Positive Relationship between Aboveground Carbon Stocks and Structural Diversity in Spruce-Dominated Forest Stands in New Brunswick, Canada

Weifeng Wang, Xiangdong Lei, Zhihai Ma, Daniel D. Kneeshaw, and Changhui Peng*

Abstract: Maintaining both the structure and functionality of forest ecosystems is a primary goal of forest management. In this study, relationships between structural diversity and aboveground stand carbon (C) stocks were examined in spruce-dominated forests in New Brunswick, Canada. Tree species, size, and height diversity indices as well as a combination of these diversity indices were used to correlate aboveground C stocks. Multiple linear regressions were subsequently used to quantify the relationships between these indices and aboveground C stocks, and partial correlation analysis was also adopted to remove the effects of other explanatory variables. Results show that stand structural diversity has a significant positive effect on aboveground C stocks even though the relationship is weak overall. Positive relationships observed between the diversity indices and aboveground C stocks support the hypothesis that increased structural diversity enhances aboveground C storage capacity. This occurs because complex forest structures allow for greater light infiltration and promote a more efficient resource use by trees, leading to an increase in biomass and C production. Mixed tolerant species composition and uneven-aged stand management in conjunction with selection or partial cutting to maintain high structural diversity is therefore recommended to preserve biodiversity and C stocks in spruce-dominated forests. FOR. SCI. 57(6):506–515.

Keywords: forest management, niche complementarity hypothesis, Shannon-Wiener index, stand structure

THE ROLE OF BIODIVERSITY in ecosystem functioning has become a central issue in ecology (Loreau et al. 2001, Diaz et al. 2009). In particular, in the context of biodiversity conservation and the mitigation of global warming, the relationship between biodiversity and carbon (C) sequestration has become more and more a focal point. Stand structural diversity can be an indicator of overall biodiversity (Staudhammer and LeMay 2001) and is commonly used in the characterization of spatial distribution, species diversity, and variation in tree dimensions such as tree size and height or a combination of these factors (Staudhammer and LeMay 2001, Pommerening 2002, McElhinny et al. 2005). It can also be logically linked to forest management practices and objectives (Lei et al. 2009). The idea that biodiversity can be maintained by managing the structural diversity of stands is a common argument among researchers (Buongiorno et al. 1994, 1995, Lindenmayer and Franklin 1997, Sullivan et al. 2001, Franklin et al. 2002, Kant 2002, Varga et al. 2005). In developing appropriate forest management strategies to preserve biodiversity and mitigate the effects of climate change, a more comprehensive understanding is needed concerning the effect of stand structural diversity on C sequestration capacity within forest ecosystems (Bosworth et al. 2008).

Numerous studies have investigated the relationship between species diversity and productivity in forest ecosystems (e.g., Caspersen and Pacala 2001, Bunker et al. 2005, Creed et al. 2009). The literature suggests that the relationship between productivity and species diversity is often positive (Whittaker and Heegaard 2003, Balvanera et al. 2006, Gillman and Wright 2006). The effect of plant diversity on carbon storage has also been explored. For example, Chen (2006) reported a positive relationship between tree species diversity and soil organic carbon content in the top 30-cm soil layer in an old-growth forest in Northeast China. Fornara and Tilman (2008) suggested that there was a positive impact of plant diversity on soil carbon accumulation in agriculturally degraded soils at Cedar Creek, Minnesota, USA. Saha et al. (2009) observed that soil C stocks increased with an increase in plant species diversity in tropical homegarden systems. One hypothesis contributing to explaining this relationship is the niche complementarity hypothesis, which proposes that species-rich communities are able to more efficiently access and use limiting resources (Tilman 1999). However, Szwagrzyk and Gazda (2007) found that a negative relationship exists between aboveground biomass and tree species diversity in natural forests of Central Europe. In addition, Jonsson and Wardle (2009) also reported in their structural equation modeling

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study that plant diversity has a weak effect on belowground C storage for carbon storage drivers in boreal forest ecosystems.

Although studies on species diversity effects on productivity and C stocks are numerous, information concerning forest structural diversity, especially spatial structure, is as yet poorly understood in a comprehensive ecosystem perspective. For example, Lei et al. (2009) reported a positive relationship between structural diversity and forest growth in spruce-dominated forests. In contrast, Edgar and Burk (2001) indicated that productivity was negatively correlated to stand composition and canopy vertical structure in aspen (*Populus tremuloides* Michx.) forest stands. Moreover, Liang et al. (2005, 2007) found negative and unimodal relationships between productivity and tree size diversity for Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco)-western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and mixed coniferous stands, respectively. In addition, Long and Shaw (2010) recently observed that stand growth is not strongly influenced by either compositional or structural diversity in ponderosa pine (*Pinus ponderosa* C. Lawson) stands in the western region of the United States. However, little information exists concerning relationships between structural diversity and carbon storage at the stand scale. Do high levels of stand structural diversity, therefore, increase C storage, decrease it, or leave it unaffected?

Lei et al. (2009) have previously investigated the relationship between structural diversity and forest growth. Little, however, is known of the relationship between structural diversity and aboveground carbon stocks in spruce-dominated forest stands in New Brunswick, Canada. Spruce-dominated forests are an important boreal forest ecosystem constituent that possess simple tree composition but complex forest age and tree size structure. Forest managers tend to be more interested in developing silvicultural solutions to enhance forest growth and C stocks for multiple-use management. According to the niche complementarity hypothesis, a greater overall C pool is assumed in black spruce-dominated forests featuring complex forest structure. Therefore, the objectives of this study were to test the hypothesis stating that increased structural diversity enhances aboveground C stocks and discuss potential managerial implementations to increase stand structural diversity in spruce-dominated forests to enhance C stocks.

Data and Methods

Data

Data were compiled from the New Brunswick Permanent Sample Plot Database (Porter et al. 2001). Spruce–balsam fir plots were selected where the proportion (in volume) of spruce trees was greater than 0.6 and, as a result, designated as spruce-dominated forest stands. In total, we selected 411 plots for which trees were measured once. Permanent Sample Plot Database sampling is conducted in 400-m^2 circular plots. Because height data were only available for trees greater than 9 cm dbh (in centimeters), trees with dbh less than 9 cm were excluded from our analysis. Stand age reported for the studied permanent sample plots ranged from 32 to 200 years (Porter et al. 2001). Stands were then assigned to forest stand developmental stages defined as young (less than 45 years), immature (46–70 years), mature (71–110 years), and overmature (greater than 111 years) (Porter et al. 2001). One to seven tree species were found within each plot, and a total of 21 tree species were cataloged after plots were combined. The most frequent tree species observed were black spruce (*Picea mariana* [Mill] BSP), white spruce (*Picea glauca* [Moench] Voss), red spruce (*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* [L.] Mill) (Table 1). For each plot the following stand variables were calculated (Table 2): stand density (N, stems/ha), stand basal area (BA, m^2/ha), quadratic mean dbh (Dq, cm), and site productivity (Sp, m^3/ha/year), measured as the mean annual increment by stand volume.

Aboveground C Stock Estimation

For each component (wood, bark, branches, and foliage) of tree biomass, the following allometric equation was used:

$$y = \beta_1 D^{\beta_2}, \tag{1}$$

where y is the dry biomass component of living trees, D is the dbh, and β_1 and β_2 are the model parameters to be estimated. This type of model estimates the biomass of the whole tree based on dbh measurements. Model parameters for different species were provided by Lambert et al. (2005). The aboveground biomass of the whole tree was calculated by summing up the aforementioned four tree components. The total biomass of a plot was computed by tallying all trees together. Aboveground C stock was then estimated by way of the product of all tree dry biomass calculated from the biomass equations and a constant factor of 0.5 as suggested by the global C cycle community.

Stand Structural Diversity Indices

The method to determine stand structural diversity indices was described in detail in an earlier study (Lei et al. 2009). These authors addressed six Shannon-Wiener indices related to tree species (Hs), tree size (Hd), tree height (Hh), and their combined interactions. These include the integrated diversity of species and size (Hsd), the integrated

Table 1. Summary of species composition (percentage of volume).

Tree species	Mean	SD	Minimum	Maximum
Black spruce	0.45	0.44	0	1
White spruce	0.08	0.23	0	1
Red spruce	0.32	0.37	0	1
Spruce subtotal	0.85	0.12	0.6	1
Balsam fir	0.05	0.08	0	0.38
Others[a]	0.10	0.11	0	0.40

[a] Tree species besides spruce and balsam fir: white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), eastern white cedar (*Thuja occidentalis* L.), eastern hemlock (*Tsuga canadensis* [L.] Carière), tamarack (*Larix laricina* [Du Roi] K. Koch), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), gray birch (*Betula populifolia* Marsh.), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), largetooth aspen (*Populus grandidentata* Michx.), black ash (*Fraxinus nigra* Marsh.), and balsam poplar (*Populus balsamifera* L.).

Table 2. **Stand characteristics during all four developmental stages.**

Characteristic	Young	Immature	Mature	Overmature	Total
No. stands	24	116	213	58	411
Age (yr)	40 (4)[a]	61 (6)	87 (8)	136 (18)	84 (27)
Height (m)	11.3 (2.1)	12.4 (2.5)	12.9 (2.6)	13.1 (3.0)	12.6 (2.6)
BA (m^2/ha)	26.2 (7.4)	27.5 (8.6)	28.4 (8.8)	31.2 (10.2)	28.4 (8.9)
V (m^3)	134.7 (45.4)	160.1 (57.3)	173.2 (61.0)	198.4 (76.9)	170.8 (63.3)
Dq (cm)	14.2 (2.1)	17.1 (3.3)	18.4 (3.1)	19.8 (4.6)	18.0 (3.6)
Sp (m^3/ha/yr)	3.4 (1.2)	2.7 (1.0)	2.0 (0.7)	1.5 (0.5)	2.2 (1.0)
N (stems/ha)	1682 (534)	1270 (487)	1118 (415)	1041 (337)	1183 (457)
ACS (Mg/ha)	47.4 (13.9)	54.2 (18.1)	58.0 (19.4)	66.5 (24.7)	57.5 (20.1)
Hs	0.508 (0.423)	0.554 (0.426)	0.517 (0.368)	0.496 (0.344)	0.524 (0.384)
Hd	1.267 (0.306)	1.480 (0.278)	1.586 (0.282)	1.717 (0.344)	1.556 (0.309)
Hh	1.292 (0.288)	1.349 (0.207)	1.417 (0.211)	1.496 (2.245)	1.402 (0.226)
Hsd	2.205 (0.491)	2.323 (0.404)	2.356 (0.374)	2.417 (0.395)	2.347 (0.394)
Hsp	1.086 (0.404)	1.165 (0.455)	1.151 (0.408)	1.275 (0.436)	1.169 (0.426)
Hsdh	1.987 (0.542)	2.161 (0.410)	2.192 (0.373)	2.267 (0.373)	2.182 (0.398)
GCd	0.266 (0.058)	0.306 (0.065)	0.335 (0.077)	0.380 (0.094)	0.329 (0.080)
GCh	0.090 (0.023)	0.093 (0.018)	0.100 (0.021)	0.115 (0.029)	0.099 (0.023)

BA, stand basal area per ha; V, standing volume per ha; Dq, quadratic mean dbh; Sp, site productivity; N, stand density; ACS, aboveground C stock. Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 3.
[a] The value in parentheses is the SD.

diversity of species and height or the species profile index (Hsp), and the average structural diversity index (Hsdh) of all three diversity indices of species, dbh, and height, as well as two Gini coefficient indices calculated by means of both tree diameter (Gcd) and height (Gch) values (Table 3). The Shannon-Wiener index was calculated using the proportion of tree species basal area, diameter class, and height class (Table 3). Use of the Shannon-Wiener index approach (based on species richness and evenness) meant that dbh and height had to be grouped into discrete classes. We used 4-cm dbh classes and 2-m height classes. According to Lei et al. (2009), tree size diversity described using 4-cm dbh classes and tree height diversity using 2-m classes exhibited high correlation coefficients with comparable indices based on other class widths for spruce-dominated forests. The Gini coefficient does not require arbitrarily determined diameter classes and performs better than other stand structural diversity measurements applied to forest management planning and practices (Lexerød and Eid 2006). It has a minimum value of 0 when all trees are of equal size and a theoretical maximum of 1 when all trees but one have a value of 0. Higher values, therefore, indicate greater structural diversity.

Statistical Analysis

The normality of distribution of the structural diversity indices and the aboveground C stock for the entire data set and subgroup data sets were tested throughout all developmental stages using the Shapiro-Wilk test. When and if distributions were approximately normally distributed, Pearson's correlation coefficients (r) were calculated between the eight structural diversity indices and the aboveground C stock. When and if distributions were not normal, Spearman's rank correlation coefficients (ρ) were computed instead.

Because stand density, age, and site quality are known to influence stand growth (Fridley 2002, Pretzsch 2005, Firn et al. 2007, Liang et al. 2007, Larson et al. 2008) and may also affect relationships between structural diversity and aboveground C stocks, stand age, site productivity, and stand density were chosen as potential additional independent variables to quantify the effects of site factors and initial stand conditions to these relationships. Multiple linear regressions (SPSS, Inc., Chicago, IL) were used to fit the data and to identify the effects of independent variables selected by way of the stepwise procedure in relation to aboveground C stocks. Multicollinearity diagnosis was performed using the variance inflation factor (VIF) because multicollinearity may cause inaccurate model parameterization and decreased statistical power and exclude significant predictor variables (Graham 2003). Variables with VIFs larger than 5 were excluded from the model.

Eight aboveground C stock models were tested in total (Equation 2) because they were developed for aboveground C stocks and the eight explanatory diversity variables separately:

$$\text{ACS} = b_0 + b_1\text{diversity} + b_2N + b_3\text{Age} + b_4\text{Sp}, \qquad (2)$$

where ACS is the aboveground C stock, diversity is the stand structural diversity index (Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh), N is stand density, Age is stand age, and Sp is site productivity. Model fitting and performance were assessed using the adjusted coefficient of determination (R^2) and significance (F value and P value) measurements. Partial correlation coefficients for each predictable variable for all models were described. These measure the degree of association between stand structural diversity indices and aboveground C stocks with the effect of removing a set of controlling random variables (e.g., stand density, age, and site productivity for stand structural diversity). Variables with high partial correlation coefficients indicate a strong relationship to aboveground C stocks.

Table 3. **Stand structural diversity indices used in this study.**

No.	Index	Formula	Description
1	Tree species diversity index	$Hs = -\sum_{i=1}^{s} p_i \cdot \log p_i$, where p_i is the proportion of basal area for the *i*th species and *s* is the number of species.	Shannon-Wiener index for species (Magurran 2004)
2	Tree size diversity index	$Hd = -\sum_{i=1}^{d} p_i \cdot \log p_i$, where p_i is the proportion of basal area for the *i*th diameter class and *d* is the number of diameter class.	Shannon-Wiener index for tree size (Buongiorno et al. 1994)
3	Tree height diversity index	$Hh = -\sum_{i=1}^{h} p_i \cdot \log p_i$, where p_i is the proportion of basal area for the *i*th height class and *h* is the number of height class.	Shannon-Wiener index for tree height class (Staudhammer and LeMay 2001)
4	Integrated diversity index of tree species and size	$Hsd = -\sum_{i=1}^{s}\sum_{j=1}^{d} p_{ij} \cdot \log p_{ij}$, where p_{ij} is the proportion of basal area in the *j*th diameter class of the *i* th species, *s* is the number of tree species, and *d* is the number of the diameter class.	Integrated Shannon-Wiener index for species and tree size (Buongiorno 1994)
5	Species profile index	$Hsp = -\sum_{i=1}^{s}\sum_{j=1}^{3} p_{ij} \cdot \log p_{ij}$, where p_{ij} is the proportion of basal area of the *j*th height class of the *i*th species, *s* is the number of tree species, height class 1 is 100 − 80% of maximal tree height (h_{max}), height class 2 is 80 to 50% of h_{max}, and height class 3 is 50 to 0% of h_{max}.	Integrated Shannon-Wiener index for the proportion of species in different stand layer (Pretzsch 1997)
6	Mean structural diversity index	$Hsdh = (H_s + H_d + H_h)/3$	Mean value of tree species, size, and height indices (Staudhammer and Lemay 2001)
7	Gini coefficient for dbh	$GCd = \frac{\sum_{i=1}^{n}(2j-n-1)\,ba_j}{\sum_{i=1}^{n} ba_j\,(n-1)}$, where ba_j is the basal area of the tree with rank *j*, *j* is the rank of a tree in ascending order from 1 to *n* by dbh, and *n* is the number of trees.	Measurements of the deviation from perfect equality (Lexerød and Eid 2006)
8	Gini coefficient for height	$GCh = \frac{\sum_{i=1}^{n}(2j-n-1)\,ba_j}{\sum_{i=1}^{n} ba_j\,(n-1)}$, where ba_j is the basal area area of the tree with rank *j*, *j* is the rank of a tree in ascending order from 1 to *n* by height, and *n* is the number of trees.	Measurements of the deviation from perfect equality (Lexerød and Eid 2006)

Modified from Lei et al. (2009).

Results

Stand Characteristics

Tree height and dbh ranged from 6.7 to 24.9 m and from 9.1 to 56.9 cm, respectively. The most obvious general stand-level trend was that dbh, height, volume, basal area, and the structural diversity indices (Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh) increased as the age of the stands increased. The only exceptions to this trend were seen in stand density, productivity, and species diversity (Hs) (Table 2). Diameter distribution exhibited the typical inverse J curve that was exhibited in many old natural forest stands (Figure 1). The pattern of expansive larger range of tree dbh in conjunction with stages of stand development was accompanied by decreasing density and productivity (Table 2). Although younger stands possessed smaller stand volume overall, it is assumed that they undergo higher growth rates and possess greater stem density. Older stands, on the other hand, possessed higher structural complexity both horizontally and vertically (Table 2; Figures 1 and 2). Tree species diversity did not follow this pattern. It increased during the young to immature stages and then decreased in the following stages of stand development.

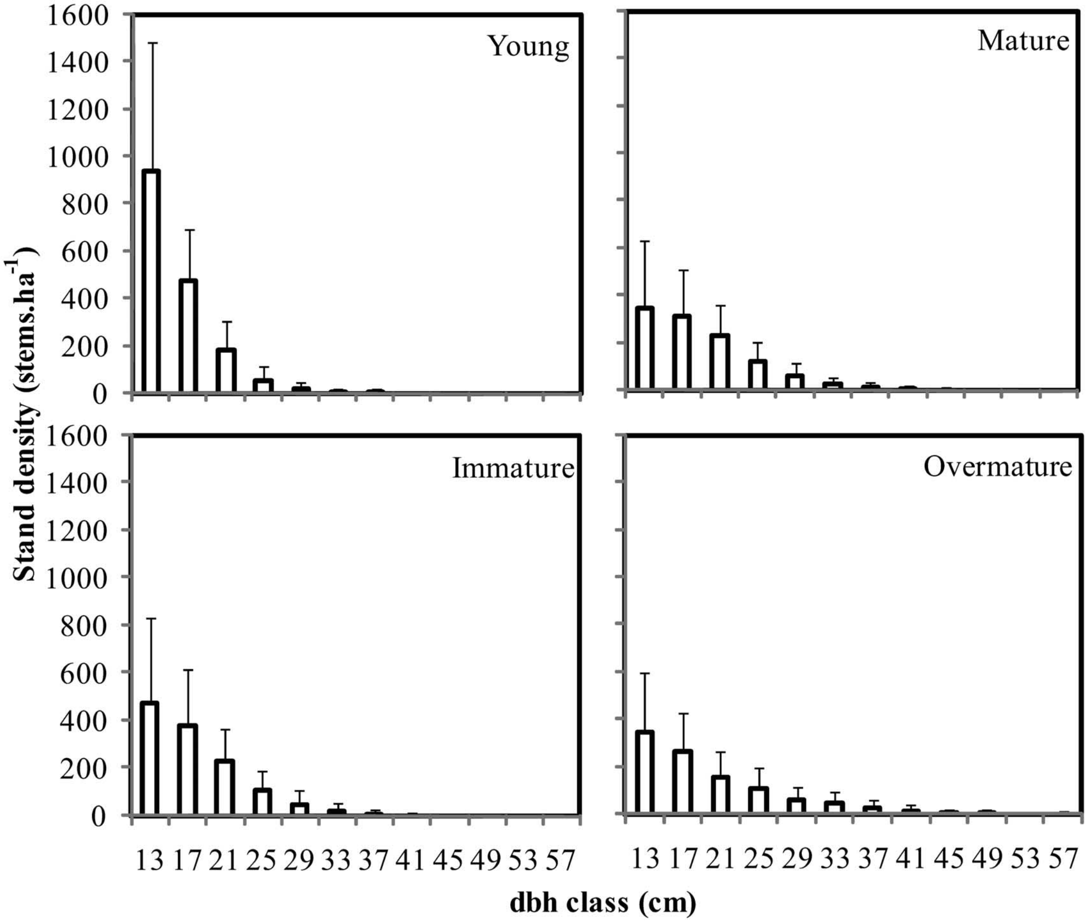

Figure 1. Diameter distribution for spruce–balsam fir stands throughout all four developmental stages.

Aboveground C Stocks

Aboveground C stocks in spruce-dominated forests ranged from 13.58 to 110.12 Mg ha^{-1} (with an average of 57.49 Mg ha^{-1}). In addition, aboveground C stocks exhibited a general increasing trend throughout all stand developmental stages (Figure 3). Older forests, therefore, possess both greater quantities of C and a more complex stand structure than younger forests.

Relationships between Aboveground C Stocks and Structural Diversity

Significant positive relationships were found in the data set between the eight structural diversity indices and aboveground C stocks (Table 4; Figure 4). Results showed that correlation coefficients changed from 0.314 (Hs) to 0.600 (Hd) throughout all eight diversity indices, all of them being significant at the 0.01 level. Positive relationships between three of the eight correlation coefficients (Hs, Hsd, and Hsdh) generally increased throughout the stand developmental stages (Table 4). With the exception of Hs, Hsd, Hsp, and Hsdh that occurred during the early stages, all relationships between the structural diversity indices and aboveground C stocks were significant. However, tree height diversity (Hh and GCh) was related to aboveground C stocks to a lesser extent during the immature stage than it was during the other three stages.

Multicollinearity analysis ascertained the correlations from the explanatory variables used in the multiple regression models such as stand age, productivity, stand density, and the structural diversity indices themselves. These models showed nonsignificant multicollinearity because the VIFs of the stand structural diversity indices, stand density, productivity, and stand age were less than 5 (Table 5). Multiple linear regression analysis integrating stand age, stand density, site productivity, and structural diversity explained more than 80% of the variation in aboveground C stock. All predictable variable parameters for the models were significant with the exception of stand density to height diversity (Hh) (Table 5). Among the predictable variables, stand age and productivity always exhibited high values in relation to the partial correlation coefficients (Table 5), whereas stand density and the structural diversity indices exhibited low values in relation to the partial correlation coefficients. Results show that stand age and productivity played the most important roles in terms of aboveground C stock. Stand structural diversity indices differed for correlations involving aboveground C stocks. For example, Hd produced the maximum partial correlation coefficient ($r = 0.396$, $P < 0.001$) and Hh produced the minimum partial correlation coefficient ($r = 0.131$, $P < 0.01$) (Table 5). All parameters as well as the partial correlation coefficients used for the structural diversity indices of all models were positive and, as a result, aboveground C stocks increased with an increase in the stand structural diversity indices (Table 5).

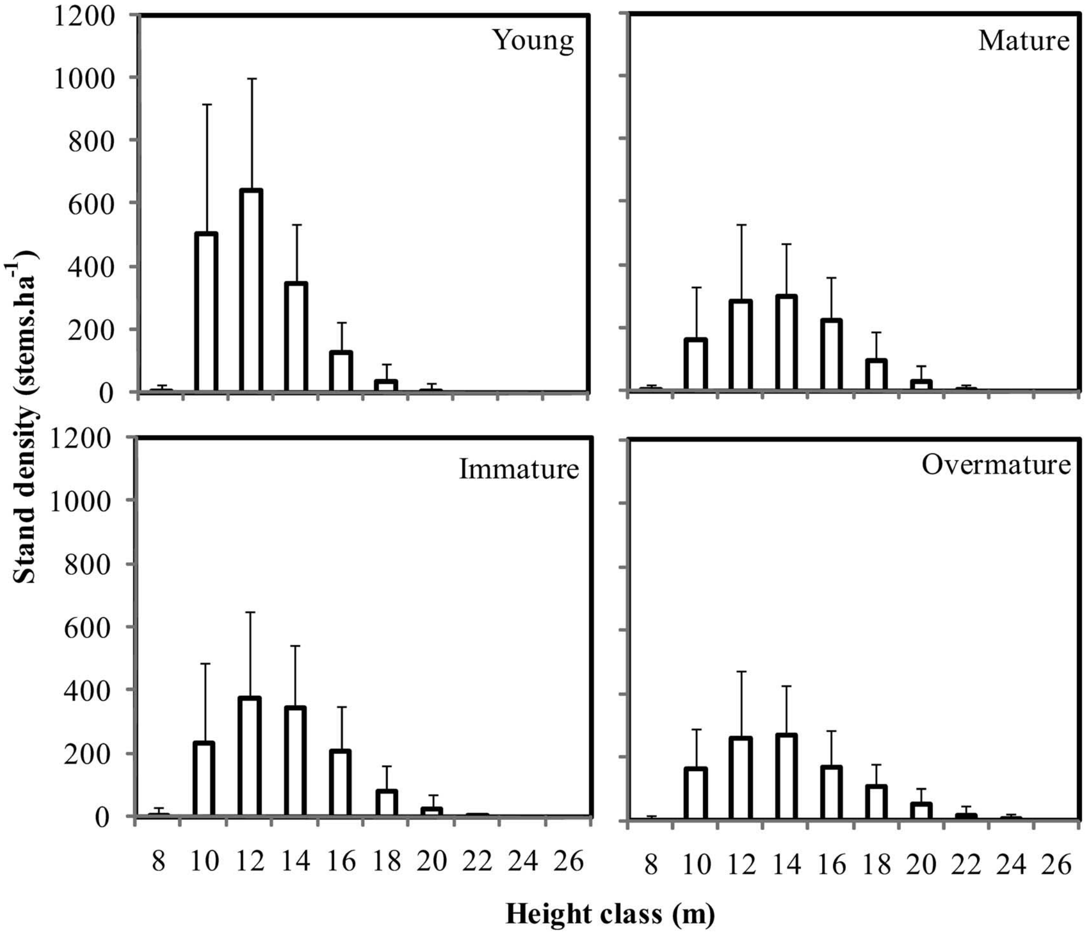

Figure 2. Height distributions for spruce–balsam fir stands throughout all four developmental stages.

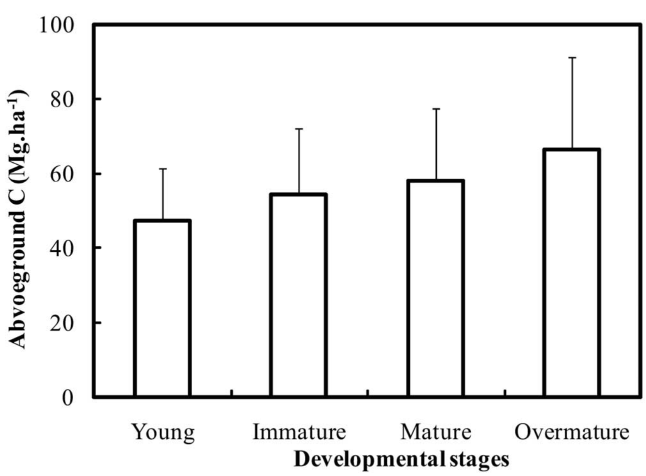

Figure 3. Mean aboveground C stocks during all four developmental stages.

Discussion

Aboveground C Stocks throughout Forest Developmental Stage Gradients

It was ascertained that C stocks showed a general increasing trend throughout all forest stand developmental stages (Figure 3). Many other studies have found a similar increasing trend for both aboveground and belowground C stocks that addresses age dependence of forest biomass or C stocks (Peichl and Arain 2006, Taylor et al. 2007). As a result, forest developmental stages play a determining role in the distribution of C pools for different forest ecosystems (Pregitzer and Euskirchen 2004).

A greater C stock accumulation was found in older stands with high structural diversity compared with young spruce-dominated forest stands because older stands are more likely to incorporate a greater variation in tree size distribution due to the fact that they possess a greater number of large trees overall (Figures 1 and 2). Moreover, because the coefficients of the original bivariate correlation for each diversity index (Table 4) were greater than that of the partial correlation (Table 5), it has been determined that the effects of controlled variables (stand density, stand age, and productivity) influence both structural diversity and C stocks and structural diversity itself also partially influences C stocks.

Effects of Species Diversity on Aboveground C Stocks

Results indicate that significant and positive relationships exist between tree species diversity and aboveground C stocks in spruce-dominated forest stands (Table 5; Figure 4). Several authors have reported positive relationships between species diversity and biomass in forest ecosystems (Vilà et al. 2007). Ishii et al. (2004) also suggested

Table 4. Relationship between structural diversity indices and aboveground C stocks.

Variables	Total data set (n = 411)	Young (n = 24)	Immature (n = 116)	Mature (n = 213)	Overmature (n = 58)
Hs	$\rho = 0.314^a$	$\rho = 0.189$	$\rho = 0.201^b$	$\rho = 0.397^a$	$\rho = 0.425^a$
Hd	$\rho = 0.600^a$	$r = 0.561^a$	$r = 0.487^a$	$\rho = 0.553^a$	$\rho = 0.724^a$
Hh	$\rho = 0.380^a$	$r = 0.508^b$	$r = 0.218^b$	$r = 0.379^a$	$\rho = 0.539^a$
Hsd	$\rho = 0.552^a$	$r = 0.307$	$r = 0.447^a$	$\rho = 0.589^a$	$\rho = 0.632^a$
Hsp	$\rho = 0.421^a$	$\rho = 0.265$	$\rho = 0.241^a$	$\rho = 0.447^a$	$\rho = 0.617^a$
Hsdh	$\rho = 0.484^a$	$r = 0.229$	$r = 0.350^a$	$\rho = 0.523^a$	$\rho = 0.585^a$
GCd	$\rho = 0.410^a$	$r = 0.521^a$	$r = 0.280^a$	$r = 0.366^a$	$\rho = 0.598^a$
GCh	$\rho = 0.319^a$	$r = 0.445^b$	$r = 0.177$	$r = 0.247^a$	$\rho = 0.574^a$

r, Pearson's correlation coefficient; ρ, Spearman's rank correlation coefficient. Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 3.

[a] P value significant at $\alpha = 0.01$.

[b] P value significant at $\alpha = 0.05$.

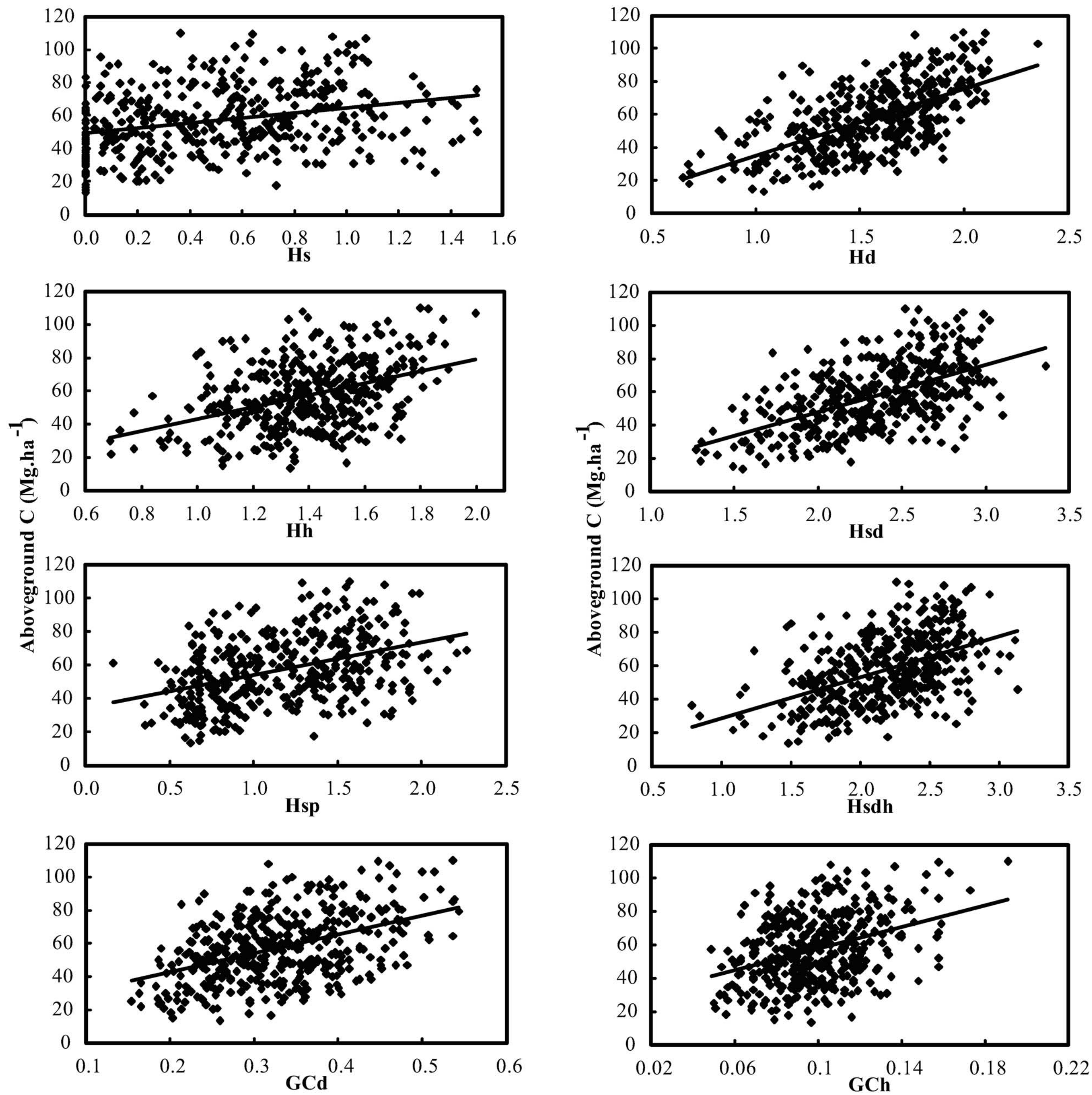

Figure 4. Relationships between aboveground C stocks and structural diversity indices (n = 411). Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 3.

Table 5. Summary of multiple linear regression models for aboveground C stocks.

Structural diversity indices	Parameter estimates and partial correlation coefficients													Adjusted R^2	F value
	b_0	b_1	r_1	VIF_1	b_2	r_2	VIF_2	b_3	r_3	VIF_3	b_4	r_4	VIF_4		
Hs	−38.421	4.835	0.196[a]	1.276	0.003	0.125[b]	1.378	19.953	0.876[a]	1.704	0.553	0.843[a]	1.375	0.830	503.1[a]
Hd	−52.203	17.311	0.396[a]	2.587	0.007	0.298[a]	1.911	16.668	0.777[a]	2.928	0.448	0.733[a]	2.183	0.851	587.8[a]
Hh	−39.003	4.512	0.109[c]	1.227	NS	NS	NS	20.515	0.812[a]	1.552	0.538	0.888[a]	1.608	0.826	648.6[a]
Hsd	−49.476	7.892	0.280[a]	1.748	0.004	0.177[a]	1.469	18.467	0.823[a]	2.389	0.517	0.812[a]	1.589	0.838	529.5[a]
Hsp	−40.766	5.767	0.243[a]	1.452	0.003	0.158[a]	1.464	19.399	0.861[a]	1.900	0.535	0.830[a]	1.462	0.834	516.4[a]
Hsdh	−44.772	5.380	0.207[a]	1.521	0.003	0.133[c]	1.402	19.399	0.849[a]	2.069	0.531	0.819[a]	1.539	0.831	505.9[a]
GCd	−45.891	44.102	0.315[a]	1.784	0.005	0.215[a]	1.614	18.930	0.858[a]	1.928	0.495	0.786[a]	1.783	0.841	544.1[a]
GCh	−40.780	68.516	0.153[c]	1.506	0.002	0.111[b]	1.411	20.090	0.873[a]	1.743	0.530	0.802[a]	1.696	0.828	493.7[a]

Regression df = 4,406; b_0 is the intercept; b_1 to b_4 refers to the regression coefficients of diversity, stand density, stand age, and site productivity, respectively; r_1 to r_4 are the partial correlation coefficients of the corresponding explanatory variables; VIF_1 to VIF_4 are the variance inflation factors corresponding to the four explanatory variables; Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 3. NS, not significant.

[a] P value significant at $\alpha = 0.001$.

[b] P value significant at $\alpha = 0.05$.

[c] P value significant at $\alpha = 0.01$.

that structural complexity may in itself increase forest growth by promoting complementary resource utilization among plant species. These findings are consistent with the positive, monotonic relationships between productivity and plant species richness (Whittaker and Heegaard 2003, Balvanera et al. 2006, Gillman and Wright 2006). Other studies have produced contrasting results. For example, Firn et al. (2007) reported a significant negative relationship between tree species diversity in the overstory and total basal area of tropical plantations. Negative relationships between tree species diversity and biomass were also reported in the temperate forest ecosystems of Central Europe (Szwagrzyk and Gazda 2007, Jacob et al. 2010). The appearance of conflicts is not surprising and reconfirmed the complexity of the ecosystem structure and function. Nevertheless, our findings robustly support the niche complementarity hypothesis, which states that aboveground carbon stocks increased with increasing tree species diversity in spruce-dominated forest stands.

Effects of Tree Size and Height Diversity on Aboveground C Stocks

Tree size diversity (Hd or GCd) exhibits the strongest positive effects on aboveground C stocks and shows the largest partial correlation coefficient among all eight structural diversity indices (Table 5). This may be the result of high resource use efficiency due to complex tree size structure, supporting niche differentiation between intraspecific species competition. Tree height diversity (Hh and GCh) showed relatively weak effects on aboveground C stocks. This could be the result of tree height being close to the maximum value in both the mature and overmature stages thereby producing a lack of variation in tree height values. Spatial structure diversity indices indicate that greater variation in tree size and height results in a multilayered foliage structure and enhanced structural complexity and, hence, allows for more efficient light infiltration, thereby supporting the hypothesis of better resource utilization by trees. The consequence of this better resource use leads to a greater accumulation of biomass and overall C production. Findings that support intraspecific complementary effects were presented by Lei et al. (2009) who investigated the relationship between structural diversity and forest growth in Canadian spruce-dominated forest stands. In one of the few studies that investigated the effects of tree size and height diversity on C stocks, Merino et al. (2007) reported that unmanaged European beech (*Fagus sylvatica L.*) stands in central Europe obtained higher values for C accumulation in tree biomass compared with managed forests because unmanaged stands possess a more heterogeneous tree structure that induces soils and trees to act as long-term C sinks.

Effects of Combined Structural Diversity on Aboveground C Stocks

This study found that the effects of combined structural diversity indices (Hsd, Hsp, and Hsdh) were unexpectedly weaker than the effects of tree size diversity (Hd) on aboveground C stocks (Table 5). The combined effects, therefore, produce negative side effects. This unpredicted condition may result from the offset between the effects of tree species diversity and tree size or tree height diversity in combination with stand development. Combined effects (Hsd) were found to contribute the most to net stand growth (Lei et al. 2009). There is an obvious need for this result to be further explored; however, the focus of this study was centered on structural diversity measures of living trees deemed as overstock. Thus, it is recommended that other attributes of structural diversity such as shrub species richness, coarse woody debris, and dead wood be investigated in the future.

Implications for Forest Management Initiatives

Silvicultural practices are commonly applied to control forest establishment, composition and structure, and growth with the purpose of producing timber and other forest products (Smith et al. 1997). Results show that spruce-dominated forests composed of shade-tolerant species (spruce and balsam fir) possess higher C stocks than mono-dominated spruce stands. A recent study conducted by

Cavard et al. (2010) within the Canadian boreal forest concluded that the mixing effects of shade-tolerant species could lead to significantly higher C pools compared with mono-specific forest stands. A plausible explanation for this condition is that both species retain different ecological niches as a result of complementary effects. Our results suggest that silviculture can be used to increase aboveground carbon stocks by increasing tree species composition and stand structure as our study confirms that stand structural diversity including tree composition, size, and height and combined indices have a significant positive relationship with aboveground C stocks. This finding also supports the initial hypothesis of this study. Therefore, a logical silvicultural decision is to select tolerant species that occur naturally in a region.

In the intervening time, uneven-aged management practices that apply selective or partial cutting may increase structural diversity and enhance C sequestration. This suggestion agrees with the results reported by Lei et al. (2009) in their study on stand growth. For instance, green tree retention has been encouraged as an alternative management strategy to create structurally complex forest stands (Sullivan et al. 2001, Zenner 2000). In their process-based model study, Garcia-Gonzalo et al. (2007) concluded that the initial forest structure (in terms of species and age class distribution), if not taken into account, may affect C stocks and timber production. Future forest management practices could be determined by the research presented above.

Conclusions

This study confirms that stand structural diversity in terms of tree species, size, and height as well as the application of the combined indices exhibited a significant positive relationship with aboveground C stocks, supporting the initial hypothesis of this study. As key constituents of structural diversity, the selected tree species, size, and height components can be logically linked to management practices and objectives. For the purpose of maintaining biodiversity and C stocks in spruce-dominated forests, it is recommended that managers apply uneven-aged silvicultural practices by means of selection or partial cutting and choose a mixed tolerant species composition to maintain both high structural diversity and C stocks.

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