UNDERSTORY VEGETATION COMPOSITION AND ABUNDANCE IN RELATION TO LIGHT, WATER, AND NUTRIENT SUPPLY GRADIENTS IN UPLAND OAK WOODLANDS

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ABSTRACT

Introduction

The Ozark Highlands of Missouri have experienced a complicated series of exploitive events (Flader 2004). The area was heavily cut over for timber at the turn of the last century and was overgrazed by privately owned livestock through the early 1900s. Decades of fire suppression since the 1940s further altered plant composition and structure. The current state of forest and woodland herbaceous communities may be quite unlike those seen historically.

The main difference between a woodland and a forest lies in the abundance of woody species in the midstory and understory, which affects the ground layer vegetation by blocking sunlight. Forests generally have a well-developed midstory and understory, and therefore have more spring ephemerals and shade-tolerant herbaceous species such as spotted geranium (*Geranium maculatum*) and black baneberry (*Actaea racemosa*). Woodlands have an open midstory and understory; more light penetrates to the ground layer to support a rich diversity of shade-intolerant species like goldenrods (*Solidago* spp.) and tick-trefoils (*Desmodium* spp.).

Ground layer vegetation composition has been shown to be closely aligned to light, water, and nutrient supply gradients. The relationship between environmental gradients and the distribution of woodland and forest plant indicators in the absence of disturbances is poorly understood. The objective of this study was to examine ground vegetation across gradients of light, moisture, and nutrient availability to determine how the composition and abundance of forest and woodland indicator plant species are affected by these gradients in undisturbed stands.

Methods

This study was conducted on the Sinkin Experimental Forest, which is operated and maintained cooperatively by the U.S. Forest Service, Northern Research Station and Mark Twain National Forest. The Sinkin Experimental Forest is located in Dent County, Missouri, approximately 40 km southeast of the town of Salem. It is located in the Current River Hills subsection of the Ozark Highlands, a dissected plateau with steep slopes, narrow ridges, and local relief of about 61 m. The soils of the ridgetops and upper hillsides are highly weathered, droughty, and strongly acidic. The soils of the lower hillsides are less weathered, are underlain by dolomite, and have greater cation exchange capacity and water holding capacity.

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Site selection was based on the presence of mature, fully stocked, closed-canopy oak stands that have not undergone substantial disturbance within the last 15-20 years. The stands were oak-pine and mixed oaks. The dominant trees were shortleaf pine (*Pinus echinata*), white oak (*Quercus alba*), and black oak (*Q. velutina*), which each make up about 20 percent of the basal area. Scarlet oak (*Q. coccinea*), hickories (*Carya* spp.), and northern red oak (*Q. rubra*) were less common. Elm (*Ulmus* spp.), flowering dogwood (*Cornus florida*), blackgum (*Nyssa sylvatica*), black walnut (*Juglans nigra*), and red maple (*Acer rubrum*) were least common (Villwock et al. 2011).

Data were collected in 2008. We sampled one hundred twenty 12.6-m-radius vegetation plots across twenty 4.9-ha stands. Plots in each stand were oriented across a moisture and site quality gradient. To describe the terrain, the aspect, location (shoulder, backslope, footslope), position (upper, middle, lower), and shape (concave, linear, convex) of the slope were recorded at plot center. Below-canopy light was measured to obtain photosynthetically active radiation (PAR). Soil samples were collected and analyzed for available water, cation exchange capacity (CEC), and pH. Diameter at breast height (d.b.h.) was recorded for overstory and midstory trees >5.0 cm d.b.h. Understory vegetation was recorded in four 1-m^2 subplots; all species were identified and percent cover was estimated in 10-percent classes. Herbaceous species were categorized as forest or woodland indicators, or generalists.

Statistical methods included multivariate ordination, Spearman correlation, regression trees, and multiple linear regressions. Regression trees and multiple linear regressions were used to examine the site, soil, and overstory factors important to forest and woodland indicator species abundances.

Results

A total of 165 species were identified in the 120 plots. Herbaceous plants were categorized as forest indicators (29 species), woodland indicators (65 species), and generalists (14 species). The most common forest indicators were false Solomon's seal (*Maianthemum racemosum*), pointedleaf ticktrefoil (*Desmodium glutinosum*), bearded shorthusk (*Brachyelytrum erectum*), and bellwort (*Uvularia grandiflora*). The most frequently occurring woodland indicators were shining bedstraw (*Galium concinnum*), Bosc's panic grass (*Panicum boscii*), and rue anemone (*Thalictrum thalictroides*). For analyses, the oak species were grouped into the red oak group (mostly black and scarlet oak) and the white oak group (mostly white and post oak).

Nonmetric multidimensional scaling was used to investigate the understory species composition. Aspect was the strongest determinant of ground flora composition; red oak stocking, pH, and CEC were also important factors. Northeast-facing slopes had higher pH and CEC, and greater stocking of non-oak species such as slippery elm (*Ulmus rubra*), pawpaw (*Asimina triloba*), and ash (*Fraxinus* spp.). Rattlesnake fern (*Botrychium virginianum*), *Geranium maculatum* (geranium), bellwort, and *Polygonatum biflorum* (Solomon's seal) were common species on northeast slopes. On southwest-facing slopes, soils were more acidic and red oak stocking was greatest; wild quinine (*Parthenium integrifolium*), late purple aster (*Symphyotrichum patens*), bracken fern (*Pteridium aquilinum*), and blueberry species (*Vaccinium pallidum, V. arboreum*, and *V. staminium*) were common in the understory.

Forest indicators (29 species) attained greatest percent cover and richness on northeast-facing slopes. Forest indicators had greatest cover where aspect was between 4 and 90°, total overstory basal area was <18.2 m^2/ha, plots were not on upper or lower shoulder slopes, and stocking of non-oak species was >52 percent. Forest indicators had the least cover where aspect was between 110 and 290° and pH was <5.26. A multiple regression model ($R^2 = 0.54$; $p < 0.001$) with soil pH, red oak stocking, pine stocking, and density of red oak stems best explained the variation in forest indicator cover. Soil pH positively affected forest indicator cover, but all tree covariates in the model had negative effects on cover.

Woodland indicators (65 species) did not show preference for aspect; they had similar percent cover and richness on northeast- and southwest-facing slopes. Soil pH was the most important factor influencing woodland indicator cover; the greatest cover occurred where pH was >5.9. However, the majority of plots had pH <5.9; on these more acidic soils, this group of woodland species was tolerant of a wide range of conditions. The following associations are for plots with soil pH less than 5.9. Where non-oak stocking was <30 percent, woodland species cover was maximized on plots with more available water and hill shape was either linear or convex (not concave). Alternatively, where non-oak stocking was >30 percent, woodland species maximized cover on mid-footslopes, lower backslopes, and lower shoulder slopes. This complex pattern may indicate specific woodland species' requirements for measured or unmeasured site factors, or competitive interactions with generalist species. A multiple regression model ($R^2 = 0.38$, $p < 0.001$) with soil pH, available water, total red oak stocking, and overstory pine stocking best explained the variation in woodland indicator species cover. Soil pH and water availability both positively affected woodland species cover; red oak and pine stocking had negative effects.

Discussion

Aspect, tree stocking, and soil pH are currently the dominant forces structuring the ground flora in these undisturbed stands. The cover of both forest indicators and woodland indicators was negatively affected by pine and red oak stocking. High stocking levels may indicate less light penetration or leaf litter accumulation, or a combination thereof, representing a physiological limitation and a mechanical barrier to herbaceous growth. Increases in soil pH led to greater cover of both forest and woodland plants, whereas aspect is a limitation only to forest indicator species.

Midstory tree abundance and PAR were expected to be influential as they both are indicative of the amount of light available to the ground layer plants. We expected to find the forest indicator species strongly correlated with low PAR, high woody density in the midstory and understory, and shadier protected slopes (northeast aspect). Woodland indicator species were expected to be strongly correlated with high PAR, less dense woody vegetation in the midstory and understory, and sunny exposed slopes (south and west aspects). However, because there was minimal variation in midstory basal area and PAR in these undisturbed stands, these covariates were not informative for describing patterns in the understory composition or abundance.

These findings will provide important baseline data for planned future studies, which will examine the interactions among environmental gradients and disturbances including prescribed burning, timber harvesting, and the combination of burning and harvesting.

Literature Cited

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