OVERSTORY COMPOSITION AND STAND STRUCTURE INFLUENCE HERBACEOUS PLANT DIVERSITY IN THE MIXED ASPEN FOREST IN NORTHERN MINNESOTA

Alaina L. Davis and Klaus J. Puettmann[1]

ABSTRACT.—Controversy exists about whether there is a tradeoff between forest management for timber productivity and forest management for biological diversity. We investigated the relationship between overstory composition (monoculture vs. mixtures) and stand structure (single vs. multiple canopy layers) and herbaceous plant diversity and composition in the mixed aspen forest of northern Minnesota. We selected 23 sites that contained aspen in monoculture or in mixture with boreal conifer or northern hardwood species. Each site was placed in a cover type group based on its overstory composition. Stand structure was described by the relative size or positioning of the different overstory tree species, shrub height and cover, average amount of plant material intercepted within the vertical profile, and an index of the plant occupancy within the vertical profile. Positive relationships were found between herbaceous diversity and proportions of aspen basal area; diversity was negatively related to proportions of hardwood basal area and not related to proportions of conifer basal area. Higher diversity in stand structure in the conifer group corresponds to a decreased diversity of the herb layer. In the aspen group, mean shrub height was positively related to the diversity of the herb layer. Presence or absence of balsam fir basal area could be used to group understory plant species. While managing for mixed species forests could be a strategy for improving diversity on a landscape level, it may not necessarily increase diversity for every component within a stand, e.g. herbaceous species diversity.

Biodiversity and its relationship to ecosystem characteristics within forests has become an important topic of research. It is unclear if management of forests for biological diversity is incompatible with management for timber productivity. Patterns of diversity are related to numerous processes such as species interactions. It is probable that these processes are related to the structural complexity within the forest and can occur at several scales from stand to landscape levels.

HYPOTHESES TESTED

- Understory herbaceous plant species diversity is determined by overstory species composition,
- Understory herbaceous plant species diversity is related to stand structure and the interaction of stand structure with overstory species composition, and
- Understory herbaceous plant composition differs based on overstory composition and stand structure.

[1]*Alaina L. Davis, Research Fellow, Department of Forest Resources, University of Minnesota, 115 Green Hall, St. Paul, MN 55108,* and *Klaus J. Puettmann, Associate Professor, Department of Forest Resources, University of Minnesota, 115 Green Hall, St. Paul, MN 55108.*

METHODS

Study Sites

We selected study sites were selected that contained mature aspen in monoculture or in mixture with balsam fir or northern hardwood species. Study Location Areas (SLA's) are located in southern St. Louis County, MN (fig. 1). The average age of the dominant tree species in the SLA's was 37 years, and average stand basal area [BA] was 40 m^2 /ha.

Field Collection and Description of Data

Vegetation plots were systematically placed with an average of 22 vegetation plots in each SLA (fig. 1). Each vegetation plot included a 1-m^2 diversity plot, and on every other plot the 1-m^2 plot was nested inside a 3-m^2 plot. Herbaceous plant diversity and stand structure were characterized for each plot. SLA's were placed into overstory composition groups: Aspen (>90% BA in aspen), Conifer (>15% BA in balsam fir and other conifer species), and Hardwood (>15% BA in hardwood species).

Data Analysis

Diversity in this discussion is characterized by the Shannon Weiner index (H'). The first hypothesis was

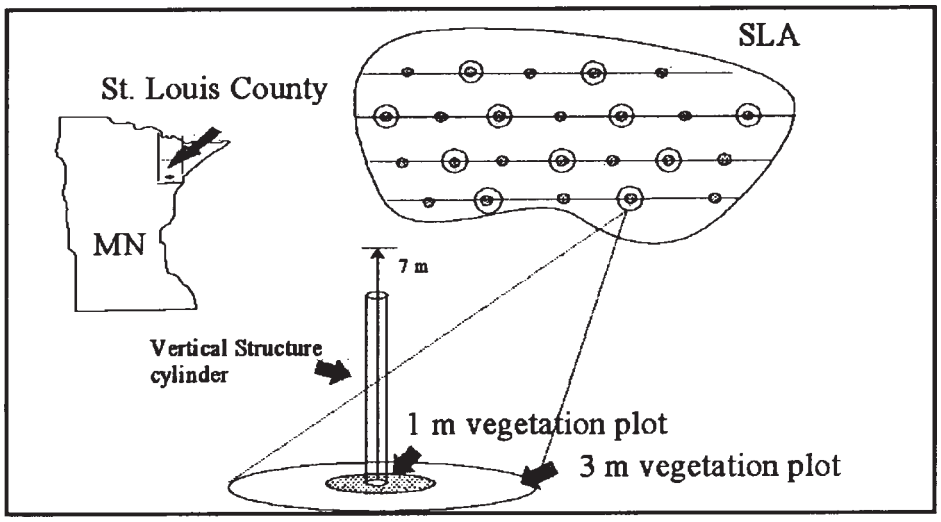

Figure 1.—*Study location area layout and plot design.*

tested by investigating (1) the proportion basal area of cover type species and (2) the variability of overstory species - CV of dbh (coefficient of variation of the mean tree diameters) and their relationships to the diversity parameters. The second hypothesis was examined by using the following stand structure variables in relation to the proportions of overstory basal area: (1) relative size of overstory species - dbh-ratio (based on balsam fir within the SLA), (2) average shrub height (3) average percent cover of shrubs within all diversity plots, (4) average number of ticks (based on number of times vegetation was intercepted on plot center up to 3 m), and (5) Foliage Height Diversity (FHD). FHD is based on all vegetation present and is calculated like the Shannon Weiner Index. Interactions between overstory and stand structure variables were tested using models including variables that showed relevance in the previous tests. The third hypothesis was tested by examining the species composition within overstory groups by using a random "allocation" of plots using Multi-Response Permutation Procedure (MRPP). The terms significant and highly significant refer to $p \leq 0.05$ and $p \leq 0.01$, respectively.

RESULTS

Overstory Composition and Diversity

Regression analysis of all SLA's (n = 23) indicated a highly significant positive relationship between diversity (H') and proportions of aspen basal area (fig. 2a). The proportion of balsam fir did not show significant trends with diversity (fig. 2b). A highly significant and negative relationship was found between the proportion of hardwood basal area and diversity (fig. 2c). Size variation of trees within individual tree species groups showed a slightly negative but non-significant relationship with diversity.

Vertical Structure and Diversity

Over all SLA's, structure measures were not significantly related to any of the diversity measures (all p values $\geq$ 0.30). However, for the Conifer and Hardwood groups (n = 11 and 8, respectively), mean shrub height and the dbh-ratio of balsam fir, respectively were both related to diversity. In the Hardwood group, shrub cover and mean number of ticks were negatively related to diversity.

Interaction of Overstory and Stand Structure

Models were constructed using overstory basal area proportions and the structure variables highlighted in the previous analysis, average number of ticks for the Hardwood group and dbh-ratio for the Conifer group. Neither of these interactions was significant within the cover type groups. To see if the cover type groups were defined too narrowly for this analysis, these models were run with all SLA's containing either hardwood (n=22) or conifer (n=13) basal area. The revised hardwood model was highly significant and the revised conifer model was significant (p=0.004, and p=0.05, respectively).

Community Composition

The difference in species composition between the three cover type groups (Aspen, Conifer, and Hardwood) was not significantly different from that of a random allocation of plots (p = 0.19). However, the species composition

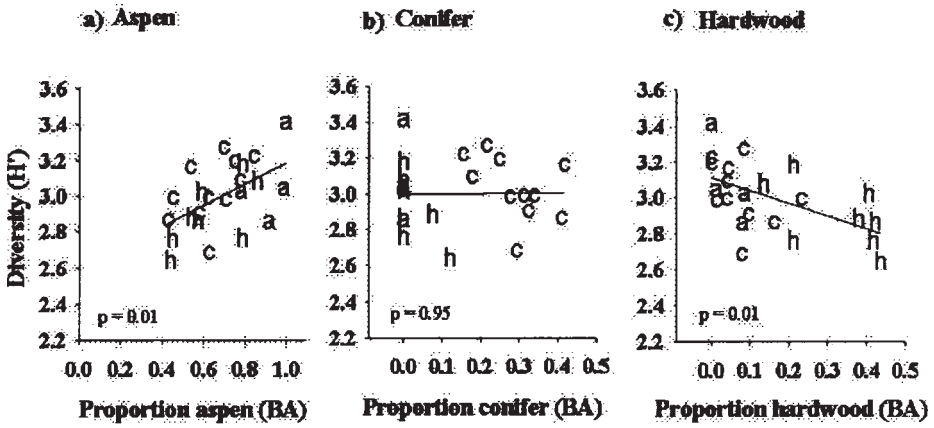

Figure 2.—*Proportion cover type basal area as related to herbaceous plant diversity (H') n=23 a) >90% aspen, c) >15% conifer, and h) >15%hardwood.*

differed between the two more general groups (with and without conifer) (p = 0.005).

DISCUSSION

In our study, mixtures of overstory species were conducive to providing conditions for a variety of stand structures that consist of shrubs, subcanopy trees, or the overstory trees themselves. Different components of stand structure were more sensitive to diversity patterns depending on the cover type composition. In our study, the understory conditions are likely different depending upon the vertical placement of balsam fir within the stand. In stands with multiple canopy layers, the midstory component had a strong influence on herbaceous plant diversity; in stands with a single overstory canopy layer, the shrub layer had more influence. These patterns may be influenced by the interaction of a variety of resource levels and climate conditions, which in turn are controlled by a variety of factors. For example, the quality and amount of light reaching the forest understory is influenced by the shade tolerance of overstory trees.

Infrared radiation and light transmittance is lower for evergreen tree species than for deciduous tree species. Our results indicate that presence of conifers in the overstory is related to understory species composition. One possible explanation is that leaf phenology patterns of herbaceous forest understory plants are adapted to the phenology of the canopy tree species. However, overstory composition may not be the best indicator of understory patterns and in fact may be weakly linked because of their differential responses to community resources and disturbances. The different layers may have different rates of colonization in response to disturbance, leading to a lag in species shift. Our sites were likely just beginning to reach a point in their development where a shift in understory species could be seen due to succession.

CONCLUSION

This study supports the hypothesis that components of biodiversity are not all positively correlated. We found that understory herbaceous plant diversity is related to overstory composition, but information about stand structure is crucial to understanding this relationship. In aspen-dominated forests, managing for mixed species forests is a strategy of improving diversity on a landscape level. However, it may not necessarily increase diversity for every component within a stand. Aspen monocultures may provide growing conditions for a more diverse understory.