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ABSTRACT.—The relationship of herbaceous plant diversity to overstory composition and stand structure in the mixed aspen forest of northern Minnesota was investigated on 23 study sites that contained aspen in monoculture or in mixture with boreal conifers or northern hardwood species. On each site overstory species were placed into species groups: conifers, aspen and hardwoods other than aspen. Each site was then placed in one of three cover-type groups based on proportion of the overstory species groups: Aspen (>0.9 basal area in aspen), Aspen-Conifer (>0.15 basal area in conifer species) and Aspen-Hardwood (>0.15 basal area in hardwood species other than aspen). The relationships between diversity of herbaceous vegetation and the following factors were tested: (1) overstory composition, defined as the proportion of basal area by species group in the overstory and (2) stand structure. Stand structure was described by the vertical position and horizontal arrangement of balsam fir within the stand. In addition, relationships were tested with respect to other stand structural features such as shrub height and cover, average amount of plant material intercepted within the vertical profile and an index of plant occupancy within the vertical profile (modified Foliage Height Diversity Index-FDH).

Understory herbaceous diversity (H′) and proportion of aspen basal area were significantly positively related whereas understory herbaceous diversity was significantly negatively related to proportion of hardwood basal area and not related to proportion of conifer basal area. Mixtures of overstory tree species provided a range of stand structures that can be represented by shrubs, subcanopy trees or the overstory trees. In the three cover-type groups different structural components were related to herbaceous diversity indicating that (1) overstory composition and stand structure interactively influence understory diversity patterns and (2) it is difficult to characterize stand structure for the range of stand conditions with a single measure. Increased diversity of structure (modified FHD) in the Aspen-Conifer group is negatively related with diversity (H′) of the herb layer. Composition of herbaceous species varied depending on presence or absence of conifers in the overstory. These patterns may be influenced by the interaction of a variety of resource levels and climate conditions, which, in turn, are controlled by factors such as tree architecture or shade tolerance of overstory trees.

INTRODUCTION

Investigation of diversity and its relationship to ecosystem characteristics within forests has become an important topic of research. It is not clear what future values of forests will arise so it is important to devise management practices that maintain diversity of both plants and animals (Day and Harvey, 1981; Burton *et al.*, 1992; Edwards and Abivardi, 1998). Many investigators regard the mixed aspen forest as one of the most diverse forests in North America (Ohman and Ream, 1971; Ahlgren and Ahlgren, 1983; Thorpe, 1992). The mixed aspen forest, which is dominated by quaking aspen (*Populus tremuloides* Michx.), is an important cover type in Minnesota, covering approximately 2 million ha (Miles *et al.*, 1995). Consequently, management of this cover type has implications for a large portion of the landscape.

Few studies of plant species diversity in the mixed aspen forest in the Midwest exist. Maycock and Curtis (1960) conducted an extensive investigation into the relationship between overstory and understory plant composition in the Great Lakes region. More recent investigations have focused on patterns in understory vegetation within a range of forest communities from hardwood to old-growth, boreal coniferous forest (Rogers, 1981; Pearsall, 1995; Okland and Eilertsen, 1996). Recently, Schluter and Ricklefs (1993) proposed that diversity and patterns of diversity are the result of numerous factors including biogeographical relationships, ecological processes and historical events. Most commonly, species interactions and disturbances are identified as ecological processes that influence biological diversity. These processes affect structural complexity within the forest and can occur at several scales from plant to landscape levels. For example, Crozier and Boerner (1984) investigated how stemflow and throughfall precipitation influence soil nutrient levels around trees. They concluded that tree mixtures are important in maintaining spatial heterogeneity in forest floor resources and therefore could influence understory species diversity. An investigation of mixed species plantings suggested that overstory conditions were primarily responsible for the ground flora composition and that mixed species communities were often more diverse than nearby monocultures (Simmons and Buckley, 1992). On the other hand, a study of mixed aspen forest in the Great Lakes region revealed that a pronounced correlation between tree, shrub and herb diversity was dependent on inherent structural and dynamic characteristics of forests (Auclair and Goff, 1971). The diversity of shrubs and herbs was highly correlated, whereas tree diversity was not correlated with herb diversity.

In our study diversity refers to herbaceous vascular plants except graminoids. Typically in the mixed aspen community there are relatively few species of graminoids present compared to the number of herbaceous plant species (Almendinger and Hanson, 1998). Auclair and Goff (1971) reasoned that correlation between shrub and herb diversity was due to their similarity in form and resource requirements. Thus, patterns of herbaceous diversity reflect diversity patterns within the forest community. The primary objective of this study was to determine if overstory composition in the mixed aspen forest is related to the diversity of herbaceous vegetation. Four hypotheses were tested: (1) stand structural features are related to overstory composition, *i.e.*, proportion of basal area by overstory species group, (2) herbaceous plant species diversity is related to overstory species composition, (3) herbaceous plant species diversity is related to stand structural features and (4) herbaceous plant community composition differs based on overstory composition and stand structure.

METHODS

Site description.—All study sites contained aspen in monoculture or in mixture with balsam fir (*Abies balsamea* (L.) Mill.) or northern hardwood species such as paper birch (*Betula papyrifera* Marsh.), sugar and red maple (*Acer saccharum* Marsh., *Acer rubrum* L.), red oak (*Quercus rubra* L.) and basswood (*Tilia americana* L.). In general, the hardwood species occupied the upper stratum of the canopy and were scattered throughout the stand. On the other hand, balsam fir occupied a range of vertical positions (in the upper canopy and as a subcanopy tree) and occurred both in scattered spatial patterns and clumped patterns within the stand. Study sites were located in southern St. Louis County, Minnesota (Fig. 1). The St. Louis County Land Department provided a list of potential stands from which study sites were chosen. Study sites were selected based on: (1) stand composition, (2) age, (3) density, (4) lack of recent disturbance, including insect or disease problems and (5) homogeneity. Through site selection we ensured a wide range of mixture proportions while minimizing variation in age, soils and site quality. Later analysis indicated that this was accomplished as neither age, soil or site quality variables were significantly related to her-

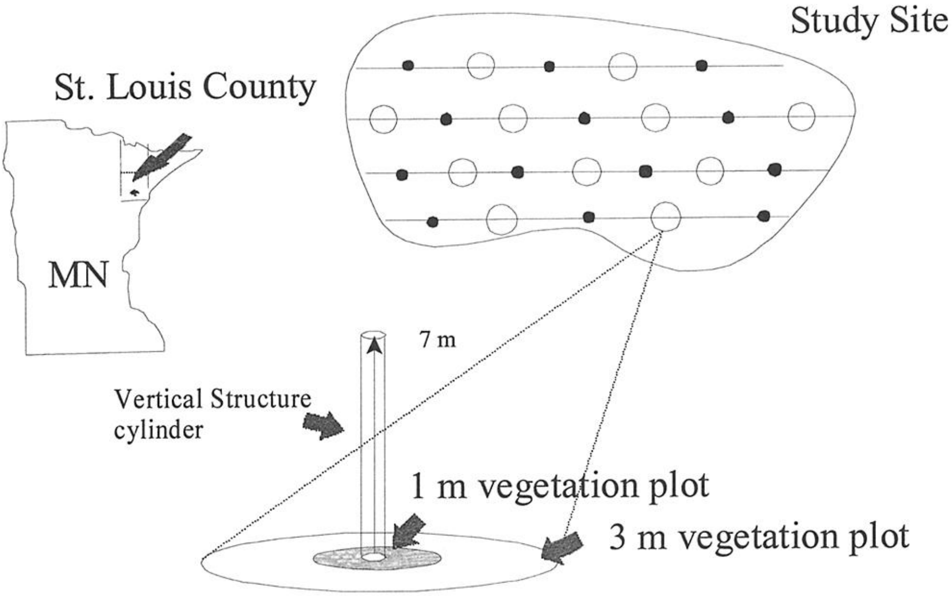

FIG. 1.—Study site location and plot layout

baceous diversity (α values > 0.05). We identified and mapped 23 study sites during the summer of 1996. Study site boundaries delineated areas that were visually observed to be uniform in overstory and understory composition and structure. Stand age of study sites ranged from 26–62 y. Study site size varied from 0.15 to 0.45 ha with an average size of 0.22 ha. The perimeter of each study site was mapped with the hand held survey station Criterion™ Series 400.

Climate, geology and soils.—Northeast Minnesota has a temperate climate with mean monthly temperatures ranging from −18 to 17 C and a mean annual temperature of 1.6 C. Average annual snowfall is about 380 cm. Average seasonal precipitation ranges from 144 mm in winter to 122 mm in the summer. Most soils in Northern Minnesota are derived from till plains, outwash and moraines laid down by glacial advances (Anderson *et al.*, 1996). Soil texture data indicated similar soil texture classes of sandy-loam and loamy sand on all study sites.

FIELD COLLECTION OF DATA

Plot layout.—Vegetation plots were systematically placed along parallel transects forming a grid of plots (Fig. 1). Spacing varied with size of the study site and was never less than 5 m × 5 m and most often 5 m × 10 m, resulting in an average of 22 vegetation plots (ranging from 17–25). In each of these vegetation plots herbaceous plant and stand structure data were collected. The vegetation plots were circular with 1-m radius on odd numbered plots and 3 m radius on even numbered plots. A single or, where space allowed, two circular overstory plots were established on each study site. We adjusted the plot size (typically 6 to 8 m radius) to include at least 18 overstory trees and located the plot center in areas representative of study site composition.

Understory vegetation.—All herbaceous plant species within the 1-m and 3-m radius vegetation plots were recorded. Nomenclature was based on Gleason and Cronquist (1991). Cover of herbs by species was estimated on each vegetation plot in cover classes of 0%, 1–5%, 6–25%, 26–50%, 51–75% and 76–100%. Cover of shrubs was estimated on all 1 m radius vegetation plots and the inner 1 m radius circle of the 3 m radius vegetation plots using the same cover classes.

Stand structure.—We used four measures to quantify stand structure on each vegetation plot: (1) point intercept with a height pole (0–3 m), (2) intercept within a height cylinder (0–7 m), (3) height of tallest shrub layer and (4) average diameter of trees by species. On the center of each vegetation plot a telescoping height pole was used to characterize the vertical vegetation profile from 0 m to 7 m. Vertical distribution of vegetation was characterized using an imaginary cylinder (25 cm radius guided by a ruler) around the pole extending from the ground to 7 m. The cylinder was divided into sections 0.5 m long. These cylinder sections were grouped into height strata. To define strata heights we visually estimated vegetation layers commonly found in the range of conditions represented in this study. The height strata were 0 to 0.5 m, >0.5 to 1 m, >1 to 2 m, >2 to 3 m, >3 to 5 m and >5 to 7 m. For each cylinder section we determined the presence (*i.e.,* occupied) or absence (*i.e.,* non occupied) of live foliage and noted the total number of occupied cylinder sections in each stratum.

Overstory.—Stand age and overstory composition were measured on the overstory plots. Increment cores were taken at breast height from two aspen in the upper canopy and breast height age was determined. For each site, stand age was calculated by averaging breast height ages and adding 3 y. Upper canopy trees are defined as trees where the crown receives full light from above and partially from the side. Additional data collected on each tree on overstory plots were: DBH (cm), measured with a diameter tape, and total height (m), measured with the hand held survey station Criterion™ Series 400.

Soil texture.—Soil texture class was determined for the top 15 cm of the soil profile. In each study site five 15 cm × 15 cm × 15 cm samples were collected. The study site was divided into four quadrants of similar size and a single sample was taken at a point approximately centered in each quadrant. A fifth sample of the same size was taken on one overstory plot. Care was taken at each sample point to ensure that an equal amount of soil was collected from the top 15 cm of the soil profile. The four samples taken in each quadrant were pooled to create one composite sample for each study site. The fifth sample was analyzed separately. Particle size distribution was determined using an adapted hydrometer method (Grigal, 1973).

DESCRIPTION OF VARIABLES

Overstory composition.—Overstory tree species were combined as aspen, conifer and hardwood other than aspen. Each study site was then placed into a cover-type group based on the proportion of these overstory species groups: Aspen (>0.9 basal area in aspen), Aspen-Conifer (>0.15 basal area in conifer species, mostly balsam fir) and Aspen-Hardwood (>0.15 basal area in hardwood species other than aspen, Table 1). Based on these criteria, two study sites qualified as both Aspen-Conifer and Aspen-Hardwood cover-type groups, but they had higher proportions of balsam fir and were placed in the Aspen-Conifer cover-type group. Aspen site index was calculated for each site as a measure of potential site productivity by using the following functions (Lundgren and Dolid, 1970):

$$S = \frac{H_{obs}}{1.48(1 - e^{-0.0214Aobs})^{-0.9377}}$$

TABLE 1.—Study site descriptions: Mean (range) proportion of basal area for cover-type groups, total basal area, aspen age, aspen 50-y site index, height of aspen and herbaceous plant diversity (H′)

	Basal area proportion			Basal area				
Cover-type group	Aspen	Hardwood*	Conifer	(m^2/ha)	Age (y)	Site index (m)	Height (m)	H′
Aspen (n = 4)	0.96 (0.91–1.0)	0.04 (0–0.09)	0	35 (23–48)	48 (38–58)	21 (18–23)	23.5 (21.8–25.5)	3.09 (2.86–3.42)
Aspen-Conifer (n = 11)	0.64 (0.43–0.84)	0.07 (0–0.23)	0.29 (0.16–0.42)	33 (24–71)	43 (26–61)	23 (21–27)	22 (20–24)	3.04 (2.69–3.28)
Aspen-Hardwood (n = 8)	0.64 (0.44–0.86)	0.33 (0.14–0.44)	0.03 (0–0.12)	34 (30–49)	41 (26–62)	22 (15–27)	22 (19–24)	2.89 (2.64–3.18)

* Hardwood species other than aspen

where S is the site index, H_{obs} is the observed mean height of upper canopy aspen and A_{obs} is the observed mean age at breast height of upper canopy aspen.

Measures of diversity.—Herbaceous plant diversity was evaluated using: (1) richness (S), the number of species, (2) rarefaction estimate of richness (E[S(50)]) which was originally promoted by Sanders (1968) and later revised (Simberloff, 1979) and (3) Shannon Weiner index (H'), which combines evenness and richness (Hutcheson, 1970; Magurran, 1988). These measures were determined by using the data collected on the 1 m and the 3 m radius vegetation plots. Frequency of species occurrence in each study site was calculated as the percent of vegetation plots on which each species was recorded. Species frequency was weighted to adjust for the different sampling areas within a site. Frequencies of species occurring in the outer portions of 3 m radius vegetation plots (*i.e.,* outside the inner 1 m radius circle) were multiplied by 0.125, the ratio of the area in the outer 2-m ring (25.13 m^2) divided by area in the inner 1 m radius circle (3.14 m^2). Rarefaction estimates were used to account for differences in sampling intensity between sites. It has been generally accepted that the number of species increases with the area sampled (McArthur and Wilson, 1967; Connor and McCoy, 1979; Palmer and White, 1994). Thus, any estimate of diversity needs to take area sampled into account. Our rarefaction estimates are standardized to 50 individuals. Rarefraction estimates of richness are based on a distribution free method using the following equation:

$$E(S) = \sum \left\{1 - \left[\binom{N - N_i}{n} \Big/ \binom{N}{n}\right]\right\}$$

where E(S) is the expected number of species, n is the standardized sample size, N is the total number of individuals recorded and N_i is the number of individuals in the ith species.

H' is based on the following equation:

$$H' = -\sum p_i \log p_i$$

where p_i is the proportion of individuals found of the ith species. All three measures of diversity were highly correlated for the data set ($n = 23$, Pearsons correlation coefficients ≥ 0.87). Thus, for ease of interpretation in further discussion only the results for H' will be presented.

Stand structure.—Measures of stand structure included average shrub cover, average shrub height, the average number of point interceptions (0 m to 3 m) and a modified Foliage Height Diversity Index (FHD) (0 m to 7 m). The calculation of the modified FHD index followed MacArthur and MacArthur (1961), with two modifications. First, earlier studies measured foliage density directly, *e.g.,* number of leaves or leaf area (MacArthur and MacArthur, 1961; Aber, 1979, respectively). We recorded presence or absence (occurrence) of live foliage in cylinder sections in each stratum and calculated the proportion of cylinder sections with foliage present. Second, rather than using strata of equal height (*see* MacArthur and Mc Arthur, 1961; Aber, 1979), we divided the vertical profile into strata that reflect estimated vegetation layers.

For each sample point the vertical profile of foliage was generated by calculating the proportion of cylinder sections with foliage present (*i.e.,* occupied sections) in each height stratum. For example, the >1–2 m height stratum includes two cylinder sections. The proportion of cylinder sections with foliage present in this stratum can be 0, 0.5 or 1, if zero, one or two cylinder sections contained live foliage, respectively. Next, we followed the standard calculation of the FHD (Hunter, 1990) using the proportion of cylinder sections with foliage present within a stratum analogous to the number of leaves (MacArthur and MacArthur, 1961) or leaf area (Aber, 1979). For each site we calculated the relative proportions of occupied cylinder sections by summing the proportion of occupied cylinder sections in each stratum and dividing this sum by the total sum of all proportions (strata 1 through strata 6) of occupied cylinder sections. The modified FHD index was calculated for each site using the formula of the Shannon Weiner index (*see* MacArthur and MacArthur, 1961), *i.e.,* for calculation purposes, the relative proportion of occupied cylinder sections for each strata is equivalent to species frequency and the number of strata which contained at least one occupied cylinder is equivalent to the number of species. Since the strata heights were chosen to reflect vegetation layers (Hunter, 1990), lower vegetation layers, which have a greater influence on the understory vegetation than vegetation in the upper vertical profile (Roberts, 1992), are weighted more heavily in the calculation of the modified FHD index.

Some balsam fir existed as an upper canopy tree, individually spaced and with crowns limited to the upper portions of the stems. Alternatively, balsam fir was found as a subcanopy tree in conspecific clumps and with a crown from the top to the bottom of the tree. Since tree height is highly correlated with tree diameter (Nilsson, 1994) and diameter is influenced by stem density, we used a diameter based variable, balsam fir DBH ratio (the ratio of the average diameter of balsam fir to the average diameter of all other trees), to represent these structural patterns. DBH ratio was not used for aspen and other hardwood species, as they did not show this range of horizontal and vertical structures.

DATA ANALYSIS

Herbaceous species diversity indices were calculated using the computer program BIODIV (Baev and Penev, 1995). Linear regression analysis was used to test the first three hypotheses using JMP 3.1 (SAS Institute, 1996). Visual observation of residuals was used to assess the appropriateness of linear models and need for weighting. PC-ORD ordination software (McCune and Mefford, 1997) was used to conduct multivariate analysis for the fourth hypothesis. Throughout the analysis the terms significant and highly significant refer to $\alpha \leq 0.05$ and $\alpha \leq 0.01$, respectively.

Linear regression was used to test the first hypothesis, that stand structural features in mixed aspen forests and aspen monocultures are related to overstory composition, by using the following structure variables as dependent variables: (1) balsam fir DBH ratio, (2) average shrub height, (3) average % cover of shrubs, calculated using the midpoint of each cover class, (4) average number of point interceptions of plant material and (5) modified FHD. Proportion of basal area by overstory species group was used as the independent variable.

The second hypothesis, that herbaceous plant species diversity is related to overstory species composition, *i.e.,* proportion of basal area by species group, was tested by using linear regression of herbaceous plant diversity as the dependent variable and the proportion of overstory basal area by species group as the independent variable.

The third hypothesis, that herbaceous plant species diversity is related to stand structural features, was tested by using linear regression of herbaceous plant diversity as the dependent variable on the following independent variables: (1) balsam fir DBH ratio, (2) average shrub height, (3) average % cover of shrubs, (4) average number of point interceptions (0–3 m height profile) of plant material on vegetation plots and (5) modified FHD (0–7 m height profile). Interactions between overstory and structure variables were tested using linear regression models including overstory and structure variables that showed significance in the previous tests.

The fourth hypothesis, that understory herbaceous plant composition differs based on overstory composition, was tested using a multivariate analysis technique. Specifically, differences in understory plant composition between cover-type groups were tested by relating

TABLE 2.—Slope parameter (P values) for linear regressions. Proportion of basal area for each overstory species group was regressed on mean values of stand structure variables across all study sites (n = 23)

	Stand structure variables				
Overstory	Shrub height (m)	Shrub cover (%)	Point interceptions	FHD	Balsam fir DBH ratio
Aspen	+1.51 (0.01)	+31.43 (0.09)	−0.18 (0.93)	−0.22 (0.0003)	NA
Conifer	−1.20 (0.14)	−11.97 (0.70)	−0.82 (0.83)	+0.27 (0.001)	−0.26 (0.57)
Hardwood*	−0.27 (0.71)	−19.03 (0.37)	−2.64 (0.20)	+0.03 (0.70)	NA

* Hardwood species other than aspen

them to a random allocation of plots using Multi-Response Permutation Procedure (MRPP) developed by Mielke (1984). The understory species frequency data matrix was reduced by excluding species that occurred on less than 90% of all study sites resulting in a species by site matrix with 66 species.

RESULTS

Overstory and stand structure.—Across all study sites (n = 23) the proportion of aspen basal area was significantly positively related to mean shrub height but not significantly related to mean shrub cover (Table 2). Mean shrub height and mean % shrub cover values were not related to the proportion of balsam fir or hardwood (other than aspen) basal area. The mean number of interceptions of plant material in a study site was not related to the proportion of basal area for any species group but the modified FHD index was highly significant and positively related to proportions of balsam fir basal area ($r^2_{adj} = 0.53$ $P = 0.0001$). However, the structural arrangement of balsam fir, as represented by balsam fir DBH ratio, was not significantly influenced by the proportion of balsam fir basal area ($r^2_{adj.} = 0.14$ $P = 0.12$).

Since the relationship between overstory composition and structural variables was not consistent among cover-type groups we tested the previous relationships within each of these groups, with the exception of the Aspen group due to the limited sample size (n = 4). Within the Aspen-Conifer and Aspen-Hardwood groups (n = 11 and 8, respectively) mean site values of stand structure were related to overstory composition (Table 3). A highly significant negative relationship was found between the proportion of conifer basal area and mean shrub height ($r^2_{adj} = 0.48$ $P = 0.01$), and a highly significant positive relationship existed between proportion of conifer basal area and the modified FHD index ($r^2_{adj} = 0.50$ $P = 0.01$). There was no significant relationship between hardwood basal area and structure variables.

Overstory composition and diversity.—Regression analysis of all study sites (n = 23) indicated a highly significant positive relationship between proportion of aspen basal area and diversity (H′) of herbaceous understory plants ($r^2_{adj.} = 0.25$ $P = 0.01$) (Fig. 2A). One study site was a potential outlier. Regressions were run without it and, due to little change in overall interpretation of results (P values did not fall below significant levels), the study site remained in the analysis. Visual assessment of residual plots revealed that variance of diversity (H′) decreased as the proportion of balsam fir increased. In order to account for the nonconstant variance weighted least squares regression (Weisberg, 1985) was used with weights inversely proportional to the proportion of balsam fir. The proportion of balsam fir did not show significant trends with diversity (Fig. 2B). Heteroscedasticity was not evident

TABLE 3.—Slope parameter (P values) for linear regressions within the Aspen-Conifer and Aspen-Hardwood cover-type groups >15% basal area in conifer or hardwood species other than aspen, respectively. No analysis was performed on the Aspen group due to small sample size (n = 4)

Cover-type group	Independent variable	Shrub height (m)	Shrub cover (%)	Point interceptions	FHD	Balsam fir DBH ratio
Aspen-Conifer (n = 11)	Proportion of conifer basal area	−2.97 (0.01)	−71.13 (0.18)	−4.94 (0.47)	+0.35 (0.01)	−0.59 (0.40)
Aspen-Hardwood (n = 8)	Proportion of hardwood* basal area	−0.25 (0.83)	−4.93 (0.86)	+3.07 (0.22)	+0.09 (0.15)	NA

* Hardwood species other than aspen

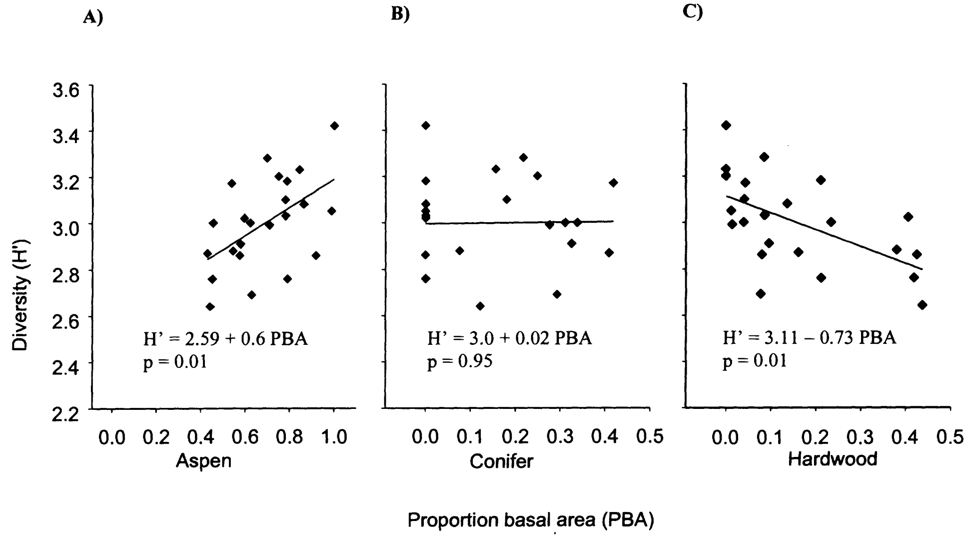

FIG. 2.—Regression plots of herbaceous plant diversity (H′) versus proportion basal area of overstory species groups across all sites (n = 23) (A) Aspen, (B) Conifer, and (C) Hardwood (other than aspen)

in residuals for the regressions of diversity on hardwood study sites. A highly significant and negative relationship was seen between the proportion of hardwood basal area and diversity ($r^2_{adj.} = 0.29$ $P = 0.01$) (Fig. 2C).

Stand structure and diversity.—Over all study sites (n = 23), no structure measure was significantly related to any of the diversity measures (all P values ≥ 0.30). However, when analyzed within cover-type groups, mean site values of structure measures were related to diversity within the Aspen-Conifer and Aspen-Hardwood cover-type groups (Table 4). In the Aspen-Conifer cover-type group mean shrub height and the balsam fir DBH ratio were significant and positively related to H′ (*e.g.*, $r^2_{adj.} = 0.43$ $P = 0.02$ for balsam fir DBH ratio). Other structure variables such as mean shrub cover and the modified FHD index were not significantly related to H′ within the Aspen-Conifer cover-type group. In the Aspen-Hardwood cover-type group shrub cover and mean number of interceptions of plant material revealed negative relationships to H′ (*e.g.*, the mean number of interceptions of plant material explaining 79% of the variation in H′ P = 0.002).

Interaction of overstory and stand structure.—Models were constructed using interaction

TABLE 4.—Slope parameter (P values) for linear regressions within the Aspen-Conifer and Aspen-Hardwood cover-type groups with >15% basal area in conifer or hardwoods, respectively. Mean structure variables were regressed on herbaceous plant diversity (H′). No analysis was performed on the Aspen group due to small sample size (n = 4)

Cover-type group	Shrub height (m)	Shrub cover (%)	Point interceptions	FHD	Balsam fir DBH ratio
Aspen-Conifer (n = 11)	+0.34 (0.03)	+0.006 (0.14)	+0.014 (0.70)	−2.39 (0.09)	+0.70 (0.02)
Aspen-Hardwood (n = 8)	−0.24 (0.27)	−0.01 (0.12)	−0.22 (0.002)	−4.06 (0.27)	NA

TABLE 5.—Slope parameter (P values) for regression models using revised groupings of study sites. Sites were assigned to revised groups based on the presence (rather than a minimum proportion of 0.15) of conifer and hardwood* basal area. Twelve sites had both conifers and hardwoods present and were placed in both groups. The independent variable was the proportion of basal area in conifers or hardwoods* for sites with conifer and/or hardwoods

	Model terms		
Revised group	Proportion conifer or hardwood*	Average point interceptions	Proportion conifer or hardwood* × average point interceptions
Conifer (n = 13)	+1.38 (0.08)	+0.07 (0.05)	−0.63 (0.01)
Hardwood (n = 22)	+5.27 (0.08)	+2.96 (0.04)	−6.12 (0.09)

* Hardwood species other than aspen

between overstory basal area proportions and the structure variables highlighted in the previous analysis, *i.e.,* average number of interceptions of plant material for the Aspen-Hardwood cover-type group and balsam fir DBH ratio for the Aspen-Conifer cover-type group. Neither of these interactions was significant within the cover-type groups. In order to see if these cover-type groups were defined too narrowly for this analysis these models were run with all study sites containing any proportion (rather than a minimum of 0.15) of basal area in hardwood species other than aspen (n = 22) and/or conifer species (n = 13). Twelve sites had both conifers and hardwoods present and were placed in both groups. Thus, the revised model does contain overlap in the groups. Using these broader categories, the revised Aspen-Hardwood model was highly significant and the revised Aspen-Conifer model was significant ($r^2_{adj.} = 0.43$ $P = 0.004$ and $r^2_{adj.} = 0.41$ $P = 0.05$, respectively, Table 5).

Understory composition.—Using MRPP herbaceous species composition similarity was tested for cover-type groups (Aspen, Aspen-Conifer, and Aspen-Hardwood). The differences among the three cover-type groups were not significantly different from that of a random allocation of plots ($t = -0.83$ $P = 0.19$). However, species composition between sites with conifers (n = 13) and sites without conifers (n = 10) were significantly different ($t = -3.54$ $P = 0.005$). The most common herbaceous species in the group with conifer were: *Anemone quinqefolia* (L.), *Arisaema triphyllum* ((L.) Schott), *Athyrium filix-femina* (L.) Roth), *Cornus canadensis* (L.) and *Coptis groenlandica* ((Oeder) Fassett), whereas the most common herbaceous species in the group without conifer were; *Dryopteris cristata* (L.), *Galium triflorum* (Michx.), *Lathyrus ochroleucus* (Hook.), *Linnaea borealis* (L.), *Maianthemum canadense* (Desf.), *Polygala paucifolia* (Willd.), *Polygonatum pubescens* ((Willd.) Pursh.), *Pyrola minor* (L.), *Thelypteris phegopteris* (L.) and *Uvularia grandiflora* (J. E. Smith.).

DISCUSSION

The results of this study support the hypothesis that understory herbaceous plant diversity is related to overstory composition (proportion of aspen basal area) but the complex interaction of overstory composition and the resultant structure of the midstory components are related to the compositional patterns in the understory herbaceous community. We found a higher herbaceous diversity in aspen monocultures. In other studies variation of overstory species composition contributed to greater diversity of understory vegetation in Norway spruce and oak stands as well as pine and beech stands (Simmons and Buckley, 1992). We hypothesize that a variety of resource and environmental conditions are interacting within the gradient of overstory and midstory conditions to determine this relationship. These conditions include differential rates of decomposition of litter (due to timing of litter fall and/or litter composition) and variation in light conditions and soil temperatures on the forest floor (Barkman, 1992). The contradictory results imply that the relative importance of these factors is specific to the ecosystem and overstory species. For example, Auclair and Goff (1971) found that herbaceous plant diversity differed between evergreen and deciduous cover types. They hypothesized that this might be due to persistent canopy cover not allowing differentiation of understory species phenologically. A study investigating variation in light transmission in oak and northern hardwood forest found that the reduction of incident radiation in the lower layers was related to the shade tolerance of overstory trees (Canham *et al.,* 1994). Also, Purohit *et al.* (1990) found that the infrared radiation and light transmittance was lower for evergreen species than for deciduous species.

In our study mixtures of overstory tree species provide a range of stand structures that can be represented by shrubs, subcanopy trees or the overstory trees themselves. The interactions between overstory composition and stand structure and their effects on understory herbaceous diversity differ and are specific to the overstory composition. The proportion of aspen in the overstory was related to shrub height. While we did not have a sufficient sample to test the relationship between shrub height and herbaceous diversity in the aspen cover type, a study located just south of our study area found a significant negative correlation between hazel (*Corylus cornuta,* Marshall) height and understory species richness (Sloan, 1981). In contrast to aspen, which is limited to the overstory layer, balsam fir can exist in the subcanopy as a densely packed cohort or can form a more scattered pattern within the stand, extending into the upper canopy with aspen. Our results indicate that within the Aspen-Conifer cover-type group, the vertical position and horizontal arrangement of balsam fir within the stand rather than the proportion of balsam fir are related to the diversity of herbaceous vegetation. This interaction between stand structure and overstory indicates that resources are being partitioned or intercepted by the various structural components. For example, as balsam firs grow (with crowns positioned higher on the stem) potential exists for more light to reach the forest floor. Shade tolerant midstory trees (*e.g.,* balsam fir) have been shown to influence understory resources and/or growing conditions (Roberts, 1992; Smidt and Puettmann, 1998). The negative relationship between the modified FHD index and herbaceous diversity indicates that in stands with higher vertical diversity, fewer herbaceous species occupy the understory. Our results agree with patterns in Michigan aspen-hardwood forests where overstory composition did not control the composition of the understory vegetation as much as did the structure and composition of the midstory (Roberts, 1992).

This study shows that understory species composition can partially be explained by the overstory composition but results of other studies on this topic vary. Sagers and Lyon (1997) were able to group riparian forest sites based on understory vegetation, but the groupings were not based on overstory composition; instead they were related to environmental variables such as pH and elevation. Whitney and Foster (1988) investigated the influence of overstory composition and age on understory composition and found various microclimatic conditions created by a gradient of overstory conditions were important in supporting a variety of plants. Only two understory species differed in occurrence across the gradient of overstory cover types (Whitney and Foster, 1988). There are several hypotheses that may explain our result that the presence of coniferous trees in the overstory is related to understory species composition. Uemura (1994) found that leaf phenology patterns of herbaceous forest understory plants are adapted to the phenology of the canopy tree species. It is also possible that the conifer overstory and herbaceous understory species have similar edaphic requirements. Edaphic conditions such as pH, moisture and nitrogen availability were more important than overstory species composition in identifying understory compositional patterns in the forests of Vancouver Island (Qian *et al.,* 1997). Other studies link understory plant species composition to nitrogen availability and soil moisture which, in turn, were related to the ground litter composition (Zak *et al.,* 1986; Pastor and Post, 1986; Zak and Pregitzer, 1990). Adaptations of understory herbs to litter and soil moisture conditions were seen in differing growth forms and rooting habits (Anderson *et al.,* 1969; Whitney and Foster, 1988). Mixed species forests differ in structural complexity and, therefore, the effects of the overstory composition on herbaceous diversity may vary. Managing for mixed species forests could be a strategy of improving diversity on a landscape level, it may not increase diversity of every component within a stand.

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