juniper trees were used as building materials, firewood, and various other objects. Hundreds of Ancestral Pueblo settlements on Chapin Mesa in Mesa Verde NP have been recorded by archeologists. The piñon-juniper stands on the mesa were altered to provide space for their farmsteads and villages that contained numerous pit structures, aboveground rooms, storage features, and agricultural fields. It is unknown if CMM was utilized by the Ancestral Pueblo people, however the seeds are not known to be poisonous (Rondeau pers. obs.).

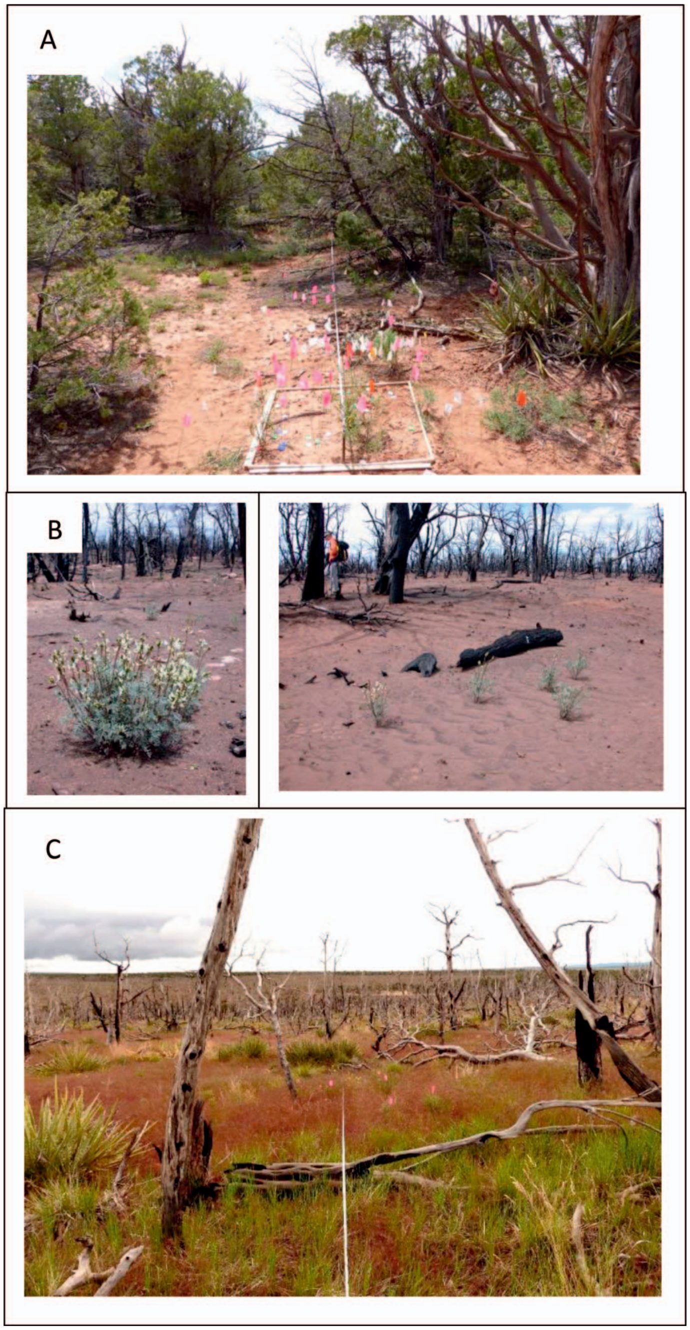

Figure 1.—A: Representative photo of old-growth piñon-juniper woodland (flags mark Chapin Mesa milkvetch [CMM] individuals). B: One-year post burn with CMM flowering (closeup on left). C: 17 y post-fire; cheatgrass is brownish-red and western wheatgrass is green (pin flags mark CMM).

Climate: The Chapin Mesa weather station is located at the northern edge of CMM habitat and was used to describe the climate. The climate (Colorado Climate Center 2020; http://climate.colostate.edu/data_access.html) is best characterized as cool winters, winter days having an average low of –7 °C and an

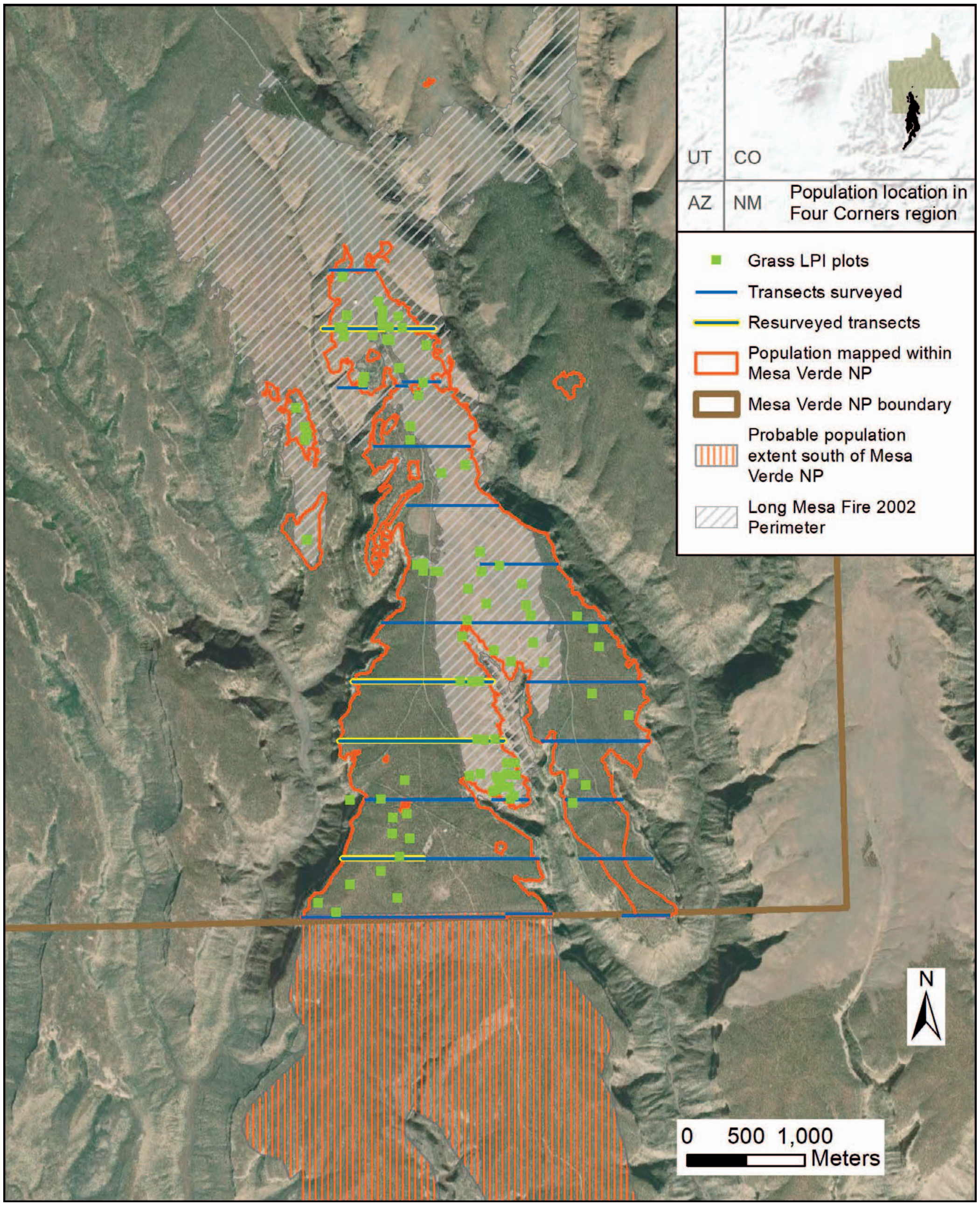

Figure 2.—Chapin Mesa study area within Mesa Verde NP. Sample plot locations: transects, resurveyed transects, and grass line-point intercept (LPI) plots.

average high of 5 °C. Summers experience an average high of 28 °C and low of 12 °C. Annual precipitation averages 468 mm, but is highly variable (251–670 mm). Winter precipitation averages 117 mm, primarily in the form of snow, and summer averages 107 mm. May (31 mm) and June (13 mm) are the driest months. During the course of this study (2001–2019), average annual temperature was 0.8 °C warmer than the 1971–2000 average and annual precipitation was close to the natural range of variation. Droughts are fairly common; the last 2 decades experienced significant long and extreme droughts in 2002, 2012, and 2018 (Abatzoglou et al. 2017; accessed 2020 from https://droughtindexportal.colorado.edu/).

Study Design and Field Methods

Precipitation data from Mesa Verde NP on Chapin Mesa (Colorado Climate Center 2020) were used to identify a 30 y average (1971–2000) for winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov) seasons. We compiled precipitation data for each sampling year as well. We used this information to determine if seasonal precipitation was correlated with annual variation in (observable) density counts of all age classes pooled.

To estimate density of Chapin Mesa milkvetch we established 197 belt transects (10 × 100 m; Figure 2). All transects were within Mesa Verde NP on Chapin Mesa. We established the first line of transects at the southern park boundary, running east to west. Transects on an east–west line were contiguous to each other, that is, where one transect ended, the next transect began. We placed subsequent lines of transects 500 m north of the previous line (Figure 2) to the limit of the distribution of CMM. We conducted density sampling of 197 transects in May of 2001 and 2019. For each transect, a center line was established on the northing UTM (NAD83) and we counted all plants within a 5 m perpendicular distance on both sides of the transect center line. We tabulated seedlings, noted by the presence of cotyledons, separately from juvenile and adult plants. We report density as the number of visible plants/m^2. The 2002 Long Mesa fire completely burned 63 transects; 29 transects were either partially burned in 2002 or partially mechanically treated after 2002 to reduce the fire risk. We removed these 29 transects from our analysis. Thus in 2019 we resampled 63 burned (described as to-be-burned in 2001 data) and 105 unburned transects.

In order to determine temporal changes in density, we resampled a suite of nonrandomly, logistically feasible, subset of transects that represented the north–south and east–west gradient. Sampling occurred in 2003 and annually from 2011 to 2019 (Figure 2), utilizing the same methods as above ($n = 17$ burned transects; 22 unburned). We label these as "trend density transects."

We estimated grass cover in burned areas in 2011 and 2015–2019 using the line-point intercept method, at 0.5 m intervals (Canefield 1941). In 2011 this was based on 82 randomly selected, 60 m long transects on Chapin Mesa (Figure 2), 61 burned and 21 unburned; measuring the dominant species: cheatgrass, western wheatgrass, smooth brome, muttongrass, and Indian ricegrass. From 2015 to 2019 grass cover in the burn was assessed with a subset ($n = 10$) of our trend density transects, based on line-point intercepts along a 50 m transect, collecting cover for only the dominant grass species: cheatgrass and western wheatgrass. In order to characterize year-to-year changes in grasses, we also acquired remote sensing data from Rangeland Analysis Platform (Jones et al. 2018; https://rangelands.app) for the Long Mesa fire area. This dataset distinguished annual grasses combined with annual forbs from perennial grasses combined with perennial forbs. We use both data sets to describe changes in herbaceous cover 2001–2019.

In order to understand potential belowground interactions (competition) among the different species, we conducted a literature review of root structure and biomass depth for the common species in both the burned and unburned area.

Data Analysis

To determine if annual variation in CMM density was associated with annual precipitation patterns, we used ordinary least-squares to ascertain if there was a correlation between seasonal deviation from 1971–2000 average precipitation and annual emergence (apparent density), based on 11 sampling years (2001, 2003, and 2011–2019). Because the burn first increased density and later decreased density (this paper), we based the correlations solely on unburned transects ($n = 22$). CMM density was not normally distributed, thus densities are reported as median rather than mean. A linear regression equation was developed from the relationship between median density and winter precipitation to estimate expected apparent density among years of varying precipitation.

Chapin Mesa precipitation patterns are considered to be nearly identical within a given year, regardless of burned/unburned status, therefore we can compare annual median densities between burned vs. unburned condition. We first compared densities of all individuals between burned and unburned transects in 2001 and 2019, then contrasted the age classes separately (seedlings distinguished from all older individuals). As the correlation between winter precipitation and CMM density was based on all individuals, expected densities were available to reference only the former comparison (i.e., all individuals counted on burn vs. unburned plots in 2001 and 2019). Since the data were not normally distributed, we used a Mann-Whitney *U*-test for statistical testing.

To assess the trend difference between burned and unburned transects 2001–2019 we plotted the raw median densities and displayed a linear regression line to visualize overall change over time. To remove the influence of winter precipitation, we calculated annual residuals for each transect ($n = 39$) for the years 2011–2019. The residuals were based on our winter precipitation linear regression model, which provided expected density for each year. We regressed the transect residuals to estimate time trend for each transect independently. We contrasted the normally distributed slopes between burned ($n = 17$) vs. unburned ($n = 22$) transects with a two-sample *t*-test, assuming unequal variances.

In this work we estimate pre-burn grass cover and its change over time in burned areas, using both plot and remote-sensing data, but we conducted no statistical tests of temporal change.

RESULTS

Seasonal Precipitation and CMM Density

Winter precipitation correlated positively with CMM density $r^2 = 0.76$, $P < 0.00001$ (Figure 3A); no other season was correlated. The linear regression estimated plant density $y = 0.065x + 0.043$ plants/m^2, where x is the deviation from average winter precipitation. No CMM emerged following winters in which Chapin Mesa received less than 40% of average winter precipitation. Such extreme winter droughts occurred in 2002, 2006, 2014, and 2018. We recorded zero densities in forested plots in 2014 and 2018 and did not observe any plants outside the plots in the unburned area. George San Miguel (Mesa Verde NP Chief of Natural Resources in 2002) stated that he did not observe any plants in 2002, however he did not sample all of the transects; we have no direct observations for 2006 but we assume that the plants remained dormant in that year as well.

Density in 2001 and 2019

In 2001, the winter precipitation (Dec–Feb) of 2000–2001 was –27% of the 1971–2000 average, thus the expected median density for all age classes in spring 2001 was 0.030 plants/m^2, using the regression above. The soon to-be-burned (63 transects) and the to-remain-unburned (105 transects) closely matched this expectation (Figure 3B). The median density in 2001 to-be-burned areas was 0.036 plants/m^2 (InterQuartile Range [IQR]: 0.01 to 0.08); median in unburned areas was 0.043 plants/m^2 (IQR: 0.01 to 0.09). In 2018–2019 winter precipitation was 87%

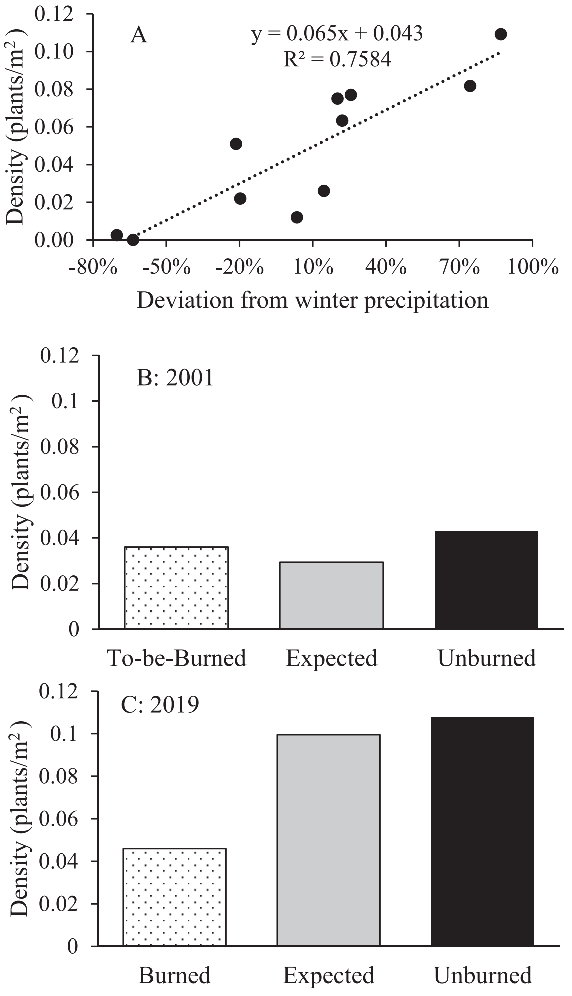

Figure 3.—A: Chapin Mesa milkvetch (CMM) median density (all age classes) vs. deviation from 1971–2000 average winter precipitation, in unburned transects ($n = 22$). Each dot represents a sample year (2001, 2003, 2011–2019). The precipitation values are from the Chapin Mesa weather station. B: CMM median density in 2001 and 2019 (C) comparing burned and unburned transects to the expected values derived from the regression equation in A. In 2001, prior to the burn, densities were similar between to-be-burned and unburned transects; in 2019 transects that burned were approximately one-half of the expected density (see text for full discussion).

above the 1971–2000 average; the expected median density for all age classes in spring 2019 was 0.100 plants/m^2. The unburned area closely matched expectations: median density was 0.108 plants/m^2 (IQR: 0.02 to 0.24); burned median density was approximately half of expected at 0.046 plants/m^2 (IQR: 0.02 to 0.09; Figure 3C).

We analyzed the same dataset as above, separating juveniles and adults from seedlings. There was no statistical difference between to-be-burned and unburned transects in 2001. By 2019, unburned transects had over twice the median density of adults and juveniles as burned transects: 0.089 vs. 0.046 plants/m^2 ($P <$ 0.008). Seedlings were not observed in 2001. In 2019, a good seedling year, seedlings were rare in burned transects (4 in 63 transects) and abundant in unburned areas (6079 seedlings in 105 transects). We detected significant differences between 2019 burned and unburned transects using Mann-Whitney *U*-Tests ($P < 0.008$ for juveniles/adults and $P < 0.001$ for seedlings).

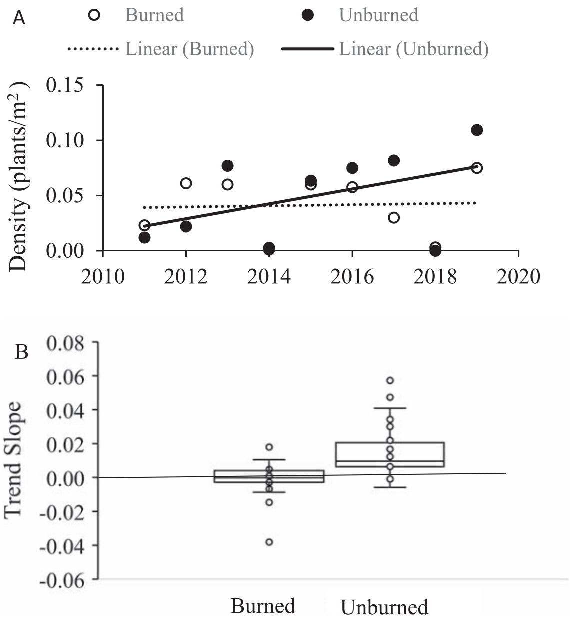

Figure 4.—Density trend of Chapin Mesa milkvetch (CMM) from burned and unburned belt transects, 2011–2019, by two metrics. A: The lines represent linear regressions of median annual densities, represented by open circles for burned, and closed circles for unburned. B: The trend slopes were generated by calculating residuals for each transect's annual count in relation to the count expected on the basis of the preceding winter's precipitation (Figure 3). We used linear regression to estimate overall slope of each transect's nine annual counts (2011–2019). Positive slopes represent an overall increase in CMM population adjusted for precipitation and values below zero represent a declining population. Individual transects are represented by open circles ($n = 17$ burned, 22 unburned, some concealed by overlap). The two treatments differed: $P = 0.0003$.

Density Trend from Repeated Belt Transects

In 2001, prior to the 2002 Long Mesa Fire, CMM median density was nearly identical in unburned ($n = 22$) and to-be-burned transects ($n = 17$), 0.50 and 0.51 plants/m^2, respectively. Following the fire, relative density increased in the burned transects and was higher than unburned transects in 2011 and 2012 (Figure 4A). In 2013 this pattern reversed; density in burned transects was less than in unburned transects (Figure 4A). In 2014, another serious winter drought suppressed emergence. In 2016–2019 the gap between burned and unburned density widened, except during the 2018 drought year, when no difference was recorded due to most plants not emerging (Figure 4A). We displayed the linear regression slope for the median density data from the 2011–2019 consecutive years for burned and unburned transects (Figure 4A). The burned transects had a flat slope and the unburned transects had a positive slope. In unburned transects the slope of residuals was positive (only 13% of the transects had a negative slope; i.e., decreased), while the majority (53%) of the transects in the burned had a negative slope (Figure 4B). The trend slopes in residual plant density were significantly lower in the burn compared to the unburned ($P < 0.0003$).

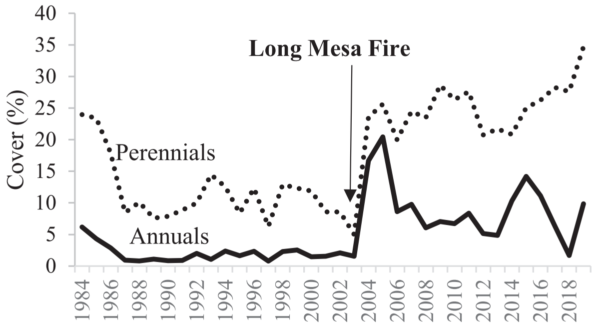

Figure 5.—The aggregate cover of perennial grasses and forbs (dashed) and annual grasses and forbs (solid) from the Rangeland Analysis Program (Jones et al. 2018; https://rangelands.app). The values shown are means for the entire Long Mesa Fire burn area.

Herbaceous Cover

Herbaceous cover, especially annual and perennial grasses, increased in the burned areas (Figure 1C) while they remained steady in the unburned areas (Figure 1A). In 2003, 1 y after the burn, the ground was barren and black with ash (Figure 1B) with CMM a conspicuous exception. Anderson (2004) noted a few additional species emerging in the burned area, especially Canada thistle (*Cirsium arvense* (L.) Scop.). Anderson (2004) also noted an abundance of CMM seedlings in both the burned and unburned areas. The Rangeland Analysis Platform also depicted a paucity of herbaceous cover in 2003 (Figures 5 and 6). Muttongrass, the dominant grass in the unburned areas, averaged around 15% cover in 2011, and our annual observations did not detect any change over the time we have been collecting data. In the burned area, grasses progressively gained cover, especially in non-drought years. In 2011, annuals averaged 19% cover and perennials averaged 21% cover in the Rangeland Analysis Platform dataset for burn areas (Figure 5). The Rangeland Analysis Platform results were similar to our on-the-ground 2011 observations; cheatgrass averaged 19% cover and perennial grasses averaged 22%. In our data collection in 2019, cheatgrass (annual) averaged 26% cover and western wheatgrass (perennial) 20% cover; the Rangeland Analysis Platform app detected a 35% average cover of aggregated perennial grasses and forbs (all species) at that time and 10% cover of annuals. We believe that Rangeland Analysis Platform

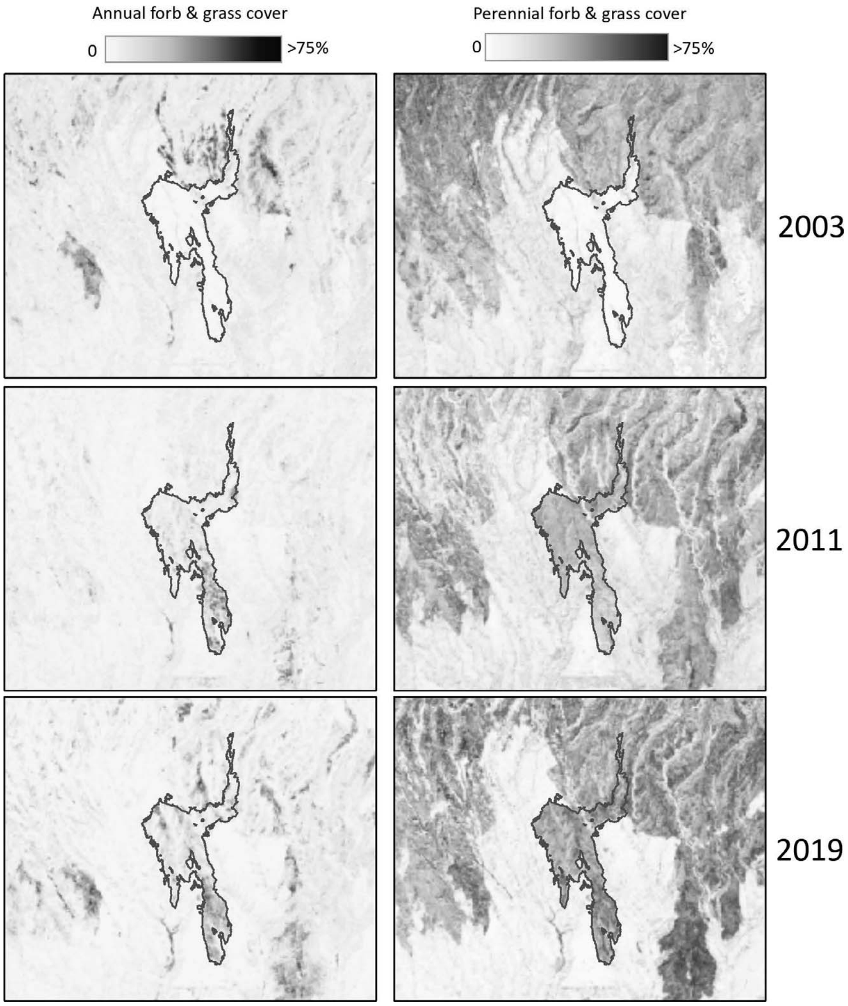

Figure 6.—Maps from Rangeland Analysis Program depicting the cover of herbaceous annuals (left column) and perennials (right column) for 2003 (upper row), 2011 (middle row), and 2019 (bottom row). Darkness of shading indicates relative cover. The area burned by the Long Mesa Fire, 2002, is outlined. The light areas outside of the polygon (easily seen in the perennial panel) are vegetated by forest.

Table 1.—Rooting depth, depth of ≥50% root mass, and lateral root length for the dominant species on Chapin Mesa, Mesa Verde NP.

Species	Maximum root depth (cm)	Depth of ≥50% root mass (cm)	Lateral root length (cm)	Source
Forbs				
Chapin Mesa milkvetch (*Astragalus schmolliae*)	50	40	15	Friedlander 1980; Rondeau pers. obs.
Toadflax penstemon (*Penstemon linarioides*)	20	15	30	Rondeau pers. obs.
Grasses				
Cheatgrass (*Bromus tectorum*)	87–150	1–30	10	Spence 1937; Hulbert 1955; Harris and Wilson 1970; Arredondo et al. 1998
Squirreltail (*Elymus elymoides*)	50	1–30	minor	Reynolds and Fraley 1989
Needle-and-thread (*Hesperostipa comata*)	60	1–20	50	Melgoza and Nowak 1991
Western wheatgrass (*Pascopyrum smithii*)	200	1–150	Long rhizomes	Weaver 1919; Coupland and Johnson 1965
Mutton grass (*Poa fendleriana*)	25	1–20	5	Rondeau pers. obs.
Shrubs				
Mountain mahogany (*Cercocarpus montanus*)	100–150	30	150–300	Berndt and Gibbons 1958
Rubber rabbitbrush (*Ericameria nauseosa*)	183	1–100	few lateral roots	Klepper et al. 1985
Bitterbrush (*Purshia tridentata*)	150–250	1–30	60	Cline 1960; McConnell 1961; Baker and Torrey 1979
Trees				
Piñon pine (*Pinus edulis*)	600	23–38	twice the crown radius	Foxx and Tierney 1987; Gottfried 1992; Rau et al. 2009; Schwinning et al. 2020
Utah juniper (*Juniperus osteosperma*)	450	30–90	300	Skau 1960; Tiedemann 1987

was better at detecting perennials than annuals, thus if we combine Rangeland Analysis perennials (35% cover) and onsite-measured cheatgrass cover (26%) the estimated herbaceous cover was about 61% in 2019, an increase of some 20% over 2011 estimates.

Root Structure and Biomass of Common Species

A literature review of root structure of the dominant species in an unburned old-growth woodland revealed stark differences from the dominant species in the burned site (Table 1 and Figure 7). In the old-growth site, CMM adult plant roots were in an intermediate root-depth zone, a zone where other species had fewer roots. The dominant trees, piñon pine and juniper, had much of their shallow root biomass in the 25–30 cm depth, primarily at the edge of the tree crown (Schwinning et al. 2020), and a tap root reaching depths of up to 6 m. Bitterbrush, the dominant but low cover shrub in the unburned forest, had a shallow root biomass (10–30 cm) in addition to a tap root that reached the 1.5 m depth (Cline 1960). In sharp contrast, the dominant cheatgrass and western wheatgrass in the burned area had fine and dense roots that densely occupied the 1–30 cm depth, as well as a column all the way down to a depth of 1.5 m for western wheatgrass (Table 1 and Figure 7).

DISCUSSION

Explaining variation in annual population estimates is fundamental to establishing a population trend. Understanding how populations vary in space and time and identifying the sources of that variation are important for predicting species responses to environmental change (Buckley et al. 2010). CMM has large year-to-year fluctuations in emergence, leading to high variation in annual density counts. This variation was statistically associated with winter precipitation; wet winters ensured high emergence of adults and juveniles; dry winters led to negligible emergence. The tight association between winter precipitation and annual emergence (Figure 3) allowed us to estimate expected density for any given year in response to weather fluctuations.

In 2001, we collected baseline density data across the Mesa Verde CMM population. In 2002, a stand-replacing wildfire swept through 38% of the NP population, completely altering the landscape (Figure 1B). CMM was able to withstand the fire due to its woody caudex, positioned 5–10 cm under the soil. Therefore, it was able to emerge as soon as favorable conditions returned. Prior to the burn, the density of CMM in unburned and to-be-burned transects was nearly identical (Figure 3B), thus any change in that ratio would suggest an effect of habitat alteration from the fire. CMM's vigor (number of stems, flowers per plant, and fruit set) one year after the fire (2003) was unprecedented in the burned area (Anderson 2004). Anderson also reported numerous seedlings emerging concurrent with the adults, reflecting a seed bank that had survived the fire. He attributed these results to a lack of competition for resources (water, sunlight, nutrients, and pollinators; Figure 1B). Nine years post-fire (2011), the CMM population in the burn was still thriving, as indicated by a density in burned transects about two times those in the unburned area (Figure 4A). Eleven years post-fire (2013), the tide began to shift and the pattern reversed. Seventeen years post-fire (2019), the density in the burn area was cause for conservation concern. The population of adults and juveniles in the burned area in 2019 was just half of that in the unburned area. Not only were adults and juveniles comparatively depopulated in the burned area, but recruitment (seedlings) was virtually nonexistent: we counted 4 seedlings in 63 transects in the burned area compared to over 6000 seedlings found in 105 transects of the unburned area. Poor recruitment, likely combined with elevated adult mortality, was presumably responsible for the population reduction observed in the burn. If this trend continues, CMM is at high risk of extirpation within the burned area. In contrast, despite three episodes of severe-

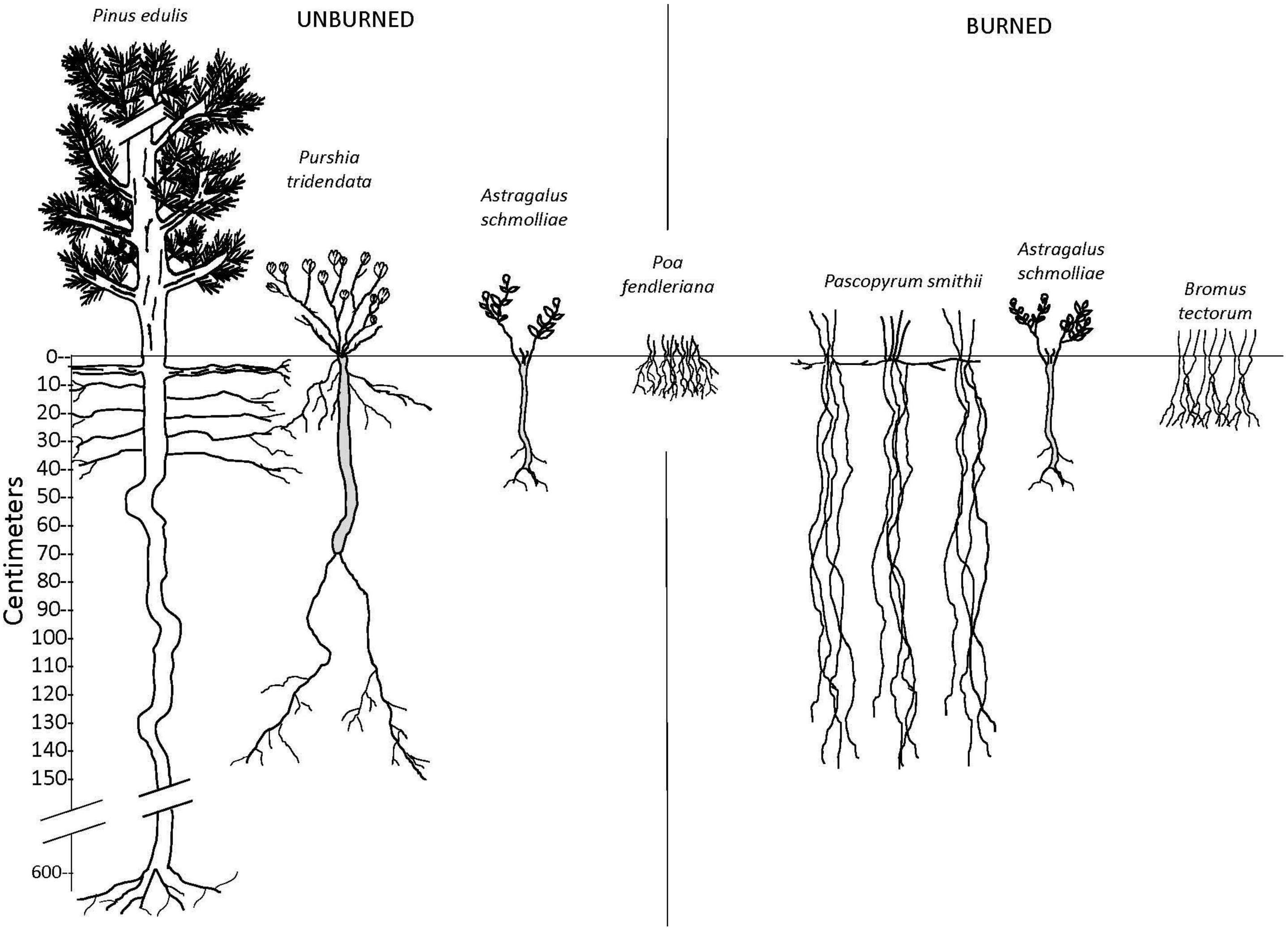

Figure 7.—Shoots and roots of the dominant species in the unburned and burned Chapin Mesa site. Note that adult and juvenile *Astragalus schmolliae* (CMM) experience little competition with roots in the unburned area, but are vulnerable to the aggressive spread of roots of *Pascopyrum smithii* (western wheatgrass) introduced into the burn area. *Bromus tectorum* (cheatgrass) in the burn intercepts moisture that would otherwise descend to the CMM roots.

extreme winter droughts between 2001 and 2019, the population of CMM in the unburned old-growth piñon-juniper forest was stable, i.e., density met expected values based off of winter precipitation correlation. In order for the CMM population in the burned area to recover, it appears that recruitment events need to increase. Reduced herbaceous ground cover would likely allow for germination.

The post-fire grassland system has few community similarities with the old-growth piñon-juniper woodland: abundant grasses, no trees, sparse shrubs, little bare ground, poorly developed biological soil crust, etc. This disparity likely is equally distinct below ground as it is above ground. Rooting depth and biomass of fine roots are integral to the success of plant species, especially in arid systems. Schenk and Jackson (2002) confirmed that a two-layer model of soil depth partitioning between woody and herbaceous plants appeared to be most appropriate in drier regimes (<500 mm mean annual precipitation) and in systems with substantial winter precipitation. Thus, this niche partitioning between woody plants and grasses is likely to be an important driver in Mesa Verde NP. Reich et al. (2001) found relative fine root biomass to be highest in a grassland system and lowest in a wooded system.

Piñon and juniper roots are distributed in a two-tiered system (Figure 7): a central tap root that can reach a depth of 6 m or more (Gottfried 1992) and an upper tier of lateral roots in the top 35 cm (Schwinning et al. 2020). Bitterbrush, the most common shrub in the old-growth woodlands, also has a two-tiered system; however, its tap root seldom extended beyond 1.5 m (Figure 7, Table 1). Muttongrass, the dominant woodland grass on Chapin Mesa, is a bunch grass that consists of fibrous roots concentrated in the top 20 cm (Figure 7; Rondeau pers. obs.). CMM's roots occupy an intermediate depth stratum, a niche that has lower competition from other species (Figure 7). Old-growth woodlands generally have less than 15% grass and shrub cover, therefore we infer, based off of our literature review, that CMM roots are primarily competing for soil moisture with the dominant tree roots; however, shrubs, if dominant, could likely compete with CMM. McHugh and Gehring (2006) documented that the aboveground shrub removal of Apache plume (*Fallugia paradoxa* (D. Don) Endl. Ex Torr.), skunk bush (*Rhus trilobata* Nutt.), and New Mexico privet (*Forestiera neomexicana* A. Gray) under piñon pine at Sunset Crater National Monument, northern Arizona, decreased shrub root biomass. In response, piñon pines, with their shrubs removed, had three-fold greater piñon root biomass than piñon with intact shrub associations. Our observations, along with the literature review of rooting depth patterns (Figure 7), strongly suggest that trees, shrubs, and grasses compete with CMM when soil moisture is limiting.

The underground root systems of the two dominant grasses in the burned area, western wheatgrass and cheatgrass, have an extensive network of fibrous roots, overlapping with the CMM rooting zone (Figure 7). Western wheatgrass can maintain a high root biomass; this biomass extends up to 1.5 m deep, and is connected by rhizomes in the upper 5 cm (Weaver 1942). Cheatgrass roots may obtain depths up to 1 m (Harris and Wilson 1970); however, most of the root biomass is in the upper 30 cm (Spence 1937; Hulbert 1955; Hironaka 1961). Western wheatgrass seedlings have been known to produce roots that extended to a depth of 76 cm when 3 mo old (Clements and Weaver 1924). Weaver (1942) found that height and seed production of other species growing within areas dominated by western wheatgrass were reduced compared to adjacent areas without western wheatgrass. The competition for water was also severe between the individual plants of wheatgrass and other species (Weaver 1942). Weaver found soil water content was often 3–8% higher in soils that had only bunchgrasses compared to soils dominated by western wheatgrass. The soil under western wheatgrass was always drier than under the prairie without western wheatgrass (Weaver 1942). Soil moisture depth was also significantly different for the same amount of precipitation; soils were wet to an average depth of 73 cm under native prairie bunch grasses versus only 26 cm under western wheatgrass, illustrating the degree to which infiltration of water into soil covered with wheatgrass was reduced (Weaver 1942). In addition to reducing soil moisture, areas dominated by western wheatgrass diminished forb richness and cover. Forb species richness was reduced by 44% and number of stems decreased by 80% in areas dominated by western wheatgrass. This included both deep- and shallow-rooted forbs. Therefore, seeding burned areas at Mesa Verde NP with western wheatgrass resulted in competition with CMM for available soil moisture.

Cheatgrass, a nonnative annual grass, can emerge in either fall or spring and has well-documented competitive attributes, similar to western wheatgrass. Cheatgrass that germinates in the fall continues root growth throughout the winter, and initiates shoot growth earlier in the spring than native plants, whereupon it reduces soil water content and has a large size advantage over spring-emerging forb seedlings (Arredondo et al. 1998). It uses more water earlier in the growing season than many native plants by initiating root and shoot growth at lower temperatures (Arredondo et al. 1998). The seedling stage of native species is vulnerable to competition from cheatgrass (Aguirre and Johnson 1991; Yelenik and Levine 2010). Parkinson et al. (2013) tested growth rates of big-seed biscuitroot (*Lomatium macrocarpum* Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose), a tap-rooted forb with no lateral root branches (hence similar to Chapin Mesa milkvetch root), in addition to four other forbs. Total biomass after 12 wk of growth was significantly lower (50%) when grown with cheatgrass. In addition, after 12 wk of growth, total biomass of all forbs when growing with a native grass was not different from those grown alone. In contrast, the total biomass of all forbs was reduced when grown with cheatgrass (Parkinson et al. 2013). Melgoza et al. (1990) observed that cheatgrass decreased the soil moisture available to needle-and-thread grass in burned areas during April and May, which are peak seedling months for CMM. Harris and Wilson (1970) found that rapidly elongating cheatgrass penetrated the soil ahead of blue bunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) roots and used the available moisture. Cheatgrass seedlings were therefore able to gain competitive advantage over blue bunch wheatgrass seedlings by rapidly elongating their roots during winter months and using moisture throughout the soil profile (Harris and Wilson 1970). They also found that seedlings of blue bunch wheatgrass were suppressed when cheatgrass was present. They concluded that competition from cheatgrass affected soil moisture, reducing the soil moisture when blue bunch wheatgrass seedlings were germinating. This same competition may be limiting CMM seedlings.

Increased competition from high herbaceous cover is a plausible reason for the decline in CMM density, however, additional factors to consider are altered light, increased temperature, insolation, reduced pollinators, and a change in herbivory. Further studies are required to determine the causative factors.

The current 17 y post-fire seral stage has little relation to the historic seral stages that Erdman described in 1963 (Erdman 1970). Historically, grass cover never exceeded 16% cover after a fire and only reached this level in the second seral stage of perennial grass/forb state, lasting up to 24 y. In contrast, we recorded grass cover at 40% and >45% cover in 2011 and 2019, respectively. The succession into a shrub dominated state also appears to bear little relation with the historical pathway. We currently estimate an average of 3% shrub cover, 17 y post fire, compared to 20% cover in a 29-year-old post-fire stand (Erdman 1970). Shrub cover will likely increase and perhaps obtain similar cover as the historical state; however, it is too soon to make a direct comparison.

The old-growth piñon-juniper woodland appears to be the preferred habitat for CMM. It provides an environment with relatively low competition for soil moisture, adequate pollinators, few ground dwelling herbivores, and ample space for seeds to germinate and thrive. The advanced development of biological soil crusts increases the resistance of invasive species, especially cheatgrass (Deines et al. 2007). The tree canopy cover provides shade that reduces soil temperatures. Breshears et al. (1998) found that soil temperatures were as much as 10 °C lower beneath woody canopies, which can substantially reduce soil evaporation. The combination of trees interlaced with open areas of low herbaceous cover provides a habitat where CMM can thrive (Figure 1A).

Managers are often pressed into treating an area after a large fire, primarily to ameliorate erosion and invasive weeds (Peppin et al. 2010). Seeding grasses has been the most common treatment. Peppin et al. (2010) reviewed data from 16 sites contained in 14 studies assessing post-wildfire grass seeding in relation to shrub establishment in forested ecosystems of the western United States and found that shrub cover was greater in areas that were never seeded. Yelenik and Levine (2010) quantified competitive effects of annual grasses on shrub seedlings with grass removal experiments. Shrub seedlings suffered a 67% reduction in growth due to light competition from grass neighbors. In the presence of above- and below-ground grass competition, 0% of shrub seedlings survived, compared to 70% survival in cleared plots. Shrubs are considered important nurse plants for piñon pine (Phillips 1909; Kane et al. 2015), and shade from woody plants reduces the grass cover that appears to inhibit CMM survival and recruitment.

There are multiple successional pathways that may alter the CMM population in the burned area, especially in light of climate change and introduced grasses: (1) grasses retain their competitive edge, altering the fire regime and preventing shrub and tree recovery, thus ensuring a stable type conversion, further reducing CMM; (2) shrubs increase and grasses wane, but trees fail to return, likely leading to a modest increase in CMM; (3) full recovery toward a woodland occurs, providing excellent habitat for CMM. Only time will tell which path recovery will follow.

In light of a declining CMM population in the burned area and climate change–amplified wildfire risk to the remaining piñon-juniper old-growth, CMM faces serious threats in its currently occupied habitats. Ameliorating those risks, and preventing introduced grasses from hijacking normal succession, are of great importance to the long-term viability of CMM.

CONCLUSION

Climate change has increased the wildfire risk to piñon-juniper woodlands, a habitat that has a suite of obligate vertebrates, invertebrates, and plants, in addition to its cultural importance to Native Americans. CMM, a globally rare and threatened piñon-juniper obligate, is an excellent indicator to assess post-fire recovery. Long-term monitoring of post-fire succession is necessary for detecting trends during seral stage community changes. CMM survived and initially thrived following the 2001 fire, but is now at risk of extirpation in the burned area, likely due to a novel grassland induced by invasive grasses. The unintended consequence of this novel grassland is an altered successional trajectory, likely impairing the CMM population, and possibly constituting a harbinger for other piñon-juniper dependent species. In the context of a changing climate, the invasive grasses risk a type conversion away from piñon-juniper recovery. Even if they do not prevent forest recovery but only delay it, our results place a high urgency on preserving the remaining old-growth piñon-juniper woodland. Furthermore, research on post-fire vegetation management, especially as it relates to assisting succession and reducing invasive and competitive grasses, such as western wheatgrass, is urgently needed.

ACKNOWLEDGMENTS

This project was made possible by the assistance of many people. The need for the project was initially recognized by Laura Hudson, George San Miguel, Marilyn Colyer, and Anne Cully. Funding was provided to the Colorado Natural Heritage Program (CNHP), as a financial assistance project from the Colorado Plateau Cooperative Ecosystems Studies Unit with Mesa Verde National Park, administered by Chief of Natural Resources, George San Miguel, U.S. Fish and Wildlife Service, and the Colorado Natural Areas Program, administered by Brian Kurzel. Field work was performed by CNHP with assistance from National Park Service Natural Resource personnel, including Julia Aaronson, Jane Ashdown, Agnes Baldenweck, Tim Clute, Cheri Dorshak, Kyle Dougherty, Tom Greene, Jennifer Jones, Cheyenne Laeske, David Marion, Matt McEttrick, Lorraine Miller, Allen Nabors, Bethany Nickison, Melissa Nicolli, Parker Roy, David Pinigis, Kevin Puczkowski, Jabus Smith, Andrew Spear, Glen Stewart, Charlotte Thompson, Kathrine Uziel, and Bryan Wender. Gina Glenne and Ellen Mayo, both USFWS, assisted with field work. Thanks to Tara Travis and Lauren Finn, both with Mesa Verde NP, for allowing access to the Park herbarium. Kay Barnett and Chris McAllister, both Mesa Verde NP archeologists, reviewed and revised our cultural history section. We are grateful for the volunteers that generously provided their assistance in the field: Gay Austin, Cynthia Billings, Page Buono, Gordon Rodda, Duncan Rose, and Al Schneider. CNHP staff assisted with numerous aspects of this project, including map design, field work, analysis, and review: Anne Black, Sierra Crumbaker, Karin Decker, Maureen DeCoursey, Georgia Doyle, Amy Greenwell, Bernadette Kuhn, Peggy Lyon, Amber Provinzano, Gabrielle Smith, and Travis Talbot. Special thanks to Gordon Rodda for his assistance in the field, analysis, and detailed review of this manuscript. Jessica Smith and Hannah Ertl reviewed and enhanced this manuscript. Lisa Floyd-Hanna graciously provided constructive suggestions to this manuscript in addition to providing vast knowledge on the natural resources of the Mesa Verde NP.

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