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Relationships between *Pinus ponderosa* forest structure, light characteristics, and understory graminoid species presence and abundance

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Abstract

Productivity of graminoid species is known to vary in response to different *Pinus ponderosa* densities. Specific forest structural characteristics related to these differences remain elusive, yet are important for management objectives that aim at a diverse understory vegetation composition. In this study, we have addressed the effects of *P. ponderosa* forest structure and light environments on individual graminoid species presence and abundance. Graminoid species presence was positively related to mean diameter of *P. ponderosa* trees (including seedlings), but presence was poorly related to light characteristics. Larger tree diameters may relate to graminoid species presence through shade intensity because shade under larger diameter trees is less dense. The abundance of small diameter trees indicates past disturbance and exposed mineral soil which may favor some graminoid species over others. Graminoid species abundance measured as basal area cover and plant numbers were more closely related to direct sunlight. Cool-season species performed better on sites with spring/autumn or morning summer sun while the larger plants of warm-season species were on sites with midday summer sun. These results suggest that manipulation of forest structure to maintain stands of large diameter trees in a patchy distribution will create a variety of direct sun regimes needed to maintain a diverse grass understory. This type of forest structure is also consistent with pre-European southwestern *P. ponderosa* forest conditions. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

During the last century, *Pinus ponderosa* Dougl. ex Laws. forests in the southwestern United States have undergone drastic density changes caused in part due

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to management practices such as heavy grazing early this century and active fire suppression (Cooper, 1960; Savage, 1991; Covington and Moore, 1994a; Covington et al., 1994). Prior to Euro–American settlement, *P. ponderosa* forests were open and park-like and consisted mostly of large diameter trees (Covington and Moore, 1994a). Currently, tree densities are 40–50 times greater than before settlement, and the majority of these trees are <13 cm in diameter (Covington and Moore, 1994b; Covington et al., 1997). These density

and diameter changes have likely changed understory graminoid species composition through their effects on light regimes or below-ground resource availability. The influence of *P. ponderosa* overstory on biomass or cover of graminoid, forb, and shrub species understory vegetation has received considerable attention (e.g., Pase, 1958; Thompson and Gartner, 1971; Clary, 1975; Uresk and Severson, 1989; Moore and Deiter, 1992) due to the influence of declining productivity on forage availability for cattle and wildlife. However, individual species responses to *P. ponderosa* forest structure have not received much attention and were considered relatively unimportant because of low overall biomass productivity under dense stands (Clary, 1988).

In the shift from forest-level to ecosystem-level management, sustainability of all components of the forested ecosystem has become a primary objective (Kaufmann et al., 1994). An integral component of ecosystem management is the maintenance of ecosystem integrity which includes species compositional integrity. Species diversity likely promotes resistance and resilience and thus may be important to ecosystem sustainability (Schulze and Mooney, 1993; Tilman and Downing, 1994).

Dendrochronology and fire scar dating are used in the southwestern US to determine forest structure prior to European settlement. These data often serve as baseline information from which ecosystem management strategies are developed (Salwasser and Pfister, 1994; Kaufmann et al., 1994; Christensen et al., 1996). However, information on herbaceous vegetation cannot be reconstructed with these methods due to their lack of woody tissues. As a consequence, development of management plans that take herbaceous species composition into account require an understanding of processes that link overstory management to understory species dynamics and diversity.

Observational studies have documented shifts in the relative importance of individual grass species with increasing *P. ponderosa* densities (Arnold, 1950; Pase, 1958; Merkle, 1962; Pearson, 1967), but research on individual species growth performance and causes of these differences is generally lacking. In eastern Washington, decreased light and nitrogen availability negatively influenced grass productivity and reproduction (Moir, 1966). In eastern Oregon, variables related to species performance differed depending on whether

performance was measured as biomass or percent cover. Competition for below-ground resources, water in particular, appeared to control biomass productivity of most graminoids and forbs (Riegel et al., 1992), while light transmission appeared more important in controlling some species' canopy cover (Riegel et al., 1995). In eastern Arizona, light transmission, soil potassium, and stand age were the most important variables related to individual species biomass productivity (McLaughlin, 1978).

In this study, we addressed how forest structure and the subsequent light environment under *P. ponderosa* affects graminoid species. We hypothesized that the forest light environment would influence species differently both with respect to their presence (a function of getting established and surviving at a site) and their abundance when present. To this end, individual species presence and basal cover were determined under a range of forest structural and light conditions in plots representing seedling/sapling to mature *P. ponderosa* trees.

2. Methods

2.1. Site description

The study was located in the White Mountains of Arizona and encompassed 20 km² in the Beaver Creek watershed of the Apache National Forest 16 km south of Alpine, Arizona. Elevations at the site range from 2400 to 2600 m and mean annual precipitation is 560 mm. Half of this precipitation falls as snow, mostly between December and March, while the majority of the remainder occurs as rain between July and September (Laing et al., 1989).

For this study, only stands dominated by *P. ponderosa* with a negligible *Pinus flexilis* James and *Quercus gambelii* Nutt. component were selected for sampling. Soils in these *P. ponderosa* stands are clayey-skeletal mollic Eutroboralfs of moderate depth (Laing et al., 1989). Current commercial uses of the site include timber harvesting with an approximate entry cycle of 10 years, and cattle grazing. The most recent selective timber harvest and thinning occurred in 1989 in about half of the stands that were sampled in this study. A prescribed burn had been conducted over the entire area in 1976.

2.2. Vegetation characteristics

During summer of 1995, 70 plots were sampled for grass basal area cover, *P. ponderosa* forest structural and light characteristics. Plots were selected to represent various overstory tree density and diameter combinations. Low-lying locations with higher water availability and locations that showed signs of recent logging disturbance (e.g., slash piles and skid trails) were excluded from sampling to avoid confounding factors. At each plot, graminoid basal area cover (%) and density of plants (# plants/m²) were determined in a 0.5 × 2.0 m² rectangle that was subdivided into 10 sections to facilitate ocular cover estimates. Graminoid basal area cover reflects the percent ground area covered at the base of a plant. In contrast crown cover, which is frequently used in similar studies, reflects the percent ground covered by the projected crown of a plant. Of the two cover estimates, basal area is more reliable since it is less influenced by seasonal climatic and other perturbations that can influence above-ground biomass and thus crown cover (Bonham, 1989). From the grass cover data, species presence/absence was determined. A total of 12 species were tallied but only species present in >10% of the plots and were further analyzed. These included: *Carex* spp., *Koeleria cristata* (L.) Pers., *Muhlenbergia montana* (Nutt.) Hitchc., *Muhlenbergia virescens* (H.B.K.) Kunth., *Poa fendleriana* (Steud.) Vasey, and *Sitanion hystrix* (Nutt.) J.G. Smith (also known as *Elymus elymoides* (Raf.) Swezy). Finally, at a 4 m radius around the grass plot center, all *P. ponderosa* taller than 0.2 m were sampled for their distance to the plot center and their diameter at 1.4 m height if they reached that height. At an 8 m radius the same measurements were taken for trees with a diameter of at least 11.5 cm.

2.3. Light characteristics

Hours of potential direct sunlight at the grass plot center were assessed using a Solar Pathfinder (Solar Pathways, Hartford, South Dakota). With the Solar Pathfinder, images that are similar to those of hemispherical photographs are manually traced onto charts that show average solar paths for all 12 months at a given latitude. Each solar path on the chart is subdivided into 30 min sections.

From the generated charts, periods of direct sun lasting longer than ca. 10 min can be resolved. For a more detailed description of the instrument see Platts et al. (1987). Trees that were shading the grass plot center between 900 and 1600 solar hours were sampled for distance from the grass plot center and diameter to determine whether tree characteristics causing light conditions in the grass plots related to the presence and plant abundance of graminoid species.

In addition, photosynthetic photon flux density (PPFD) and red : far red ratio (R : FR, 658–662 nm: 728–732 nm) of shade light at 25 cm above the ground were determined using an LI-1800 spectroradiometer (LI-COR, Lincoln, Nebraska). These measurements were conducted between 11:00 and 14:00 Mountain Standard Time during clear sky conditions. Of the 70 plots sampled for vegetation, five did not experience any shade during the measurement period and four plots could not be measured because of smoke interference from a nearby wildfire. Therefore, shade PPFD and R : FR values were available only for 61 of the 70 plots.

2.4. Derived variables

Overstory tree data from the fixed plots were combined to form several forest structural variables that incorporate different degrees of forest structural information (Table 1). For example, density quantifies only the number of trees regardless of their size, but basal area and Reineke's stand density index combine both density and size (Table 1; Avery and Burkhart, 1983). The Hegyi and Martin and Ek indices go a step further and use density, size and distance to describe forest structure (Martin and Ek, 1984). The Hegyi and Martin and Ek indices were developed to assess among-tree competition and require a diameter for the 'target' tree, i.e. the tree for which competition will be evaluated (Martin and Ek, 1984). Since the 'target' tree in this study was a grass plot without meaningful diameter, the 'target' tree diameter was set to 'one' for the calculations. For the same reason, the selection criterion of whether a tree was considered a competitor was modified from Martin and Ek (1984) to exclude a target tree diameter: A tree was considered a competitor if its diameter (cm) divided by four was greater

Table 1
Forest structural variables generated from *P. ponderosa* trees sampled around graminoid species plots

Variable	Tree measure included	Equation ^a
Trees per hectare	number of trees (density)	n/p
Mean diameter	tree size	$(\sum \text{DBH})/n$
Quadratic mean diameter	tree size	$((\sum \text{DBH}^2)/n)^{0.5}$
Basal area	tree size and density	$n/p * 0.00007854 * \text{md}^2$
Reineke's stand density index	tree size and density	$n/p * (\text{qmd}/25.4)^{1.605}$
Hegyí index ^b	tree size, density, and distance	$\sum (\text{DBH}/(d + 1))$
Martin and Ek index ^b	tree size, density, and distance	$\sum (\text{DBH} * e^{-16d/(\text{DBH} + 1)})$

^a Abbreviations and units: n is the number of trees per hectare, p the plot size (ha), DBH the tree diameter (cm) at 1.4 m height, 'md' the mean diameter (cm), 'qmd' the quadratic mean diameter (cm) and d the tree distance from grass plot center (m).

^b Modified from Martin and Ek (1984) to account for the lack of a meaningful target tree diameter (see text).

than its distance to the grass plot center (m). Since the grass plot was centered within the *P. ponderosa* tree plots, no linear expansion term (Martin et al., 1977) was used. The importance of *P. ponderosa* seedlings was assessed by including all trees taller than 0.2 m in the calculations, and then recalculating using only trees taller than 1.4 m. For trees shading the grass plot during the day, mean and quadratic mean diameters were calculated.

The Solar Pathfinder charts were digitized and analyzed for hours of sun in the morning (sunrise–1100 solar time), midday (1100–1400) and afternoon (1400–sunset) for the months March through October. A principal component analysis using the varimax option in SAS (version 6.11) was performed on these variables. It resulted in six new variables that correlated strongly to morning, midday or afternoon sun-hours during summer (April–August) or spring/autumn (March, April, August–October).

2.5. Data analyses

To reduce the large number of potentially redundant variables, correlation matrices were generated to determine the better predictor variable incorporating the same tree information (Table 1, e.g. mean diameter versus quadratic mean diameter) and whether a variable containing seedling *P. ponderosa* was a better predictor than one excluding seedlings. From these options, the best predictor was included in multiple regression analyses. Multiple regressions used stepwise selection with an $\alpha = 0.05$ for variable entry and $\alpha = 0.1$ for removal and were conducted in SAS (version 6.11).

Shade PPF and R : FR were regressed against the forest structural variables described in Table 1, and in addition, the mean diameter (or quadratic mean diameter) and number of trees that were shading the grass plot during the midday time period. Trees shading the plot during other times were not included since they showed little influence on the radiation at the time of measurement. The six sun-hour variables obtained from the principal component analysis described above were regressed against the forest structural and shading tree variables.

To address the question of which forest structural and light variables are related to species presence, the presence data for each of the grass species was regressed by logistic regression against the structural (Table 1) and shading tree variables in SPSS for Windows (Release 6.1.2, 1995). Both forward and backward selection using the likelihood-ratio test as criterion for the entry or removal of predictor variables ($\alpha = 0.05$ for entry and $\alpha = 0.10$ for removal) were employed to determine the best model. For all species both methods resulted in the same model. Midday shade measurements were not included in this or the following regression analyses because these data were not available for all plots.

To address species abundance, individual species cover and plant density multiple regressions were only performed on those plots where a particular species was found since the question of presence/absence was addressed in the previous analyses. This resulted in the following sample sizes: *Carex* spp. $n = 37$, *K. cristata* $n = 30$, *M. montana* $n = 24$, *M. virescens* $n = 22$, *P. fendleriana* $n = 21$, *S. hystrix* $n = 53$. Both forest structural (Table 1) and shading tree variables were

included in addition to the sun variables for these regressions. An outlier occurred with *M. virescens* where cover of one sample plot was twice that of the next smaller cover value and it influenced the regression outcome. When this point was eliminated from the cover regression analysis the corresponding plant density value was high but not outside the range of the other plots, so for *M. virescens* density results of both analyses, one with and one without this outlier data point, are reported.

For all species but *M. montana* and *M. virescens*, cover and plant density resulted in models containing similar predictor variables if the significance level for model entry was raised to $\alpha = 0.10$. This suggests that individual plant sizes were independent from the predictor variables for all but these two species. To explore the plant size issue for *M. montana* and *M. virescens* further, the average cover per plant was determined by dividing the basal cover by plant density for each plot. This average plant cover for *M. montana* and *M. virescens* was then regressed against the forest structural (Table 1), shading tree, and sun-hour variables.

Plots of the relationships between the significant predictor variables and the dependent variables were generated to evaluate the appropriateness of a simple linear relationship. If a relationship appeared non-linear, either a square or square-root term of the significant variable was added to the potential predictor variables, and the multiple regression analysis was repeated including this additional variable. These transformations visually appeared to fit the data, but this method did not allow the detection of other potential relationships.

3. Results

3.1. Light conditions

Both shade PPFD and R : FR were higher under larger diameter, directly shading trees (Table 2) but the relationship between PPFD and tree diameter was poor at diameters <15 cm (Fig. 1). Exclusion of these

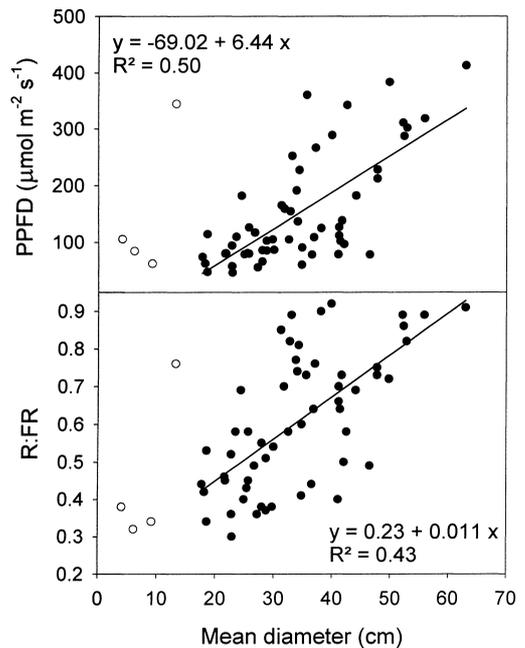


Fig. 1. Relationship between mean diameter of *P. ponderosa* trees that direct light beam was penetrating and shade intensity (PPFD) and red : far red ratio (R : FR). Solid points are data included in the regression equation.

Table 2

Significant forest structural variables in multiple regressions of sun-hour variables, shade intensity (PPFD) and shade red : far red ratio (R : FR)

Variable predicted	Predictor variables	Trend	R ²
Midday shade PPFD	mean diameter of trees that light beam penetrated	+**	0.34
	Hegyí index of surrounding trees	-**	0.10
Midday shade R : FR	mean diameter of trees that light beam penetrated	+**	0.42
Morning spring/autumn sun	quadratic mean diameter of shading trees	+**	0.13
Midday spring/autumn sun	quadratic mean diameter of shading trees	+*	0.06
Afternoon spring/autumn sun	mean diameter of surrounding trees	+**	0.10
Midday summer sun	Hegyí index of surrounding trees	-**	0.20
Morning summer sun	Reineke's stand density index including seedlings	-*	0.06
Afternoon summer sun	Hegyí index of surrounding trees	-**	0.13

smaller-diameter values (open circles in Fig. 1) improved the relationship to $R^2 = 0.50$ for PPF.

Forest structural variables were generally poor predictors of direct sun-hours at the grass plots. The best fit was obtained for midday summer sun, while the poorest fits were associated with morning summer sun and midday spring/autumn sun (Table 2). Of the significant tree variables, tree diameter variables were positively related to the sun-hours while the Hegyi index, tree density, and Reineke's stand density index had a negative influence on sun-hours received by the grass plots.

3.2. Species presence

Overall, the sun-hour variables were poorer predictors of species presence than the forest structural variables. Of the structural variables, the diameter of the surrounding trees (including seedlings) was the most important predictor (Table 3). *Carex* spp. were more likely to be found under larger diameter trees (Table 3). *M. montana* was also more likely to be found under larger diameter trees and was negatively related to tree competition (Hegyi index), the diameter of shading trees, and afternoon summer sun. *M. virescens* on the other hand, preferably grew in locations with small diameter trees in the direct vicinity

and larger diameter trees for shade. *S. hystrix* was more likely to be found under large diameter trees (quadratic mean diameter) while midday spring/autumn sun influenced *S. hystrix* presence negatively. However, while the model predicted *S. hystrix* absence well, it did poorly when the species was actually present. Neither the presence of *K. cristata* or of *P. fendleriana* was significantly related to any of the variables examined.

3.3. Cover and density

For the species' cover and density, the sun-hour variables were more significant than for species presence (Table 4). *Carex* spp. showed a positive influence of midday spring/autumn sun on plant density. *M. montana* cover increased with the mean diameter of surrounding trees, decreased in a non-linear relationship with morning summer sun, and average *M. montana* cover per plant was positively but weakly related to midday summer sun. None of the predictor variables were related to the density of *M. montana* plants. *P. ponderosa* competition (Hegyi index) had a negative influence on *M. virescens* cover while the average cover per *M. virescens* plant increased with both midday summer and afternoon summer sun. *M. virescens* plant density, however, was positively,

Table 3

Significant predictor variables in multiple logistic regression of species presence. The trend indicates whether increasing values of a predictor variable appears to increase or decrease the likelihood for a species to be present. The predictive quality of a model is represented by the accuracy (%) with which the model predicted species presence when it was actually present and absent when actually absent. Ideally both values would be 100%, while lower values indicate a lower model fit

Species	Predictor variables	Trend and significance	(%) Correct model prediction when species was actually	
			present	absent
<i>Carex</i> spp.	diameter of surrounding trees including seedlings	+ *	44	79
<i>Koeleria cristata</i>	none	—	—	—
<i>Muhlenbergia montana</i>	mean diameter of shading trees	— **	89	71
	diameter of surrounding trees including seedlings	+ **		
	Hegyi index of surrounding trees	— **		
	afternoon summer sun	— *		
<i>Muhlenbergia virescens</i>	mean diameter of shading trees	+ **	94	59
	diameter of surrounding trees including seedlings	— **		
<i>Poa fendleriana</i>	none	—	—	—
<i>Sitanion hystrix</i>	quadratic mean diameter of surrounding trees including seedlings	+ **	29	94
	midday spring/autumn sun	— *		

Table 4

Significant predictor variables in multiple regressions of species cover and plant density. If a transformed term was significant, the transformation is indicated

Species	Variable predicted	Predictor variables	Trend and significance	Model R^2
<i>Carex</i> spp.	cover	none		0.36
	density	midday spring/autumn sun	+ **	
<i>Koeleria cristata</i>	cover	none		
	density	none		
<i>Muhlenbergia montana</i>	cover	mean diameter of surrounding trees	+ *	0.53
		morning summer sun: untransformed and as squared term	- **	
	density	none	+ *	
<i>Muhlenbergia virescens</i>	avg. plant cover	midday summer sun	+ *	0.17
	cover	Hegyí index of surrounding trees	- **	0.38
		density	square root of tree density including seedlings (or mean diameter of shading trees including seedlings) ^a	
avg. plant cover	midday summer sun	+ *	0.42	
	afternoon summer sun	+ *		
<i>Poa fendleriana</i>	cover	none		0.35
	density	midday spring/autumn sun	+ **	
<i>Sitanion hystrix</i>	cover	none		
	density	none		

^a Significant variable if the outlier point is included in density analysis.

non-linearly related to the density of surrounding *P. ponderosa* (including seedlings) or negatively related to the mean diameter of surrounding *P. ponderosa* if the outlier data point was included. For *P. fendleriana*, midday spring/autumn sun increased both plant density and cover. As with the presence dataset, none of the predictor variables were related to *K. cristata* cover or density.

4. Discussion

Results of this study indicate that graminoid species distributions in southwestern *P. ponderosa* understories are influenced by two factors. First, species presence was related to stand structure and in particular to tree diameter (including seedlings). It is rather surprising that the sun variables did not significantly relate to species presence data. However, shade could indirectly relate to species presence through the link of shade PPF and R:FR to

P. ponderosa tree diameters (Fig. 1). Secondly, species abundance as measured by cover and plant density was more influenced by the amount of daily and seasonal distribution of direct sun than by forest structure. These results agree well with other studies regarding the importance of light for understory vegetation growth and performance (Liefers and Stadt, 1994; Riegel et al., 1995; Griffith, 1996; Ricard and Messier, 1996).

The importance of including *P. ponderosa* seedlings in the diameter variables for predicting species presence could be related to past plot history. *P. ponderosa* regeneration is sparse and infrequent on basalt-derived soils and highly dependent on areas with exposed mineral soil and little grass competition (Pearson, 1950). At the study site, abundant *P. ponderosa* regeneration appears limited to disturbed areas that are created during logging operations (e.g. landings; Bruce Buttrey, USFS Alpine Ranger District, personal communication 1995). The negative influence of pine seedlings in the presence of *Carex* spp.,

M. montana, and *S. hystrix* and positive influence on *M. virescens* presence would then suggest that the former do not get readily established after disturbance while *M. virescens* does. This result is somewhat surprising for *S. hystrix* since it can colonize sites quickly (Tisdale and Hironaka, 1981; Vose and White, 1987). However, *S. hystrix* was the most abundant of the species among those present in the sample plots and may thus not have significant habitat preferences. The preference of *M. virescens* for small diameter tree sites is consistent with findings by McLaughlin (1978) who showed that *M. virescens* and several forb species responded positively to younger and shorter *P. ponderosa* trees. The fact that forbs respond positively to logging damage (Arnold, 1953; Garrison, 1960) provides further evidence that the ability of pine seedlings to predict graminoid species presence is linked to prior disturbance regimes.

At increasingly larger diameters, shade light conditions could further influence species distributions, since larger tree diameters give midday shade of higher PPFD and R : FR (Fig. 1). Other studies in more mesic environments have found positive relationships between species presence and canopy openness (Griffith, 1996) or percent daily PPFD (Ricard and Messier, 1996; Lieffers and Stadt, 1994). These measures integrate diffuse and direct light since 45–55% of the daily PPFD in temperate forest understories is attributable to sunflecks (Chazdon, 1988). Direct sun in patches >10 min appears of little importance to species presence in the current study since the sun variables did not explain significant levels of variation; shade characteristics appear to be important only through their link with tree diameters. In agreement with our results, productivity studies have also shown that mature *P. ponderosa* stands of various densities tend to have higher graminoid biomass production than pole-sized stands (Reynolds, 1962). Also, in California woodlands, open grassland species are likely eliminated from woodlands despite successful germination through shade-induced mortality (Marañón and Bartolome, 1993).

In predicting species abundance expressed as basal cover and plant density, no single variable stood out as a major factor. However, in contrast to the species presence data, sun variables were important for species abundance. Two species, *Carex* spp. and *P. fendleriana*, responded positively to midday spring/

autumn sun. For these species the response of plant density was greater than that of cover. This may be an artifact of sampling, since plants of these species were consistently small and had overall cover values of <3% per plot. At such low cover values, the actual plant counts may give a more accurate reflection of the species' abundance. The two *Muhlenbergia* species were the only ones responding strongly to a forest structural variable. However, their average plant cover was also related to midday summer sun and afternoon summer sun.

The performance differences relative to the sun variables largely agree with the species' growth phenology and responses to shading that were evaluated in a separate greenhouse study. In the greenhouse, *K. cristata* and especially *S. hystrix* were less negatively affected by shading than *M. montana* (Naumburg, 1996). In the field, *K. cristata* and *S. hystrix* also showed no relationship with the sun variables. *Carex* spp. and *P. fendleriana*, the two species significantly related to spring/autumn sun, are cool-season species that grow and flower in spring (Gould, 1951). In contrast, *M. montana* is a warm-season species that does not grow until mid-summer and flowers in early autumn (Gould, 1951). This species was one of the two where individual plants performed better under midday summer sun. The second species, *M. virescens* is an exception among the local representatives of the C_4 -genus *Muhlenbergia* in that it grows and flowers together with cool-season species (Gould, 1951). Its preference here for midday summer sun, however, indicates it is functionally dissimilar to cool-season species.

Studies have shown that cool-season species show smaller increases in biomass production after *P. ponderosa* clear-cutting than warm-season species (Thompson and Gartner, 1971) and that several years after *P. ponderosa* thinning, *Carex* spp. contribute more to overall biomass at high than at low *P. ponderosa* densities (Pase, 1958). Traditional thinning operations result in even spacing of trees (e.g. see Fig. 1 in Pase, 1958) which would increase overall light levels including midday summer sun. Evidence in this study suggests that warm-season species should be favored under such conditions. This is further supported by a similar larger scale pattern found in eastern South Dakota where cool-season grasses dominated on north-facing slopes and in forested areas whereas

warm-season grasses dominated on south-facing slopes (Tiezen, 1970).

One explanation for the apparent relationships between stand structure, light conditions, and species presence and abundance relates to water relations. While belowground competition for water and nutrients can negatively affect grass biomass production in *P. ponderosa* forests (Moir, 1966; Riegel et al., 1992), growth under woody vegetation can enhance grass biomass and abundance, especially in semiarid climates (Clary and Morrison, 1973; Tiedemann and Klemmedson, 1977; Frost and McDougald, 1989; McClaran and Bartolome, 1989; Belskey, 1994). In this study, none of the sun-hour variables showed a negative relationship with the species. However, midday summer sun appeared only beneficial to the two *Muhlenbergia* species. Since early summer is the dry season at the study site when evaporative demand is also high, protection from intense sun at midday during summer may be of benefit for the cool-season species especially in light of their comparatively low water-use efficiency during mid-summer (Naumburg, 1996). Further, in pinyon–juniper woodlands soil moisture at canopy edges will vary with incident radiation and cardinal direction (Breshears et al., 1997). In these systems, graminoid species abundance varies with canopy proximity and cardinal direction (Clary and Morrison, 1973; Schott and Pieper, 1985). Since the cardinal directions with respect to a tree canopy are related to the daytime and season of incident radiation, the results of this study with respect to abundance differences of the species could be related to water availability and should be explored in further studies.

In addition, canopy shade can reduce surface soil temperatures by up to 10°C during the summer in pinyon–juniper woodlands compared to intercanopy patches (Breshears et al., 1998). C₄ grass species abundance is both over large scales and in SE Arizona highly correlated with growing season temperature (Teeri and Stowe, 1976; Wentworth, 1983; Ehleringer et al., 1997). In SE Arizona the threshold where C₄ species become less abundant than C₃ species is at an elevation of 2100 m, equivalent to 26°C mean maximum temperature during the warmest month of the year (Wentworth, 1983). The study site is located close to this elevation and temperature threshold. Thus, the *Muhlenbergia* species better performance

under midday summer sun could also relate to higher summer temperatures that may be sub-optimal for the cool-season species.

In conclusion, the results of this and previous studies indicate that graminoid species have different habitat preferences that relate to ground disturbance as well as direct and shade light conditions. Light conditions are influenced by *P. ponderosa* size and distribution. Driving forces behind these species habitat preferences may relate to greater negative shade influence on some species as well as on temperature and water conditions. Therefore, changes in forest light and structural conditions will likely change graminoid species presence and abundance over time. To promote graminoid species diversity, forest management practices should strive to produce a variety of heterogeneous stand conditions. For example, clumps of *P. ponderosa* separated by open patches would provide a variety of direct sunlight regimes. Since several of the species in this study were more likely to be present under a canopy of larger diameter trees, thinning operations should focus on the removal of smaller diameter trees and avoid large scale disturbance. This type of management would also mimic the pre-European spatial and structural arrangement of southwestern *P. ponderosa* forests (White, 1985).

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