Herbaceous Vegetation Responses (1992–2004) to Restoration Treatments in a Ponderosa Pine Forest

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Abstract

Ecological restoration treatments are widely applied in southwestern ponderosa pine forests to convert them to an open canopy structure similar to that found at the time of Euro-American settlement. An experiment was initiated in northern Arizona in 1994 to evaluate long-term ecosystem responses to 3 restoration treatments: 1) thinning from below (thinning), 2) thinning from below plus forest floor manipulation with periodic prescribed burning (composite), and 3) an untreated control. Results focus on total herbaceous and functional-group standing crop response to these restoration treatments. Pretreatment data were collected in 1992 and posttreatment responses were measured from 1994 through 2004. Total herbaceous standing crop was significantly higher on the 2 treated areas than on the control over the entire posttreatment period, but did not differ between the thinning and composite treatments. Plant functional groups responded differently to treatments and to drought. In general, the graminoid standing crop responded within several years after the initial treatments and continued to increase through time, until a series of severe droughts reduced standing crop to pretreatment levels. C_3 graminoids dominated the standing-crop response, of which bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey *ssp. elymoides*) was the primary contributor. C_4 graminoids had a minimal response to restoration treatments, possibly because they were less abundant before the experiment began or because they were adversely affected by autumn burning. Legumes and forbs exhibited a 4–5 year lag before responding to the thinning and composite treatments. Annual and biennial plants showed a large biomass increase approximately 5 years after implementation of the composite treatment. The restoration goal of optimizing herbaceous standing crop must be weighed against the competing goals of increasing the abundance of specific functional groups, increasing biodiversity or rare plants, and managing invasive plant species.

Resumen

Los tratamientos de restauración ecológica son ampliamente aplicados en los bosques de "Ponderosa pine" del sudoeste para convertirlos en una estructura de cobertura abierta similar a la que se encontró en el tiempo de la colonización Euroamericana. En 1994, en el norte de Arizona, se inicio un experimento para evaluar las respuestas a largo lazo del ecosistema a tres tratamientos de restauración: 1) aclareo desde abajo (aclareo); 2) Aclareo desde abajo mas manipulación del piso del bosque con fuego prescrito periódico (compuesto) y 3) control sin tratar. Los resultados se enfocaron en la respuesta de la biomasa total herbácea y de grupos funcionales a estos tratamientos de restauración. Los datos pre-tratamiento fueron colectados en 1992 y las respuestas post-tratamientos fueron medidas de 1994 a 2004. Durante todo el periodo post-tratamiento la biomasa total herbácea de las dos áreas tratadas fue significativamente mayor que la del área control, pero no difirió entre los tratamientos de aclareo y compuesto. Los grupos funcionales de plantas respondieron diferente a los tratamientos y la sequía. En general, la biomasa de las gramíneas respondió varios años después de iniciar los tratamientos, incrementándose continuamente a través del tiempo hasta que una serie de severas sequías redujo la biomasa a los niveles presentes antes de aplicar los tratamientos. Las gramíneas C_3 dominaron la respuesta de la biomasa, de las cuales el "Bottlebrush squirreltail" (*Elymus elymoides* (Raf.) Swezey *ssp. elymoides*) fue el principal contribuyente. Las gramíneas C_4 tuvieron una mínima respuesta a los tratamientos de restauración, posiblemente porque ellas fueron menos abundantes antes de que el experimento comenzará o porque ellas fueron afectadas adversamente por la quema de otoño. Las leguminosas y hierbas mostraron un retrazo de 4-5 años para responder a los tratamientos de aclareo y compuesto. Aproximadamente 5 años después de implementar el tratamiento compuesto las plantas anuales y bianuales mostraron un gran aumento de la biomasa. La meta de restauración de optimizar la biomasa herbácea debe ser ponderada contra las metas de incrementar la abundancia de grupos funcionales específicos, aumentando la biodiversidad o las plantas raras y manejar las especies vegetales invasoras.

INTRODUCTION

Prior to Euro-American settlement, southwestern ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forests were characterized by a productive, grass-dominated understory and a temporary accumulation of litter and woody debris that supported low-intensity surface fires every 2–20 years (Pyne et al. 1996; Swetnam and Baisan 1996, 2003). Euro-American settlement greatly altered these forests at the beginning of the 20th century by introducing large numbers of domestic livestock, removing many large-diameter trees through high-grade logging practices, and disrupting the natural fire regime (Pearson 1910; Weaver 1951; Moore et al. 1999). These factors, combined with favorable climatic conditions, resulted in the establishment of massive amounts of pine regeneration in the early 1900s (Arnold 1950; Weaver 1951; Cooper 1960; Savage and Swetnam 1990; Savage et al. 1996).

Historically, many sites in northern Arizona were described as a matrix of grass-dominated meadows interspersed with stands of pine (Pearson 1950; Cooper 1960). However, contemporary southwestern ponderosa pine forests have a closed overstory canopy with a few fragmented, remnant grass openings intermixed (Covington and Moore 1994; Covington et al. 1997). These remnant grass patches may hold only a fraction of their presettlement plant richness and diversity.

Resource management and conservation practices are challenging in these mixed woody-herbaceous systems (House et al. 2003). The ratio of woody to herbaceous plants is very dynamic and can change at decadal time scales (Archer 1996), especially in response to fire, herbivory, and climate. In response to concerns about forest ecosystem health and large crown fires in southwestern ponderosa pine forests, land managers and the scientific community in the Southwest have begun using ecological restoration thinning treatments to convert dense, closed-canopy ponderosa pine stands back to more open-stand structures. Many of these treatments and management plans also call for regularly scheduled prescribed fires, in hopes of simulating the frequent fire regime that was common in these systems in presettlement times (Agee 1993; Covington et al. 1997; Moore et al. 1999; Wienk et al. 2004). Both overstory tree thinning and prescribed burning can have mixed results on the herbaceous understory, depending upon thinning level and fire intensity, frequency, and season (Covington et al. 1997; Tiedemann et al. 2000; Wienk et al. 2004).

This study is part of a larger project initiated to restore a reasonable approximation of the presettlement ponderosa pine ecosystem and to determine the attributes that characterize the health of that system (Covington et al. 1997; Kaye et al. 2005). Three treatments—thinning from below (thinning restoration treatment), thinning from below with forest floor manipulation and periodic prescribed burning (composite restoration treatment), and no treatment (control)—were applied at the study site. Both restoration treatments return the overstory to the approximate stand structure (size, density, age distributions) of presettlement forests. The composite restoration treatment also restores the approximate fuel depth and fire characteristics of presettlement forests in the area (Covington et al. 1997).

The primary objective of this study was to evaluate the responses of the herbaceous community to the thinning and composite restoration treatments. Here we describe the effects of tree thinning and thinning plus prescribed burning on aboveground herbaceous standing crop by treatment and by plant functional group. Aboveground herbaceous standing crop was measured in 1992 (pretreatment) and another 7 times from 1994–2004 (posttreatment). Treatment differences were assessed with respect to total standing crop and the relative contributions of C_3 graminoid, C_4 graminoid, legume, nonleguminous perennial forb, and nonleguminous annual–biennial forb functional groups.

METHODS

Study Site
This study was conducted at the Gus Pearson Natural Area (GPNA), located approximately 10 km northwest of Flagstaff, Arizona in the Fort Valley Experimental Forest, Coconino National Forest (lat 35°16′00″, long 111°45′00″). The approximately 4.3-ha study site ranges from 2 195 to 2 255 m in elevation, and much of the area has flat to gently rolling topography with some southwesterly and northwesterly aspects. Soils are derived from Tertiary basalt flows and cinders, and are classified as a Brolliar stony clay loam, and a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs (Kerns et al. 2003).

The average annual temperature is 7.5°C. Average annual precipitation is approximately 57 cm, and follows a bimodal, monsoonal precipitation pattern with approximately half of the precipitation occurring as rain in July and August and half as snow in the winter (Savage et al. 1996). Drought was common during this study, with 2002 being especially severe (Fig. 1). Weather data were obtained from the Fort Valley Experimental Station weather records (USDA, Forest Service Rocky Mountain Research Station 2005), supplemented by data from the Flagstaff airport (NOAA 2005) when data were missing from Fort Valley.

The study area was fenced to exclude domestic ungulates in 1950, and so has been ungrazed by livestock for more than 50 years (Olberding 2000). In 1992, a 2.4-m electrified fence was constructed to exclude wild ungulates from GPNA. Some trees were removed from GPNA in 1894, but it did not receive commercial harvest after that time (Avery et al. 1976). The last major fire in the vicinity prior to this experiment occurred in 1876 (Dietrich 1980).

Ponderosa pine is the only overstory species on the study site. The understory is dominated by native perennial graminoid species, including *Festuca arizonica* Vasey (Arizona fescue), *Elymus elymoides* (Raf.) Swezey *ssp. elymoides* (bottlebrush squirreltail), *Muhlenbergia montana* (Nutt.) A. S. Hitchc. (mountain muhly), *Poa fendleriana* (Steud.) Vasey (muttongrass), and *Carex geophila* Mackenzie (White Mountain sedge). Dominant native perennial forb species include *Vicia americana* Muhl. Ex. Willd. (American vetch), *Senecio actinella* Greene (Flagstaff ragwort), *Houstonia wrightii* Gray (pygmy bluet), *Astragalus rusbyi* Greene (Rusby's milkvetch), *Lupinus argenteus* Pursh (silvery lupine), *Antennaria parvifolia* Nutt. (small-leaf pussytoes), *Solidago velutina* DC. (threenerve

goldenrod), *Achillea millefolium* L. var. *occidentalis* DC. (western yarrow), and *Cirsium wheeleri* (Gray) Petrak (Wheeler's thistle). Common native annuals include *Muhlenbergia minutissima* (Steud.) Swallen (annual muhly; a grass), *Lupinus kingii* S. Wats. (King's lupine; a legume), and forbs such as *Laennecia schiedeana* (Less.) Cronq. (pineland marshtail), *Chenopodium graveolens* Willd. (fetid goosefoot), *Conyza canadensis* (L.) Cronq. (Canadian horseweed), and *Helianthus annuus* L. (common sunflower). Common native biennial forbs are *Erigeron flagellaris* Gray (trailing fleabane) and *Erigeron divergens* Torr. & Gray (spreading fleabane). Six exotic species have been recorded on the study site, with the 2 dominants being the perennial graminoid *Poa pratensis* L. (Kentucky bluegrass) and the biennial forb *Verbascum thapsus* L. (common mullein). The only shrub on the study site is *Ceanothus fendleri* Gray (Fendler's ceanothus).

Experimental Design

In 1992, 15 treatment plots, each approximately 0.2–0.3 ha in size, were established and assigned to one of 3 treatments (control, thinning restoration, and composite restoration treatments). Treatment plots have also been referred to as whole plots (sensu Covington et al. 1997). The 5 control treatment plots were located nonrandomly on one side of the study site, and the thinning and composite treatment plots were assigned randomly. This design was necessary so that the fuel break created by the treated plots would protect the historical buildings of the adjacent Fort Valley Experimental Station.

Each treatment plot contained 4 patch types: presettlement tree groups, thinned postsettlement tree groups, unthinned postsettlement trees, and remnant grass openings. One circular subplot, with a radius of 2.5 m, was established within each of the 4 patch types per treatment plot. In total, 55 subplots were established: 4 per treatment plot in the thinning treatment ($n = 20$) and composite treatment ($n = 20$), and 3 per treatment plot in the control ($n = 15$, controls did not contain thinned patches). Subplots represent the range of patch types and illustrate the wide range of conditions sampled within treatment plots. Herbaceous data were scaled to the treatment-plot level ($n = 15$) by weighting the herbaceous standing crop on each subplot by the proportion of the treatment plot area occupied by the patch type in which the subplot was located (see Standing-Crop Data Collection below). Detailed results on patch-level effects can be found in Casey (2004) and Laughlin et al. (2006).

The thinning and composite treatments were thinned from below (i.e., postsettlement trees that were overtopped or in lower crown positions were removed in varying proportions; Nyland 1996) in the fall of 1993, retaining all presettlement trees (> 40.6 cm diameter at breast height [dbh]) and leaving approximately 3 replacement postsettlement trees for every dead presettlement tree or stump (Fulé et al. 1997; Mast et al. 1999). Presettlement and postsettlement tree group structure was determined through dendrochronological reconstructions (Mast et al. 1999). The thinning and composite treatments removed approximately 2 200 trees per hectare (Covington et al. 1997; Fig. 2), including most of the trees that established after 1876 (defined as postsettlement). All slash was removed by hand, and all presettlement coarse woody debris was retained.
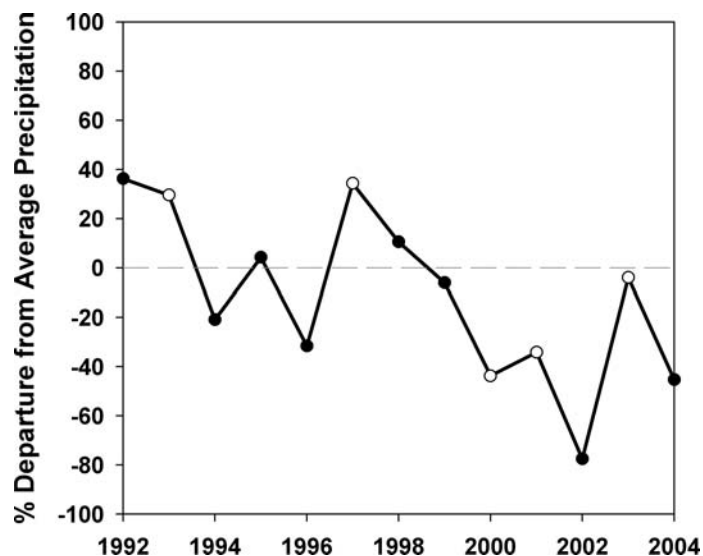

Figure 1. Annual precipitation during the study (1992–2004) as percent departure from the long-term (51-year) average. Annual totals included the 12 months of precipitation before vegetation sampling (previous September through August). Dark symbols indicate years in which vegetation was sampled.

In the composite treatment, the forest floor was manipulated by raking the litter layer aside, removing accumulated forest floor duff, and returning the current (approximately 3-year) litter layer to the site. To simulate the presettlement condition of a grass-dominated understory that carried frequent fire, approximately 670 kg·ha^{-1} of herbaceous vegetation from Hart Prairie (4.8 km to the north) was harvested in late September 1994 and scattered across the plots (Covington et al. 1997); this supplementation occurred only in 1994. The composite treatment received an initial prescribed burn in 1994, and additional prescribed burns in 1998 and 2002. All burns were conducted in October, after data collection was completed for that year. Fire history records indicate that most presettlement fires in northern Arizona ponderosa pine forests occurred in April through early July (Baisan and Swetnam 1990). Therefore, although fine-fuels loads mimic presettlement herbaceous fuels, the season of burn is not similar to presettlement fire regimes. Contemporary forest fuel loads and conditions often restrict prescribed burns to the fall. Fire intensity was low for all fires, with average flame lengths of 15 cm and soil surface temperatures of 240°C.

See Covington et al. (1997) and subsequent publications for a more detailed account of experimental design, thinning and prescribed burn characteristics, treatment protocol, and effects on other ecosystem components (Feeney et al. 1998; Kolb et al. 1998; Kaye and Hart 1998a, 1998b; Kaye et al. 1999; Mast et al. 1999; Skov et al. 2004; Boyle et al. 2005; Kaye et al. 2005).

Standing-Crop Data Collection

Herbaceous standing-crop data were collected in 1992 (pretreatment), 1994, 1995, 1996, 1998, 1999, 2002, and 2004. Field sampling occurred during a 2-week period near mid-September, which is the time of peak aboveground production and flowering for major understory species in northern Arizona (Clary 1975). Each year, we sampled 2 1-m^2 (0.5 × 2.0 m)

Figure 2. Time-series photographs of photo point 302 prior to treatment (1992, top photo), 5 years after thinning (1998, middle photo), and 11 years after thinning (2004, bottom photo). The arrows highlight the

quadrats per circular subplot. All live herbaceous vegetation rooted in the quadrats was clipped to ground level (approximately 2-cm stubble height). Quadrats were arranged in a wagon-wheel configuration around the center of the circular subplot and clipping was rotated each year so that the identical area was not sampled (clipped) for at least 4 years.

Clipped vegetation was separated by species in the field and later regrouped into functional groups. The functional groups differed among years as methods were refined. In 1992, standing crop was separated into graminoid and forb functional groups. From 1994 to 2004, herbaceous vegetation was divided into C_3 graminoids (grasses and sedges), C_4 graminoids, legumes, nonleguminous perennial forbs, and nonleguminous annual–biennial forbs.

Samples were oven-dried at 70°C for 24–48 hours and weighed to the nearest 0.01 g. Data from the 2 quadrats per subplot were averaged together to yield a single value for each functional group on each of the 55 subplots each year. Herbaceous data were then scaled to the treatment-plot level ($n = 15$).

Statistical Analyses

Standing-crop data were scaled to the treatment-plot level ($n = 5$ per treatment) and analyzed in total and for each functional group. Testing for normality and homogeneity of variances concluded that data were not normally distributed, so they were $\ln(x)$ transformed prior to analysis; annual–biennial forb standing crop was $\ln(x + 1)$ transformed to account for zeros. Treatment effects were compared in 1992 (pretreatment) using a 1-way analysis of variance (ANOVA). Posttreatment standing-crop data (1994–2004) were analyzed using repeated measures multivariate analysis of variance (MANOVA) with Greenhouse-Geisser adjustments to account for autocorrelation (Moser et al. 1990). Significant treatment effects in the MANOVA were followed by analyses comparing treatments within each year using 1-way ANOVA and Tukey's honestly significant difference (HSD) post hoc multiple comparisons tests. Significant interactions indicated that treatments differed temporally (significant differences among treatments in interannual variability in standing crop over time). All tests were conducted at $\alpha = 0.05$ using JMP-IN software (version 5.1.2; SAS 2004).

We also calculated the proportion that each functional group represented of the total herbaceous standing crop by treatment from 1994–2004. These proportions were compared between treatments using the likelihood ratio contingency test (G^2).

RESULTS

Total Herbaceous Standing Crop

After treatment, total standing crop differed significantly among treatments ($F = 8.6$, $P = 0.005$) and over time ($F = 27.0$,

$\leftarrow$

same tree (approximately 15 cm diameter at breast height) in each photo. All photos were taken in early autumn (September to early October) on the Gus Pearson Natural Area near Flagstaff, AZ. Note the difference in herbaceous standing crop between 1998, an average year in precipitation, and 2004, which was > 40% below normal. (Photo credits: Ecological Restoration Institute, Northern Arizona University)

$P < 0.001$) (Fig. 3). The treatment × time (time since treatment) interaction was also significant ($F = 3.0$, $P = 0.015$).

One-way ANOVA indicated that total standing crop differed marginally among treatments 1 growing season after thinning from below (1994: $F = 3.5$, $P = 0.06$), and differed significantly among treatments in all subsequent years (all $F > 6.3$, all $P < 0.02$). In particular, total standing crop was higher in both treated areas than in the control, but it never differed between the thinning and composite treatments (Fig. 3).

Graminoid Standing Crop

After treatment, graminoid standing crop differed among treatments ($F = 11.3$, $P = 0.001$) and over time ($F = 13.4$, $P < 0.0001$), and the treatment × time interaction was also significant ($F = 2.4$, $P = 0.04$). Graminoid standing crop was significantly higher in treated than in control plots in every posttreatment year, but never differed between the thinning and composite treatments.

Graminoids were separated into C_3 and C_4 graminoids in the years 1994–2004. C_3 graminoids had a greater response to treatment than did C_4 graminoids (Figs. 4a, 4b, and 5). C_3 graminoid standing crop differed by treatment and over time, and the treatment × time interaction was marginally significant. C_3 graminoid standing crop differed between the treated areas and the control in every posttreatment year, but did not differ between thinning and composite treatments (Fig. 4a). C_4 graminoid standing crop did not differ among treatments, times, or with the treatment × time interaction (Fig. 4b).

Forb Standing Crop

Forb standing crop differed by treatment ($F = 4.2$, $P = 0.04$) and time ($F = 42.0$, $P < 0.0001$), and there was a significant treatment × time interaction ($F = 2.4$, $P = 0.03$). Forb standing crop did not differ among the 3 treatments from 1994 to 1996 (all F less than 2.5, all $P > 0.1$), but did differ from 1998–2004 (all $F > 5.5$, all $P < 0.02$). Forb standing crop never differed between thinning and composite treatments.

Legumes and annual–biennial forbs had a greater response to treatments than did nonleguminous perennial forbs (Figs. 4c–4e). Legume standing crop differed by treatment, by time, and there was a marginally significant treatment × time interaction. Legume standing crop in the 2 treated areas differed from the control in every year from 1996–2004 (Fig. 4c). Legume standing crop peaked in 1999, which was 1 year after the 1998 prescribed burn, then declined. Legumes were higher in the composite than in the thinning treatment throughout the study period, though this difference was not statistically significant. Perennial forb standing crop did not differ by treatment, or time, and there was not a significant treatment × time interaction (Fig. 4d).

Annual–biennial forb standing crop differed by treatment and by time, and there was a treatment × time interaction. Annual–biennial forb standing crop was greater in the composite treatment than in the thinning treatment or control from 1999–2004 (Fig. 4e). This functional group peaked in 1999, following the second prescribed burn, and then declined.

Proportions of Functional Groups

In 1994, proportions of functional groups differed between treatments ($G^2 = 25.5$, $P = 0.0013$); the thinning and com-
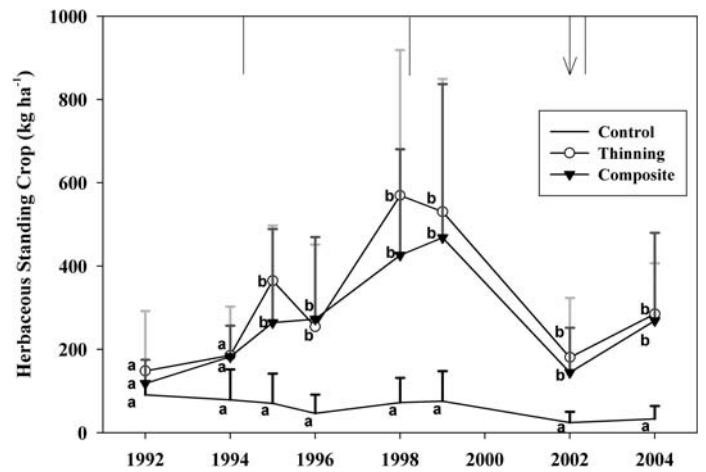

Figure 3. Total herbaceous standing crop (mean + SD) in 3 restoration treatments between 1992 and 2004. Data from 1992 represent pretreatment data. Lowercase letters indicate significant differences among treatments within years. The arrow denotes the extreme drought year (2002) and vertical lines denote prescribed burn years.

posite treatments differed from the control (both $P < 0.05$), but did not differ from each other ($P = 0.37$). In 2004, proportions of functional groups differed between treatments ($G^2 = 72.0$, $P < 0.0001$). In contrast to 1994, however, the thinning and composite treatments differed from the control and from each other.

In 1994, 1 year after thinning but prior to any prescribed burn, C_3 graminoids represented 43% of the total herbaceous standing crop in the control, 58% in the thinning, and 67% in the composite treatment (Fig. 5). These proportions varied over time, with a noted decrease around 1999, but the C_3 graminoid functional group remained dominant in all treatments in 2004 (51%, 60%, and 75% in the control, thinning, and composite treatments, respectively).

In 1994, C_4 graminoids represented less than 12% in the control and thinning treatments, and 6% in the composite treatment (Fig. 5). Again, these proportions varied over time, with a noted decrease around 1999. In 2004, C_4 graminoids represented 13% of the total herbaceous standing crop in the control, 26% in the thinning, and 5% in the composite treatment.

Perennial forbs comprised the largest proportion of the forb functional group and were 42%, 22%, and 17% of the total herbaceous standing crop in the control, thinning, and composite treatments, respectively, in 1994 (Fig. 5). By, 2004, this group was 35%, 9%, and 4% in the control, thinning, and composite treatments, respectively. Legumes represented 3%, 8%, and 10% of the total standing crop in the control, thinning, and composite treatments, respectively, in 1994 (Fig. 5). These proportions varied over time, but by 2004, the legumes accounted for less than 1%, 5%, and 8% of the total standing crop in the control, thinning, and composite treatments, respectively.

Annual and biennial forbs were negligible in 1994 in the control and represented less than 1% of the total standing crop in both the thinning and composite treatments (Fig. 5). In 1999, annual–biennial forbs were 1% and 2% in the control and thinning treatment, respectively, but 20% in the composite treatment. In 2004, annual–biennial forbs continued to account for less than 1% of the total standing crop in the control and
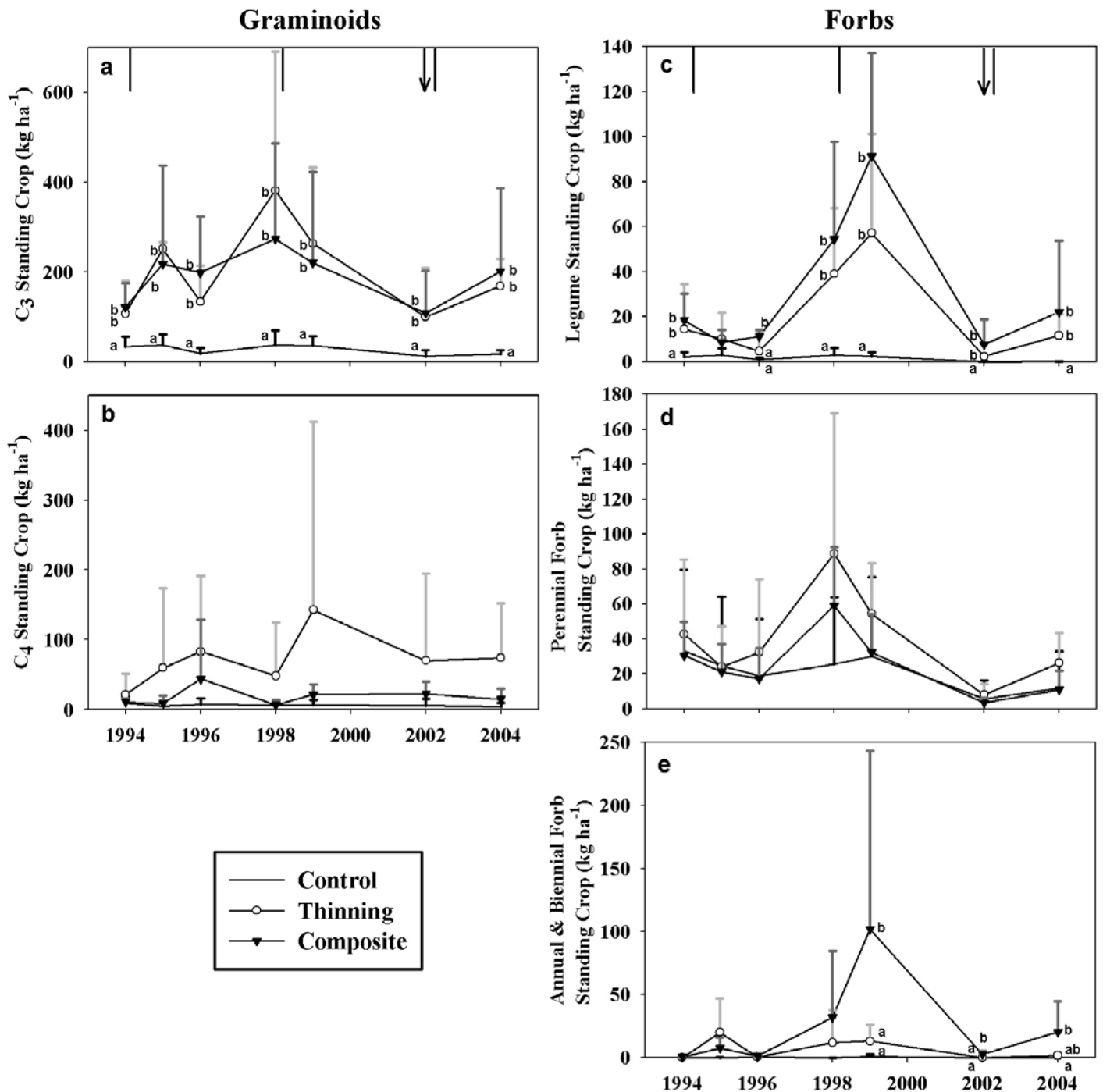
Figure 4. Standing crop (mean + SD) of: a) C_3 graminoids, b) C_4 graminoids, c) legumes, d) nonleguminous perennial forbs, and e) nonleguminous annual–biennial forbs in 3 restoration treatments between 1994 and 2004. Lowercase letters indicate significant differences between treatments within years; letters are not shown if treatments did not differ. The arrow denotes the extreme drought year (2002) and vertical lines denote prescribed burn years. Note differences in scale of the y-axis among graphs.

thinning treatments, but represented 7% of the total standing crop in the composite treatment.

DISCUSSION

The thinning and composite restoration treatments increased total herbaceous standing crop significantly over the control. Total herbaceous standing crop in the thinning and composite

restoration treatments significantly increased just 2 years after thinning and reached a maximum (approximately 5-fold over the control) in 1998 and 1999. This immediate response in herbaceous standing crop was because of the C_3 graminoid component of the understory. Forbs responded later, 5 to 6 years after the initial thinning and prescribed burning. Precipitation and drought patterns greatly influenced herbaceous standing crop (see Drought Effects below).
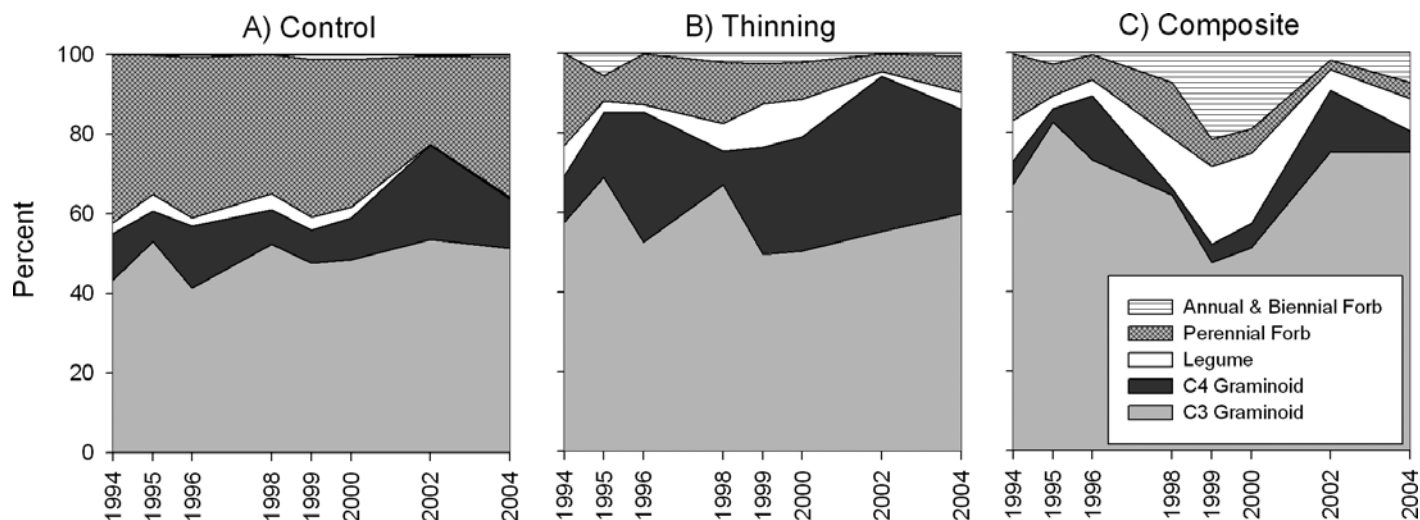
Figure 5. Distribution of total standing crop among functional groups in: A) control, B) thinning, and C) composite restoration treatments between 1994 and 2004.

Thinning Effects

Herbaceous C_3 graminoids and legumes demonstrated an immediate response to thinning. Our results are consistent with other overstory–understory studies in ponderosa pine forests and pine–oak woodlands that demonstrate that high overstory canopy cover results in low herbaceous production (Arnold 1950), and that rapid recovery of understory plant biomass can be obtained by basal area reduction (Thompson and Gartner 1971; Ffolliott and Clary 1982; Uresk and Severson 1989; McPherson and Weltzin 1998; Wienk et al. 2004). Increased light availability, resulting from tree thinning, was likely the main factor stimulating increased herbaceous standing crop (McLaughlin 1978; Riegel et al. 1995; Naumberg et al. 2001), in addition to higher nitrogen and water availability (Riegel et al. 1995; Kaye et al. 2005).

C_3 graminoid standing crop responded quickly to overstory thinning, but C_4 graminoid standing crop responded only slightly to thinning even 11 years after treatment. These results are inconsistent with reports of greater C_4 graminoid response following overstory canopy removal (Thompson and Gartner 1971; McPherson and Weltzin 1998). This apparent discrepancy might reflect differential responses among individual plant species within each functional group. In our study, for example, the native perennial bottlebrush squirreltail (a C_3 graminoid), dominated the initial herbaceous standing crop response to thinning (Casey 2004; Laughlin et al. 2006). Squirreltail can colonize sites quickly and it performs well in a variety of light conditions (Vose and White 1991; Jones 1998; Naumberg and DeWald 1999; Naumberg et al. 2001).

Unique functional-group responses compared to other investigations may also reflect the existence of different initial conditions. For example, the initial proportion of C_4 graminoids in our experiment was low ($< 12\%$ of total standing crop in 1994) relative to C_3 graminoids in all treatments. In contrast, the study by McPherson and Weltzin (1998) was conducted in southern Arizona, where C_4 grass species dominate ($> 90\%$ of total herbaceous biomass at experiment initiation) and C_3 grass species are sparse. Although little is known about the importance of graminoid functional groups in presettlement forests, it

is possible that C_4 graminoids, which are shade-intolerant, have been locally extirpated beneath the dense canopies of treed plots (Kerns et al. 2001, 2003). If so, these extinctions would have occurred many years before we initiated this experiment.

Despite the overall poor response of C_4 graminoids, we did observe a gradual increase in the proportion of C_4 graminoids in the thinning treatment over the 11-year period (Fig. 5). Mountain muhly, which drove this response (Casey 2004; Laughlin et al. 2006), has been shown to increase its biomass with increasing light availability (Naumburg and DeWald 1999; Naumburg et al. 2001).

Fire Effects

The severity of fire effects on the understory is dependent upon a number of factors, including the frequency, intensity, and season of burning, as well as species composition and abiotic factors. Research has generally shown that understory production increases following low-intensity prescribed burns in ponderosa pine forests, though increases are often species specific (Harris and Covington 1983; Andariese and Covington 1986; Vose and White 1991; Wienk et al. 2004).

In this study, effects of low-intensity autumn prescribed burns on herbaceous standing crop were confounded with overstory canopy reduction and manipulation of the forest floor prior to the first prescribed burn. However, fire may have been a major contributor to some of the functional group changes. C_4 graminoids (particularly mountain muhly) did not increase in the composite treatment, suggesting that some aspect of the periodic burning (season, frequency, intensity, etc.) was detrimental to this functional group. Other studies have also shown a decrease in C_4 grasses with fall prescribed burns. Gaines et al. (1958) found a 10% decrease in mountain muhly in ponderosa pine forests 1 year after autumn prescribed burns in eastern Arizona. Haisley (1984) found that mountain muhly production significantly decreased in aspen and ponderosa pine forests of northern Arizona after October prescribed burns.

The increase in C_3 graminoids (specifically bottlebrush squirreltail), legumes, and annual–biennial forbs in the more

disturbed environment of the composite treatment was not surprising. Low-intensity fire creates conditions suitable for early successional species by increasing bare ground for germination sites, increasing short-term nutrient availability, and removing dominant competitors (Denslow 1983; Collins and Gibson 1990; Whelan 1995; Crawford et al. 2001). Bottlebrush squirreltail is an early and rapid colonizer of disturbed sites (Jones 1998) and generally increases following low-intensity fall burns (Young and Miller 1985).

Legumes showed a delay in response to restoration treatments for the first 4 years, and then increased substantially in 1998 in both treated areas, suggesting that both restoration treatments affected legume production. Legumes are common in fire-dependent communities (Leach and Givnish 1996), and are known colonizers and increasers following fire. In the southeastern United States, frequently burned sites were reported to have a higher frequency, density, and diversity of legumes than did unburned sites (Hendricks and Boring 1999).

Annual and biennial forbs had a delayed response to treatment, similar to that observed in legumes and perennial forbs, and then showed a standing-crop increase in 1998 in both treatments. However, the largest increase occurred in 1999, 1 year after the second prescribed burn, when annual and biennial forb standing crop was significantly higher in the composite treatment than in the thinning treatment or control. By 2002, standing crop of this functional group had returned to earlier levels. Note that precipitation was near normal or above average during the first 5–6 years and then below average during the last 5 years. It is not surprising to find more annuals and biennials in a disturbed environment that includes frequent surface fires that consume most of the surface litter, leaving a suitable environment for the establishment of ruderal species. Common mullein, an exotic biennial, drove the annual–biennial standing crop response (Casey 2004). The dominant native annual and biennial forbs were pineland marshtail and 2 species of fleabane. Mullein and pineland marshtail seeds are commonly found in the soil seed bank of ponderosa pine forests in northern Arizona following thinning or burning treatments (Korb et al. 2004, 2005).

The intent of the original study was to mimic the frequency, intensity, and season of burning of the natural fire regime for the study area (Covington et al. 1997). Fire history records indicate that prior to Euro-American settlement of the region, most fires in the ponderosa pine forests of northern Arizona (and in the Southwest in general) occurred in the spring and early summer (April through early July) (Baisan and Swetnam 1990). Spring or early summer fires may suppress C_3 graminoid and enhance C_4 graminoid functional-group responses to a greater extent than those that occurred in response to October burning in this investigation. However, it is currently unsafe to conduct a prescribed burn under the weather and fuels conditions that exist in many areas of northern Arizona between April and early July.

In addition to fire effects, the composite treatment underwent extensive forest floor manipulation before the first burn, including raking to remove the litter layer and the addition of mown hay from a nearby prairie. These activities may have had additional effects on the understory, which were not examined or controlled for in this study. Raking may have affected total standing crop and species composition by

affecting the soil seed bank in the O horizon of the composite treatment (Korb et al. 2004, 2005). Although it is theoretically possible to introduce plant species by the addition of mown prairie hay, our plant surveys have not revealed any new species over the years (Casey 2004). This procedure has not been observed to result in any plant introductions in the northern Great Plains (Bakker et al. 2003). If forest floor manipulation activities are to become an integral process in restoration, they should be examined as separate treatments in future studies to determine their unique impacts.

Drought Effects

Precipitation and drought appear to be the primary forcing factors in total herbaceous standing crop in our study. Drought was common, especially during the last 5 years (Fig. 1), and severe, particularly in 2002, when precipitation was 75% below average. These droughts reduced herbaceous standing crop to levels that were similar to 1992 and 1994. C_4 graminoids were not as greatly affected by the drought as were the other functional groups. McPherson and Weltzin (1998) also report the recovery of C_4 species the second year after overstory canopy removal, even with below-average precipitation. The greater water-use efficiency of C_4 plants likely explains their ability to thrive under drought-stressed conditions (Waller and Lewis 1979; Ehleringer and Monson 1993). We suspect that when normal precipitation resumes in northern Arizona, total standing crop in both treated areas will eventually exceed the maximum experienced in 1998.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The herbaceous understory should be a prime focus of land managers involved with forest restoration and conservation biology activities in southwestern ponderosa pine forests. A productive and diverse understory protects soil from erosion, creates forage and cover for livestock and wildlife, provides fuels for surface fires, and is the repository for much of the plant biodiversity in these ecosystems. Successful restoration projects should seek to enhance the recovery of native herbaceous species.

These results demonstrate that restoration treatments that reduce dominance of the overstory canopy increase total herbaceous standing crop of the understory in ponderosa pine forests of northern Arizona. A long-term perspective is required to assess treatment responses as evidenced by the unique temporal responses among plant functional groups and the disproportionate impact of severe drought on C_3 compared to C_4 graminoid plant functional groups during the 11-year investigation. Graminoid standing crop responded within several years of the initial treatments and increased over time until a severe drought reduced standing crop to levels near those present when the experiment began. C_3 graminoids, particularly bottlebrush squirreltail, dominated this standing-crop response. C_4 graminoids, on the other hand, showed a minimal response to restoration treatments. The limited response of C_4 graminoids to restoration treatment may reflect their limited abundance at the time of pretreatment. The abundance of this functional group may have been suppressed because of its

inability to grow and reproduce under dense tree shade. However, it also appears that C_4 graminoids were adversely affected by autumn burning. Legumes and forbs showed a significant 4–5-year lag before responding to the thinning or composite treatments. There was a large pulse in annual and biennial forbs approximately 5 years after experiment initiation, driven primarily by common mullein, an exotic biennial. The restoration goal of optimizing herbaceous standing crop must be weighed against the competing goals of increasing the abundance of specific functional groups, increasing biodiversity or rare plants, and managing invasive plant species.

ACKNOWLEDGMENTS

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