Ecological Relationships between Overstory and Understory Vegetation in Ponderosa Pine Forests of the Southwest

Figure 1 Fence-line comparison of an area thinned in 2005 (foreground) and unthinned (background) ponderosa pine forest near Flagstaff, Arizona.

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Executive Summary

Southwest ponderosa pine has a rich understory of grasses, grass-like plants, shrubs, and forbs, whose community composition is determined by soils, climate, overstory composition, site characteristics and disturbance history. Many studies have focused on understanding the interactions of overstory tree density and understory productivity, but fewer studies have analyzed the effects of overstory on understory composition and species diversity. Recently, research has been focused on understanding the effects of management and natural disturbances on both the overstory tree density, and the resulting response of understory plant species. This review chronicles some of the more recent research on overstory tree canopy manipulations through mechanical thinning, prescribed burning and wildland fire, and how changes in overstory affect understory productivity and composition. Some general trends are that overstory tree density manipulation can have a profound effect on understory productivity and composition, but responses can take several years to decades before they stabilize, and individual species respond individually. Precipitation appears to be a strong determinant in how understory species respond, and recent long-term drought has compromised the ability of vegetation to respond to management. Exotic plant species abundance and diversity are affected by management, but show the strongest response to uncharacteristic wildland fire, which in many cases is the inevitable result of a lack of appropriate management for fuels reduction and ecological restoration. From an understory perspective, the thresholds for basal area (25-70 ft^2/ac) are at the low end of current treatment prescriptions. Several understory plant species appear to benefit from the reintroduction of fire as a natural ecological process through soil nutrient cycling augmentation. Mechanical treatments could be strategically located to emphasize areas of high potential for increasing understory diversity, and to avoid areas where exotic, invasive plant species may increase their spread.

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Introduction

Understory (also spelled understorey) is the term for the area of a forest which grows at the lowest height level below the forest canopy. Plants in the understory consist of a mixture of seedlings and saplings of canopy trees together with other plants. Ponderosa pine (*Pinus ponderosa* var. *scopulorum*) forests of the Southwest are capable of supporting a diverse understory of forbs, grasses, shrubs and cacti, and the composition of the understory differentiates ponderosa pine forests into several different habitat types or vegetation associations (Moir 1993, USFS 1997). Understory vegetation is important because it contributes to the suitability of an area as habitat for species of insects, birds, and mammals, and also because understory vegetation abundance and composition affect several ecological processes including fire and erosion. The understory vegetation of ponderosa pine forests of the Southwest has been studied for decades due to its economic importance as forage for cattle, and because managers and scientists have noticed significant changes to the understory that have occurred over a relatively short amount of time, with and without disturbance. While earlier studies focused on the effects of management on forage production or biomass, more recent studies have recognized the importance of species diversity and community composition to understory function, and the management actions that elicit varying responses of understory vegetation through time and across the landscape. This review derives most of its information from literature published since 1980 on understory vegetation in ponderosa pine forests of the Southwest (SW-PIPO), although it also draws upon studies in similar arid ponderosa pine forests from other parts of the western United States.

Biomass & Productivity

The earliest descriptions of SW-PIPO understory are from explorers whose early writings spoke to open, park-like forests dominated by large, widely spaced trees with an abundant understory of grasses and forbs (Beale 1858, Dutton 1882). The first scientists to study the history of fire recorded in SW-PIPO tree rings attributed the decline in understory productivity and changes in species composition to the exclusion of fire (Cooper 1960). There are several excellent reviews of ponderosa pine understory, including two that treat the earliest literature on forage production (Ffolliott and Clary 1982, Ffolliott 1983), and a more recent review focused on restoration of understory vegetation in Southwest ponderosa pine forests (Korb and Springer 2003). Many of the earlier studies came to the same conclusion illustrated by Figure 2: The productivity of ponderosa pine forest understory was inversely related to the density of overstory trees, whether expressed in basal area, trees per acre, percent canopy cover, or stand density index (e.g., Ffolliott 1983, Moore and Dieter 1992). Several studies have derived regression equation models predicting the productivity of understory vegetation as a function of basal area (BA) (Tapia and others 1990), soil parent material (Ffolliott and Clary 1975, Ffolliott and Baker 1977) and soil texture (Clary and others 1966, Clary 1969). The threshold for BA

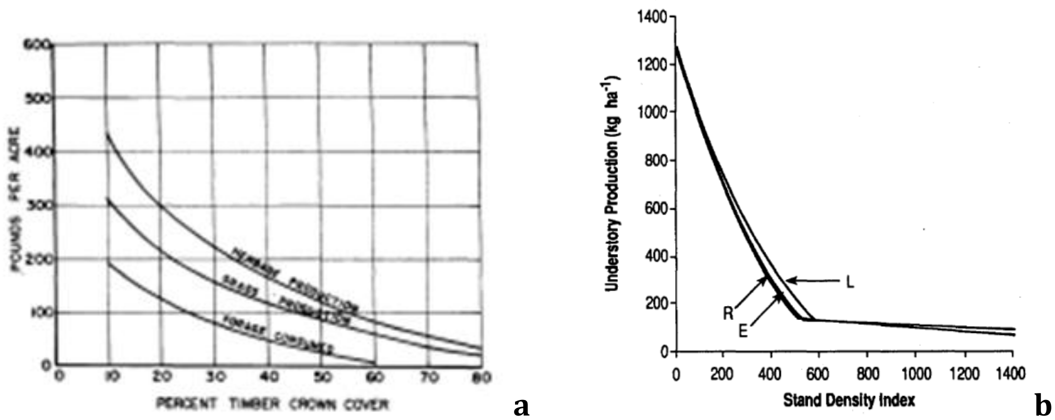

Figure 2 Relationships among a) crown or canopy cover expressed as percent with total herbage production, perennial grass production, and forage consumed (from Ffolliott 1983), and b) Stand density index (SDI) and understory production (Moore and Dieter 1992).

may be close to 70 ft^2/acre for SW ponderosa pine, as there is no significant difference in productivity between thinned and unthinned stands above this level (Clary and Ffolliott 1966).

Some of the mechanisms for overstory control of understory productivity include direct competition through the accumulation of a dense litter layer (White and others 1991), changes in sunlight quantity reaching the understory plant layer surface (Naumburg and DeWald 1999), reduced below-ground resource availability (Uresk and Severson 1989), and interactions of litter depth, soil nutrient status, light, and moisture as a result of disturbance such as fire affecting the phenology of individual species (White and others 1991). There is also evidence that changes in the understory affect overstory trees, although these effects have been less well documented (Barrett 1970, Sabo and others 2008).

Diversity, Composition & Structure

The productivity of understory vegetation is important for wildlife and cattle, but equally important is the diversity of species that compose understory vegetation, which has been estimated to arise from an available pool of between 300 to 600 species for southwestern ponderosa pine ecosystems (Daniel Laughlin, personal communication). Different species respond to different biotic and abiotic variables, and only a few species' responses are understood. In one study in eastern Arizona, the most important variables controlling individual species' biomass productivity were stand age, soil potassium, and light transmission of the canopy (McLaughlin 1978). In another study in eastern Arizona, the presence of six graminoid species was poorly related to light characteristics measured under different tree canopies, but their presence was positively related to mean diameter of ponderosa pine trees (Naumburg and DeWald 1999). Ponderosa pine forests of the North Rim of Grand Canyon National Park provide reasonable examples of reference conditions because of their relatively intact fire regimes, limited exposure to introduced grazing animals since about 1930, and few other anthropogenic disturbances. Within forests on the north rim of Grand Canyon National Park, overstory composition had a strong influence on understory community structure. Ponderosa pine with Gambel oak (*Quercus gambelii*) had greater understory plant cover, species richness, and diversity than pure ponderosa pine stands, and species richness and plant cover were negatively related to ponderosa pine basal area (Laughlin and others 2005).

Effects of Disturbance

Disturbances that affect understory vegetation include grazing, fire, windthrow of overstory trees, and climate. Several studies have examined the effects of wildfires on understory vegetation response. One such study on the North Rim of Grand Canyon National Park examined the effects of a 1999 low severity Wildland Fire Use Fire (WFUF) at Fire Point. Laughlin and others (2004) measured plant community composition one year prior to and two years after the WFUF, and established relict or reference sites on nearby plateaus (Powell and Rainbow) where a nearly intact fire regime presumably maintained a more intact understory community. They found that after the WFUF, the plant community at Fire Point shifted toward higher compositional similarity with the relict or reference sites, and that this change was due to an increase in annual and biennial forbs. Species richness, plant cover, plant layer density, and plant diversity were significantly lower at Fire Point than at reference sites, but the fire did not increase the rate of change in these variables after two years. The litter layer at Fire Point was reduced to depths more similar to reference sites (Laughlin and others 2004).

The length of time since fire occurrence has a large effect on the type of response that is measured. Lowe and others (1978) reported that grass basal area decreased one year after wildfire, with increasing grass basal area in subsequent years with a peak achieved in year seven. In a longer term study of the Rattle Burn on the Coconino National Forest, Baiteneh and others (2006) found that the most severely burned sites continued to show the greatest understory production up to 30 years after the 1972 wildfire, compared to low severity burned and unburned controls. However, species composition changed through time in a variable manner – for many species, there was an initial increase in abundance, then a decrease (Baiteneh and others 2006). They hypothesized that post-fire understory plant communities are composed of fire-resistant plants and plant species that colonize the burned site from adjacent communities. Baiteneh and others (2006) concluded that post-fire plant communities are a product of fire regime – intensity, severity, periodicity, seasonality – as well as precipitation and grazing regimes.

Effects of Grazing

The effects of grazing animals, both native and introduced, have been well documented in the literature to have a marked influence on understory productivity, composition, and diversity, but will not be treated in this review. For detailed information, see Leopold (1951), Cooper (1960), Moore and others (1999), Curtin (2002), and Sorensen and McGlone (2010). Several of these authors have documented the importance of managing grazing following silvicultural activities to allow the understory to grow and reproduce.

Effects of Climate

We found at least four studies that incorporated precipitation data into their analyses, and each reported a strong, positive correlation between annual precipitation and understory productivity and diversity (Fule and others 2002, Bataineh and others 2006, Moore and others 2006, Sabo and others 2008). For example, Moore and others (2006) reported that over a twelve-year period, graminoids (grasses and grass-like plants) responded positively to silvicultural treatment in amount of standing biomass, until severe drought reduced productivity to pre-treatment levels.

Effects of Management

Thinning & Burning

Prescribed burning and mechanical thinning are used to both mimic and prepare for the reintroduction of the historically frequent fire regime under which ponderosa pine forests evolved. Understory productivity is variable 2, 5, and 7 years after prescribed burning (Andariese and Covington 1986), with the greatest increase in productivity following the longest time period since burning, and under pole (medium-sized trees) stands compared to mature stands. White and others (1991) compared the effects of prescribed fire on four species of grass' phenology within two strata of overstory. The two strata were described as sawtimber patches (120 stems/ha and 63 cm average diameter at breast height [dbh]) and pole patches (1730 stems/ha and 15 cm average DBH). *Muhlenbergia montana* and *Festuca arizonica* failed to flower one year after prescribed burning in both strata, but in the second year following burning, a significantly higher percentage of *F. arizonica* plants flowered in the burned sawtimber patches than in the burned pole patches. *M. montana* plants did not fare as well, with fewer than half of the plants flowering regardless of strata type. The two other species of grass studied, *Poa fendleriana* and *Sitanion hystrix* (now *Elymus elymoides*) showed no difference in response to burning when compared to controls and in either stratum (White and others 1991).

In a longer term study, Moore and others (2006) reported differences in response among plant types as a result of restoration treatments begun in 1994 at Fort Valley Experimental Station: thinning from below (thinning), thinning from below plus forest floor manipulations with periodic prescribed burning (composite), and untreated control. They reported that total standing crop was significantly higher at the two treated areas compared to controls, but that there was no difference between the two treatments, thinning and composite. The graminoid species responded within three years post-treatment, and continued to increase in standing crop until severe drought reduced standing crop to pre-treatment levels (Moore and others 2006). C3 graminoids accounted for the bulk of the response, and C4 graminoids showed a minimal response. Forbs and legumes waited 4-5 years post-treatment before showing a positive response to both the thinning and composite treatments, and annual and biennial plants increased in standing biomass at five years post-treatment (Moore and others 2006). Laughlin and others (2006) found similar, differential responses among species, with standing crop of C3 and C4 graminoids responding positively within patches where all post-settlement trees were removed, but did not respond as well in patches where post-settlement trees were left standing, and within presettlement patches. In the same study, standing crop of legumes and *Festuca arizonica* did not increase through time under all patch types (Laughlin and others 2006).

Species richness and diversity are important components in describing plant community composition, which when combined with species abundance give a strong indication of habitat quality of understory vegetation for different taxonomic groups (Noss 1990). Abella (2004) published a review of understory responses to thinning and burning activities in Arizona ponderosa pine forests, and stated that no research to that point had indicated a consistent increase in ground flora diversity for the studies he reviewed. Since that time, a handful of studies have begun to elucidate the interaction of current management strategies with understory diversity. One such study (Laughlin and others 2008) reported that treatments implemented in 1994 had no effect on species richness for the first ten years, but one treatment diverged from controls and from the lesser degree of treatment in the 11th and 12th years following treatment. Laughlin and others (2008) measured understory vegetation response in the same area cited earlier in this report (Moore and others 2006) from Fort Valley Experimental Forest, in which thinning, and thinning and burning (composite), were compared with controls, both total richness and native understory species richness increased significantly when the overstory was thinned, and the understory was burned in the composite treatment (Laughlin and others 2008). In another study, Laughlin and others (2007) stratified their vegetation sampling within 11 Terrestrial Ecosystem Survey units for a total of 75 plots within the Coconino National Forest and Northern Arizona University's Centennial Forest. They used multivariate analysis techniques to quantify contribution of nine variables toward understory richness. They found that species richness was lowest when the forest overstory was densest, which they explained through indirect effects of canopy on soil organic matter, soil nitrogen and understory cover. Laughlin and others determined that understory species richness was highest at intermediate levels of understory plant cover, hypothesizing that both competitive exclusion and colonization success limit richness in this system.

In a similar study conducted on the North Rim of Grand Canyon National Park, Laughlin and Grace (2006) demonstrated that ponderosa pine overstory had a strong inhibitory effect on the abundance of understory species, which in turn influenced the richness of understory species. But in their multivariate model, time since last surface fire also had a strong, inverse effect on understory richness, with a threshold response when fires were too frequent and resulting understory plant richness was lower than expected. These results indicate that surface fire is an important and complex determinant of understory plant community composition and structure (Laughlin and Grace 2006).

Overstory composition has been shown to influence understory diversity. Abella and Springer (2008) found differences in community composition under Gambel oak (*Quercus gambelii*) when compared to pure pine and treeless openings. They found the greatest understory diversity under tree-less openings (3 species/m^2) compared to under ponderosa pine trees (1.25 species/m^2)), and intermediate levels under Gambel oak.

Response of Understory Exotic Species

Many studies have documented the influx of non-native, exotic species and its influence on the integrity of native ecological systems (Noss 1990, Vitousek and others 1996). Understory plant communities are also susceptible to invasion by exotic plant species, and the effects of management on exotic species have been documented in several studies (Knapp and others 1996, Griffis and others 2001, Korb and Springer 2003). The response of SW-PIPO native and exotic understory plants to management treatments was surveyed by Griffis and others (2001) along a gradient of disturbance, with comparisons among unmanaged (no mechanical thinning and burning; thinned; thinned and burned; and burned by stand-replacing wildland fire). They reported that exotic species responded more strongly than natives, in both species richness and abundance for exotic forbs. Total native species richness remained about the same with increasing disturbance, while native graminoid abundance increased with increasing disturbance of thinning and burning.

However, both total native species richness and native graminoid abundance decreased in the area burned by stand-replacing wildland fire. Unmanaged stands exhibited the lowest total understory diversity, which increased with disturbance intensity. The highest diversity of exotics was found in areas that had experienced stand-replacing fire (Griffis and others 2001). This study indicates that there are tradeoffs in managing stands, and that mechanical treatments have some undesirable effects, but that uncharacteristic, stand-replacing fires (as a result of not implementing treatments) may have the most undesirable effects of any option on understory plant community composition.

Discussion & Conclusions

There are strong connections between overstory structure and composition, and understory quality, abundance, productivity and diversity. Individual species of understory plants respond differently to overstory manipulations, whether through mechanical harvest, managed fire, or wildland fire. There is a pronounced lag time or delay between disturbance or management activities, and understory response, which is mitigated by precipitation and other site variables. Fire plays a crucial role in SW PIPO overstory and understory structure, composition, and diversity, and fire increases soil nutrient cycling processes. Several authors have studied varying levels of overstory manipulation, and found that the degree of understory response is dependent upon how much overstory is removed and the residual density of trees, or the level of treatment. Two such studies suggested that threshold levels for basal area exist. Above that level, understory response is minimal or nonexistent. As mentioned earlier, the basal area threshold may be close to 70 ft^2/acre for SW ponderosa pine, as there is no significant difference in productivity between thinned and unthinned stands above this level (Clary and Ffolliott 1966). Griffis and others (2001) suggested a BA of 15m^2/ha (65.3 ft^2/ac) as that threshold, while Sabo and others (2008) suggested that only SW PIPO stands thinned below a BA of 5.9m^2/ha (25.7 ft^2/ac) elicited a significant response in understory productivity. These reported thresholds are at the low end of the spectrum of current treatment levels (BA of 40-120 ft^2/ac), and continued research should focus on understanding the response of SW PIPO to treatments around and below these thresholds to determine optimal understory response, versus financial and other costs of treatment.

Exotic plant species also respond to forest management, including thinning, prescribed burning, and wildland fire management, although exotic plant invasions appear to be exacerbated to the greatest degree by uncharacteristic fire that is the result of minimal or no management. These results suggest that for areas where increasing understory productivity and native diversity are desired objectives, significant reductions in overstory density to more heterogeneous patterning of openings and moderate levels of tree density within groups are warranted across a significant portion of the landscape. However, treatments are expensive and have negative impacts. Just as it has been suggested that overstory treatments could be strategically placed to optimize cost: benefit ratios in achieving potential fire behavior reduction goals, understory focused treatments could be placed strategically to enhance native biodiversity, increase wildlife habitat connectivity, and avoid the increased spread of exotic invasive species.

Predictive Model Development

Several studies used multivariate statistical analysis techniques to develop conceptual models of understory interactions with their environment, and there has been modest development of quantitative, predictive models (McPherson 1992, Carr 2006, Laughlin and others 2006, 2007, 2008). The amount of data available supports the development of site- and species-specific predictive models of understory vegetation response to management treatments, but data are available for only a limited number of understory species, in a limited number of locations. Due to this data limitation, development of generalized models of understory response to overstory manipulations, and species-specific habitat suitability models will be problematic until more understory species' responses to treatments are better understood across a wider gradient of sites.

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