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Species Diversity and Floristic Relationships of the Understory Vegetation in Black Spruce and Trembling Aspen Stands in the Boreal Forest of British Columbia

Introduction

The boreal forest is confined to the Northern Hemisphere and is the most continuous and extensive forest in the world. In North America boreal forest extends from the Pacific to Atlantic coast spanning over 10° latitude. White spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) B.S.P.), and trembling aspen (*Populus tremuloides* Michx.) are among the dominant tree species. Black spruce and trembling aspen may form pure stands and occupy similar sites as their edaphic amplitudes overlap; however, spruce is rare on water-deficient sites and aspen does not tolerate excess water.

Despite many studies conducted in the North American boreal forest, little is known about relationships between the boreal understory vegetation and softwood or hardwood canopy species in different climate regions. Furthermore, the variation in species diversity and succession between the stands dominated by coniferous trees and those dominated by broadleaved trees within the same region is unknown. The objectives of this study are to determine (1) the difference in the species diversity and floristic composition of understory vegetation between black spruce and trembling aspen stands within the same climatic region, and (2) how the species diversity and floristic composition of understory vegetation in each stand type vary with climate, and soil moisture and soil nutrient conditions.

Study Stands and Methods

A total of 231 sample plots, each 20 x 20 m, representing black spruce and trembling aspen stand types, were located from 52° 14' to 59° 59' N latitude and from 120° 02' to 133° 17' W longitude. The stands were stratified into three climatic regions according to zonal classification of the BC Forest Service: (1) drier montane boreal (DMB), (2) wetter montane boreal (WMB), and (3) mild montane boreal (MMB). The DMB and WMB climates are delineated by the Boreal White and Black Spruce (BWBS) zone, and the MMB climate is delineated by the Sub-boreal Spruce (SBS) zone. The drier portion of the BWBS zone affected by DMB climate is west of the Rocky Mountains, the wetter portion of the BWBS zone affected by WMB climate is east and northeast of the Rocky Mountains, and the SBS zone affected by MMB climate is west of the Rocky Mountains but south of the BWBS zone.

Soil moisture regime (SMR) and soil nutrient regime (SNR) of each sample plot were estimated in the field. In this study, we used three classes for both SMR and SNR: SMR1 (moderately dry + slightly dry), SMR2 (fresh + moist), and SMR3 (very moist + wet); for soil nutrients these classes were: SNR1 (very poor + poor), SNR2 (medium), and SNR3 (rich + very rich).

Floristic similarity between each pair of the 231 sample plots was measured by Sørensen's index:

$$SI = \frac{2c}{a+b}$$

where a and b are the numbers of species in sample plots i and j, respectively; and c is the number of species common to both sample plots.

Non-metric multidimensional scaling (NMDS) was applied to detect to what extent different dominant canopy species and climatic regions in the sample plots of were segregated in an ordination space.

Results

Species richness between aspen and spruce stands in the same climatic region was not significantly different when vascular plants and cryptogams were combined (Table 1). However, when different growth forms were compared separately, trembling aspen stands were significantly more diverse in vascular plants and less diverse in cryptogams than black spruce stands in the DMB and WMB regions (BWBS zone). Spruce and aspen stands had equal species richness in the MMB region (SBS zone). In most comparisons, species richness stand types was similar between the DMB and WMB regions (BWBS zone) but significantly higher in the MMB region (SBS zone) (Table 1).

Table 1. Mean and standard deviation (in parentheses) of species richness per sample plot according to dominant canopy species and climatic regions. Means with the same uppercase superscripts within the same row between different stand types are not significantly different (t-test, $\alpha = 0.05$); and means with the same lowercase superscripts within the same column between climatic regions for the same group of plants are not significantly different (Tukey's HSD multiple comparison, $\alpha = 0.05$).

	Spruce stands	Aspen stands
Drier montane boreal		
Number of stands	24	28
All plants	20.4 (5.5)^{Aa}	21.0 (4.8)^{Aa}
Vascular plants	12.2 (4.2)^{Ba}	16.7 (2.7)^{Ab}
Woody plants	4.8 (2.0)^{Aa}	4.8 (1.5)^{Ab}
Herbaceous plants	7.4 (3.2)^{Ba}	11.9 (2.3)^{Aa}
Cryptogams	8.3 (3.1)^{Bb}	4.3 (3.6)^{Ab}
Wetter montane boreal		
Number of stands	67	60
All plants	20.2 (8.1)^{Aa}	21.6 (3.9)^{Aa}
Vascular plants	13.6 (7.2)^{Ba}	20.3 (4.4)^{Aa}
Woody plants	4.9 (2.1)^{Ba}	6.6 (1.9)^{Aa}
Herbaceous plants	8.7 (5.9)^{Ba}	13.7 (3.7)^{Aa}
Cryptogams	6.6 (3.1)^{Ba}	1.3 (1.7)^{Aa}
Mild montane boreal		
Number of stands	27	25
All plants	27.0 (6.1)^{Ab}	27.5 (6.5)^{Ab}
Vascular plants	22.1 (6.8)^{Ab}	25.2 (5.4)^{Ac}
Woody plants	6.5 (2.2)^{Ab}	7.4 (2.5)^{Aa}
Herbaceous plants	15.6 (5.7)^{Ab}	17.8 (3.8)^{Ab}
Cryptogams	4.9 (1.8)^{Bc}	2.4 (2.4)^{Aa}

Species richness of vascular plants increased with increasing nutrient availability from poor to rich while that of cryptogams decreased in both types of stands (Figure 1a). Overall species richness increased consistently with increasing soil moisture from dry to wet in aspen stands but increased and then decreased in black spruce stands (Figure 1b).

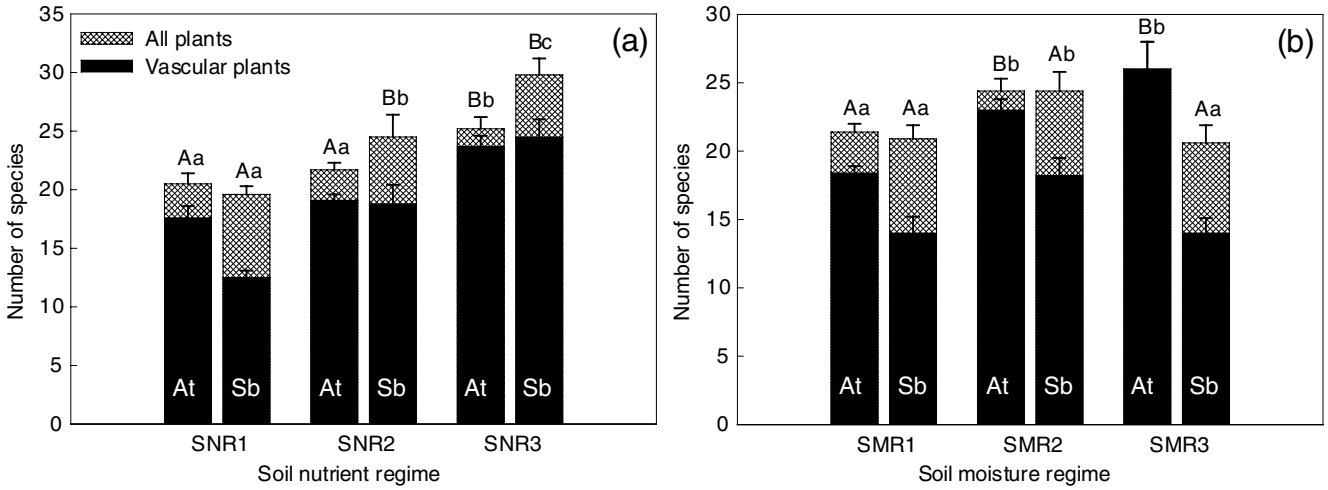

Figure 1. Comparisons of species richness (mean ± 1 SE) of overall plants and vascular plants between trembling aspen (At) and black spruce (Sb) stands on sites of different soil moisture (a) and nutrient (b) conditions. Means with the same uppercase and lowercase letters on the bars for the same stand type are not significantly different in species richness of all plants and vascular plants ($\alpha = 0.05$), respectively.

Within the same climatic region, floristic similarity was on average higher among aspen stands than spruce stands (Table 2). Furthermore, within-stand type floristic similarity was significantly higher (p <0.05) than between stands across all climatic regions (Table 2). Spruce stands in different regions were more similar than aspen stands (Table 2). The NMDS ordination differentiated well between stand types (Figure 2).

Table 2. Mean of Sørensen's indices between sample plots according to stand type (At - trembling aspen, Sb - black spruce) and climatic region (DMB - drier montane boreal, WMB - wetter montane boreal, MMB - mild montane boreal). Bold values indicate the highest mean in the row and/or column. Numbers in parentheses are the number of sample plots. Mean of Sørensen's indices with the same superscripts within the same climatic region between the two stand types are not significantly different (α = 0.05).

Climatic region/ Stand type	DMB/ At (28)	DMB/ Sb (24)	WMB/ At (60)	WMB/ Sb (67)	MMB/ At (25)	MMB/ Sb (27)
DMB/At	**0.440** [a]					
DMB/Sb	0.319	**0.378** [b]				
WMB/At	0.282	0.199	**0.461** [a]			
WMB/Sb	0.291	0.359	0.231	**0.376** [b]		
MMB/At	0.224	0.142	0.299	0.178	**0.401** [a]	
MMB/Sb	0.328	0.286	0.301	0.310	0.303	**0.394** [a]

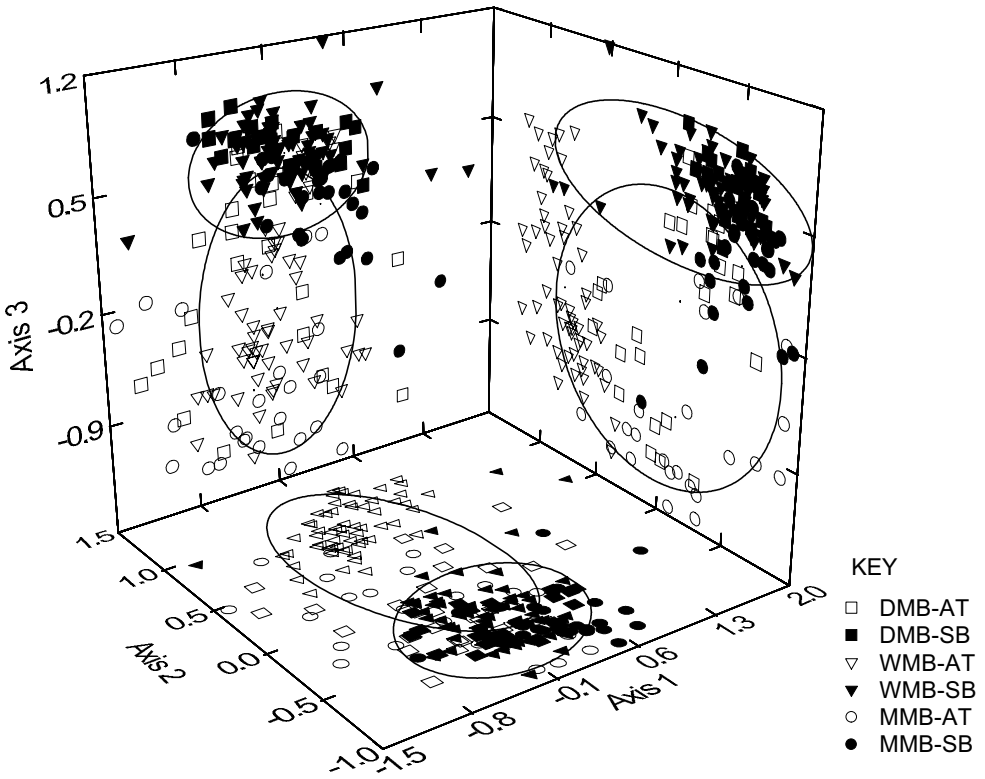

Figure 2. NMDS ordinations showing relationships among the 231 study stands differentiated according to two stand types (AT - trembling aspen, SB - black spruce) and three climatic regions (DMB - drier montane boreal, WMB - wetter montane boreal, MMB - mild montane boreal). Ellipses for the stand types were constructed with a probability value of 0.7.

Discussion

As black spruce and trembling aspen may occupy similar upland sites, what are the determinants of their understory vegetation differentiation? We suggest two principal causes: understory light conditions and forest floor quality (humus forms).

Compared to black spruce stands, trembling aspen stands have more light in the understory, indicated by the presence of shade-intolerant and moderately shade-tolerant species (such as *Epilobium angustifolium, Lupinus arcticus* and *Rosa acicularis*), more balanced temperature and soil moisture conditions, and most importantly, higher nutrient availability, as indicated by the presence of *Aster conspicuous, Epilobium angustifolium, Festuca altaica, Leymus innovatus, Lathyrus ochroleucus, Lonicera involucrata, Mertensia paniculata* and *Osmorhiza berteroi*. Probably the best indicator of high nitrogen availability is *Epilobium angustifolium* that typically inhabits cutovers and signifies rapid decomposition of forest floor materials. In contrast, black spruce stands are dominated by indicators of low nitrogen availability such as ericaceous shrubs (e.g., *Ledum groenlandicum* and *Vaccinium vitis-idaea*) and oxylophytic mosses (e.g., *Hylocomium splendens, Pleurozium shreberi* and *Ptilium crista-castrensis*).

Compared to acidic Mor humus forms (particularly Hemimors) in black spruce stands, a variety of Moder or, rarely Mull, humus forms develop in boreal trembling aspen stands. Many studies investigating relationships among humus forms, forest floor nutrient properties, and understory vegetation concluded that the regional decomposition and nutrient availability gradients are reflected in the development of different humus forms that, in turn, are associated with different vegetation. The nutrient availability (measured by plant-available nitrogen) in the forest floor increases from Mor < Moder < Mull humus forms, and vegetation changes in the same order from bryophyte and ericaceous-dominated communities to herbaceous communities. Thus, according to these general relationships, aspen stands should have richer forest floors and more diverse herbaceous understories than spruce stands.

References

Qian, H., K. Klinka and P.V. Krestov. 2001. Species diversity and floristic relationships of the understory vegetation in black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*) stands in the boreal forest of British Columbia. Submitted to Journal of Vegetation Science 01/02/25.

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