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Understorey vegetation in boreal *Picea mariana* and *Populus tremuloides* stands in British Columbia

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Abstract. We compared the species composition and species density of vascular plants in the understorey vegetation of boreal forest between *Picea mariana* (Black spruce) and *Populus tremuloides* (Trembling aspen) stands in British Columbia, Canada, and related differences in species composition and species density between the two forest types to dominant canopy tree species as well as a wide variety of environmental factors. We analysed 231 stands, distributed in three different climatic regions representing drier, wetter, and milder variations of montane boreal climate. Of these stands 118 were dominated by *P. mariana* and 113 by *P. tremuloides*. *P. tremuloides* stands had higher species density than *P. mariana* stands in all climatic regions, but species density of each dominance type varied among climatic regions. The floristic composition of the understorey vegetation was markedly different for *P. mariana* and *P. tremuloides* dominated stands.

A detailed study on the effect of canopy dominance and local environmental factors on the understorey vegetation of the boreal forest was conducted using 88 stands from one of the three climatic regions. Using a combination of ordination and variation partitioning by constrained ordination we demonstrated a small but unique effect of canopy dominance type on the understorey vegetation, while a larger amount of compositional variation was shared with other factors. Our results accord with a scenario in which differences in primary environmental factors and humus form properties, the latter accentuated by the canopy dominants themselves, are the most important causes of higher species density in *P. tremuloides* stands than in *P. mariana* stands, as well as differences in species composition among the two canopy dominance types. Processes and time scales involved in the small but significant direct and indirect effects of the canopy dominant on understorey species composition are discussed.

Keywords: Black spruce; Boreal forest; Floristic relationship; Humus form; Species richness; Trembling aspen.

Nomenclature: Qian & Klinka (1998).

Abbreviations: DMB = Drier montane boreal; MMB = Mild montane boreal; WMB = Wetter montane boreal.

Introduction

The North American boreal forest extends from the Pacific to the Atlantic coast. The evergreen conifer *Picea mariana* (Black spruce) and the broad-leaved deciduous *Populus tremuloides* (Trembling aspen) are among the few dominant, commercially important tree species with a North American transcontinental distribution, that grow in a wide range of sites. The two species have contrasting autecological and forest characteristics (DeByle & Winokur 1985; Viereck & Johnston 1990) and are typically parts of characteristic ecosystems that differ in biotic community, abiotic environment, structure, function, complexity, interactions, temporal change (e.g. Priha & Smolander 1997; Ewald 2000) and humus form development (Fons et al. 1998). *P. mariana* is less frequent on water-deficient sites and *P. tremuloides* does not tolerate water logging (DeByle & Winokur 1985; Légaré et al. 2001). Typically, *P. tremuloides* and *P. mariana* form pure stands but mixed-species stands occur where the species' ecological (climatic and local environmental) amplitudes overlap. Although the understorey species composition of the North American boreal forest has been addressed in several studies (e.g. Krajina 1969; Wali & Krajina 1973; Meidinger & Pojar 1991; Qian et al. 1998; Légaré et al. 2001), little is known about its variation relative to canopy dominants, particularly broad-leaved deciduous and evergreen coniferous species, and the extent to which *P. mariana* and *P. tremuloides* dominated stands differ in species composition and richness of the understorey vegetation in different climatic regions.

Ordination and constrained ordination methods (ter Braak 1986; R. Økland 1990; Legendre & Legendre 1998), the two main families of multivariate gradient analysis techniques (see ter Braak & Prentice 1988) that complement each other (R. Økland 1996), enable analysis of complex vegetation-environment relationships.

Ordination methods can be used to generate hypotheses about vegetation-environment relationships, while constrained ordination can test the hypotheses by partitioning the variation of species composition among different sets of explanatory variables (R. Økland 1996). Variation partitioning on many groups of variables simultaneously, as opened for by Økland & Eilertsen (1994), facilitates assessment of the relative importance of potential factors to the variation in species composition in complex cases. Disentangling of interacting effects among canopy dominance and local and regional environmental factors on understorey species composition in boreal forests is such a complex case.

Material and Methods

Study area and selection of study stands

The study area encompassed a large part of northern British Columbia (52°14' to 59°59' N and 120°02' to 133°17' W; Fig. 1). Sampling took place during the growing seasons of 1995, 1997 and 1998 in three climatic regions: (1) drier montane boreal (DMB; 24 *P. mariana* stands, 28 *P. tremuloides* stands); (2) wetter montane boreal (WMB; 67, 60); and (3) mild montane boreal (MMB; 27, 25). Both DMB and WBM were influenced by continental montane boreal climates, while DMB was located in the rain shadow of the Coast Mountains and WBM east of the Rocky Mountains on the Alberta Plateau. Forest fires are frequent in all regions, maintaining a large fraction of the area in early and mid-seral stages. For detailed descriptions of environment and vegetation see Krajina (1969), Wali & Krajina (1973) and Meidinger & Pojar (1991).

We selected 231 forest stands to cover the floristic and environmental variation of the study area. These were naturally established, unmanaged, even-aged stands with breast-height age of 50 - 175 yr, with a uniform canopy layer > 80 % dominated by *P. mariana* or *P. tremuloides*. *Pinus contorta* was occasionally present as a minor co-dominant with *P. mariana*; *Picea glauca* and *P. engelmannii* × *P. glauca* with *P. tremuloides*.

Selection of plots and vegetation data collection

One representative plot of 20 m × 20 m (0.04 ha), relatively uniform in topography, vegetation (floristic composition and structure) and soil conditions, was selected in each stand. Plots of this size have been extensively used for collecting floristic data in boreal forests of the study area, and were considered to represent the stand's floristic composition adequately. All vascular plant species in the canopy and understorey layers of each plot were identified, and their cover was estimated visually as ground percentage cover. Overstorey tree species seedlings and saplings were excluded from the species list before analysing the data.

The entire data set (231 plots) was used to achieve the first objective of this study, i.e. to investigate the extent and the pattern of variation in species composition and species density (i.e. number of species per plot of fixed size; Grace 1999) of *P. mariana* and *P. tremuloides* stands across climatic regions. We used 88 plots in the WMB region, 58 dominated by *P. tremuloides* and 30 by *P. mariana*, to achieve the second objective of this study, i.e. to test if relationships between each of species composition and species density and the environment differ between *P. mariana* and *P. tremuloides* dominated stands on edaphically similar sites within the same climatic region.

Recording of explanatory variables

We used 30 explanatory variables, stratified into five groups, R, T, M, H and C (Table 1). Canopy dominance (Dom; 1 = *P. mariana*, 0 = *P. tremuloides*) was added as group D. Among the regional variables (R), latitude and longitude were determined from topographic maps, and elevation was measured with an altimeter. Averages of five climatic variables for each 0.5° by 0.5° grid cell provided by the International Institute of Applied System Analysis (IIASA) climatic database (Leemans & Cramer 1991) were used as a basis for estimating five climatic variables for each study stand: mean annual temperature (MAT), mean temperature of the coldest month (MTCM), mean temperature of the

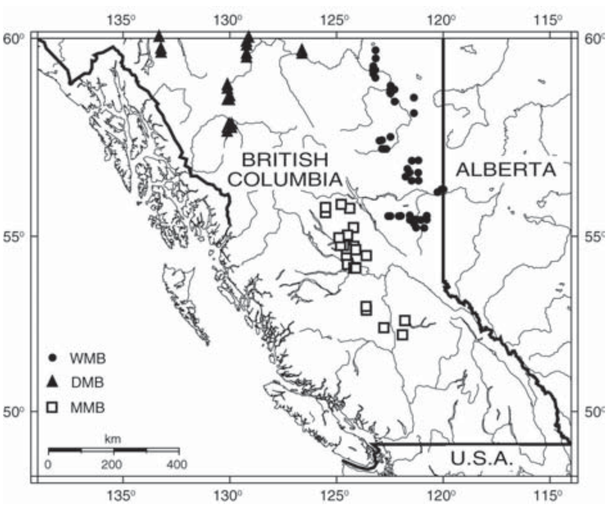

Fig. 1. Map showing the location of the 231 study stands of *Populus tremuloides* and *Picea mariana* in three climatic regions: drier montane boreal (DMB), wetter montane boreal (WMB), and mild montane boreal (MMB).

Table 1. Environmental explanatory variables for the 88-plot data set. Transformations are ln: $y = \ln(c+x)$; exp: $y = e^{(cx)} = \exp(cx)$]. For further details, see Text. Group variables with an independent contribution to total group variation ($P \leq 0.01$) included in the variation partitioning analysis have *, followed by a number denoting the selection order.

Variable name	Code	Group	Transformation Type	*c* value
Latitude	LAT	R*2	ln	– 54.912
Longitude	LON	R*3	exp	0.262
Elevation	ELEV	R*1	ln	590.7
Mean annual temperature	MAT	R	exp	0.178
Mean temp. coldest month	MTCM	R	exp	0.102
Mean temp. warmest month	MTWM	R	exp	0.440
Annual precipitation	MAP	R*5	exp	0.0078
Precipitation May – Sept.	MSP	R*4	exp	0.012
Soil moisture regime	SMR	T*2	none	
Topography type	Topotype	T	none	
Slope	Inclin	T*3	ln	0.523
Aspect favorability	AspFav	T	exp	0.00024
Heat index	HI	T*1	exp	0.891
Mineral soil pH	MpH	M*3	ln	– 3.441
Mineral soil total C	MtotC	M*4	ln	– 0.359
Mineral soil total N	MtotN	M	ln	– 0.027
Mineral soil C:N ratio	MC:Nrat	M	ln	0.094
Mineral soil mineralisable N	MminN	M	ln	– 0.434
Mineral soil extractable Ca	MCa	M*1	ln	138.46
Mineral soil extractable Mg	MMg	M*2	ln	– 5.084
Mineral soil extractable K	MK	M*5	ln	– 9.572
Humus form pH	HpH	H*1	exp	0.332
Humus form total C	HtotC	H	exp	0.089
Humus form total N	HtotN	H*4	exp	0.865
Humus form C:N ratio	HC:Nrat	H	ln	– 18.528
Humus form mineralizable N	HminN	H*2	ln	442.8
Humus form extractable Ca	HCa	H*5	exp	0.00007
Humus form extractable Mg	HMg	H	ln	528.1
Humus form extractable K	HK	H*3	exp	0.00012
Total canopy cover	Canopy	C*1	ln	– 7.962

warmest month (MTWM), mean annual precipitation (MAP), and mean summer (May to September) precipitation (MSP). The IIASA data were adjusted for elevation using data from local meteorological stations. Data from 158 stations were used to construct a linear model for the dependence of temperature on altitude and latitude ($R^2 = 0.71$, $F = 190$, $df = 2{,}155$, $P < 0.001$):

$$\text{MAT} = 47.03 - 0.0022 \text{ alt} - 0.79 \text{ lat} \quad (1)$$

Data from 387 stations were used to construct a linear model for precipitation as dependent on altitude and longitude ($R^2 = 0.34$, $F = 101$, $df = 2{,}384$, $P < 0.001$):

$$\text{MSP} = 2005 + 0.044 \text{ alt} - 14.29 \text{ long} \quad (2)$$

Amongst the topography-related variables (T) soil moisture regime was assessed in the field on a three-point ordinal scale (0 = moderately dry to slightly dry; 0.5 = fresh to moist; 1 = very moist) based on topographic properties (slope aspect, inclination and topographic position) (Klinka et al. 1989) and soil morphological properties (humus form, rooting depth, soil texture, coarse fragment content, soil aeration, soil mineralogy, and the presence and depth of growing season water table). Topographic type was assessed in the field on a five-point ordinal scale (0 = level; 0.25 = lower valley side; 0.5 = middle valley side; 0.75 = upper valley side; 1 = crest). Slope and aspect were measured in degrees for each plot. Aspect was recalculated to an index of aspect favourability according to T. Økland (1990), and given as deviation from 202.5° (the most favourable aspect) on a scale from 0 to 180. The heat index was calculated according to Parker (1988):

$$\text{Heat index} = \tan(\text{slope}) \times \cos(180° - \text{aspect favourability}) \quad (3)$$

Eight variables were measured for both mineral soil and humus. A soil pit was dug in each plot, and the humus form and soil were described and identified according to Green et al. (1993) and Anon. (1998), respectively. Composite samples of each of humus and mineral soil (from beneath the H horizon to a depth of 30 cm), were taken from each soil pit for chemical analyses. Samples were air-dried to constant mass. Mineral soil samples were passed through a 2-mm sieve, and humus samples were ground with a Wiley mill and then passed through a 2-mm sieve. Samples were analysed for basic nutrient properties according to Lavkulich (1981). Soil pH was measured with a pH meter in a 1 : 1 water suspension for mineral soil and a 1 : 5 suspension for humus. Total carbon was determined by loss on ignition at 500 ºC (induction furnace) using a LECO carbon analyzer. Total N was analysed using a Technicon Autoanalyzer (Technicon Corp., Tarrytown, NY) following micro-Kjehldal digestion. Mineralizable N was calculated by anaerobic incubation at 30 °C for 14 days (Powers 1980), and released NH_4^+ was measured colorimetrically with a Technicon Autoanalyzer. Extractable Ca, Mg, and K were quantified by extraction with Morgan's sodium acetate solution at pH 4.8 and absorption spectrophotometry with an acetylene flame.

The last variable is Canopy cover, estimated in %.

Statistical analyses

Species density (recorded separately for woody and herbaceous species as well as pooled for all vascular plant species) was tested in the 231 plots for differences between canopy dominance types (by *P. mariana* or *P. tremuloides*) and among different climatic regions by two-way analysis of variance (ANOVA). Two-sided *t*-tests were used for pairwise comparisons between canopy dominance types within each region.

Prior to analyses of the 88 plots, the cover of all vascular plant species (0.1% - 100%) was weighted to an abundance scale ranging from 1 to 8 using the equation

$$y_{ij} = 2 \cdot x_{ij}^{0.3} \quad (4)$$

where x_{ij} is the original and y_{ij} is the resulting weighted abundance of species *i* in plot *j* (van der Maarel 1979; R. Økland 1990).

All explanatory variables were transformed to zero skewness according to Økland et al. (2001) in order to allow the use of standard parametric statistical methods with the implicit assumption that all observations are drawn from the same distribution and have the same mean and homogeneous variances (homoscedasticity; Sokal & Rohlf 1995). Standardized skewness – skewness divided by $(6/n)^{0.5}$; Sokal & Rohlf (1995) – was first calculated for all variables. Two transformation formulae were used:

$$\text{exp transformation: } t_{kj}' = e^{c_k z_{kj}} = \exp(c_k z_{kj}) \quad (5)$$

$$\text{ln transformation: } t_{kj}' = \ln(c_k + z_{kj}); \quad (6)$$

where z_{kj} is the original value of variable k in plot j and c_k is a parameter determined for each variable so that the transformed variable $T' = \{t_{kj}'\}$ had zero skewness. Equation (5) was applied to left-skewed variables (standardized skewness < 0); equation (6) to right-skewed variables. After transformation, all T' were ranged to obtain new variables $T = \{t_{kj}\}$ expressed on a 0-1 scale:

$$t_{kj} = [t_{kj}' - \min(t_{kj}')] / [\max(t_{kj}) - \min(t_{kj})] \quad (7)$$

Environmental differences between dominance types

All 30 explanatory variables (Table 1) were tested for differences between canopy dominance types by separate one-way ANOVAs. The hypothesis that the frequency distribution of plots within humus types was similar in the two canopy dominance types was tested against the two-tailed alternative hypothesis by the χ^2-test (see Sokal & Rohlf 1995).

Ordination

Ordination methods were used to find and quantify the main vegetation gradients. Representatives for the two main families of ordination methods were used in parallel, as recommended by R. Økland (1990, 1996), since ordination methods may occasionally distort the true gradient structure in a data set (Minchin 1987; R. Økland 1990). Detrended correspondence analysis (DCA; Hill & Gauch 1980), representing the first family of ordination methods, was used to find gradients in species composition (ordination axes) as hypothetical environmental variables which best fit species' abundances to an explicit model of species' responses to environmental gradients. Global non-metric multidimensional scaling (NMDS; cf. Minchin 1987), representing the second main family of ordination methods and being a geometrical method, was used to configure plots in an ordination space with a fixed number of dimensions and to optimize the rank-order correspondence between sample-plot distances in the ordination diagram and between-plot floristic dissimilarities. DCA was run using CANOCO Version 4.0 (ter Braak & Šmilauer 1998) with standard options for detrending by segments, non-linear rescaling of axes, and no down-weighting of rare species. NMDS was run using PC-ORD version 4.17 (McCune & Mefford 1999) using the quantitative form of the Sørensen index as a measure of between-plot dissimilarity. A two-dimensional solution was obtained with a maximum of 200 iterations and 30 runs with randomized data.

Axes of the NMDS and DCA ordinations were compared by calculating pairwise Kendall rank correlation coefficients (τ; Sokal & Rohlf 1995). Strong correlations were interpreted as favouring the main data gradient structure (R. Økland 1996). Where the two methods produced congruent axes, ecological interpretation using Kendall's τ between plot scores and explanatory variables was restricted to DCA (see R. Økland 1990, 1996).

Differences in species density

Species density was ln-transformed to zero skewness using Eq. 6 and was tested for differences between canopy dominance types in the 88-plot data set by one-way ANOVA. In case of differences significant at the $P \leq 0.05$ level, the degree to which species differed among climatically and edaphically similar sites within the two stand types was tested by ANCOVA (Sokal & Rohlf 1995) with species density as the dependent variable, the first two DCA ordination axes as covariates and the SB variable as factor.

Variation partitioning

Partial canonical correspondence analysis (CCA; ter Braak 1986) was used to partition the variation in species composition on several groups of environmental variables (Økland 1999). Variation, expressed in arbitrary 'inertia units' (IU), is additive and can be distributed on several groups of variables analogous to sums of squares. We used R. Økland's (unpublished) s-group generalization of the two-group approach of Borcard et al. (1992) and Økland & Eilertsen (1994). The analysis was set up with $s = 6$ to highlight the relationship between variation due to canopy dominance and variation due to other factors (Table 1). We initially tested the variables in each group for independent, significant contributions explaining the variation in species abundance. The forward selection procedure in CANOCO, which invokes a distribution-free Monte Carlo simulation test (ter Braak 1990) to assess the significance of each variable in the regression model, was used with 9999 permutations. Only variables that had a significant independent contribution ($P = 0.01$) were included in further analyses.

In the two-group case – notation follows Økland & Eilertsen (1994) – the total variation attributable to the joint group $A + B$, $A \cup B$, is the sum of eigenvalues for the $n_A + n_B$ constrained axes in a hybrid CCA with $A + B$ as constraining variables (n_A and n_B are the number of significant variables in A and B, respectively). The variation explained by A, not shared by B, $A \mid B$, is found by partial CCA, using B as covariables and A as constraining variables. The significance of variation $A \cup B$ and $A \mid B$, can be tested by the Monte Carlo test. Shared variation, e.g. between A and B, $A \cap B$, is found as:

$$A \cap B = A - A \mid B = B - B \mid A = A \cup B - A|B - B \mid A \quad (8)$$

Generalization of this process to s groups of variables $A_1, A_2, \dots A_s$ is possible because the equation of the total variation explained (TVE) = $A_1 \cup A_2 \cup \dots \cup A_s$ can be distributed on $2^s - 1$ (here: 63) unique, non-overlapping partial intersections among the s groups of variables, $P \mid Q$, where $P = A_{p1} \cap A_{p2} \cap \dots \cap A_{pi}$ and $Q = A_{q1} \cup A_{q2} \cup \dots \cup A_{q(s-i)}$. Q comprises all groups not included in P; i is the order of the partial intersection. The variation attributable to each partial intersection can be found recursively from the variations explained by the 2^s–1 partial unions $R \mid Q$, where $R = A_{p1} \cup A_{p2} \cup \dots \cup A_{pi}$; $R \mid Q$ can be determined directly by partial constrained ordination.

The partitioning results were simplified by distributing low and insignificant amounts of variation on intersections of successively lower order by a stepwise procedure. First, we selected the average variation explained by the 63 unique partial intersections, TVE/(2^n–1) = 2.125/63 = 0.0337 IU, as a threshold limit. Next, starting with the partial intersections $P_i \mid Q$ of the highest order ($i = 6$), we distributed the variation of all intersections that explained ≤ 33 IU on all intersections of order ($i - 1$), that only contained variable groups also included in P_i. We continued the process until only partial intersections with explained variation above the threshold remained. Partial intersections were emphasized that explained ≥ 0.075 IU, corresponding to $P \leq 0.01$ from Monte Carlo tests of partial unions (9999 permutations).

Results

The 231-plot data set

Excluding seedlings and saplings of canopy tree species, 211 species of vascular plants were found in the understorey of the 231 plots. The 113 plots dominated by *P. tremuloides* had 168 species, 54 of which were absent from *P. mariana* plots; the 118 *P. mariana* plots had 157 species, 43 of which were absent from *P. tremuloides* plots. Most species common in *P. mariana* plots were also common in *P. tremuloides* plots (Table 2).

Table 2. Frequency (% of plots in which a given species is present) of common species (frequency > 30%; in bold) in plots of the 231-plot data set dominated by *Picea mariana* (n = 118) and/or *Populus tremuloides* (n = 113). Data are pooled over three climatic regions in British Columbia.

Species	Canopy dominant species *Picea mariana*	*Populus tremuloides*
Aster conspicuus	9	**39**
Calamagrostis canadensis	17	**39**
Cornus canadensis	**79**	**74**
Epilobium angustifolium	**45**	**72**
Fragaria virginiana	21	**45**
Galium boreale	23	**47**
Geocaulon lividum	26	**36**
Lathyrus ochroleucus	7	**52**
Ledum groenlandicum	**53**	**39**
Leymus innovatus	12	**35**
Linnaea borealis	**64**	**76**
Lonicera involucrata	**31**	**31**
Maianthemum canadense	3	**36**
Mertensia paniculata	**36**	**40**
Mitella nuda	**33**	19
Orthilia secunda	**36**	**41**
Petasites frigidus	**53**	**55**
Pyrola asarifolia	9	**36**
Rosa acicularis	**67**	**79**
Rubus pubescens	25	**44**
Shepherdia canadensis	29	**53**
Spiraea betulifolia	9	**35**
Vaccinium vitis-idaea	**58**	**42**
Viburnum edule	**39**	**58**

In all three climatic regions species density was, on average, higher in *P. tremuloides* plots than in *P. mariana* plots (Table 3). The difference in species density between the two stand types tended to increase with latitude. Under *P. tremuloides*, the understorey contained 1.1 × as many vascular plant species as under *P. mariana* in the MMB region ($P \geq 0.05$), while the corresponding ratios were 1.4 and 1.5 in DMB and WMB, respectively ($P \leq 0.05$ for all species groups except woody plants in DMB).

Table 3. Mean and standard deviation (in parentheses) for species density (number of species per plot) by canopy dominant and climatic region in the 231-plot data set. Means with the same superscripts within the same row are not significantly different at the $P \leq 0.05$ level (t-test).

Climatic region	*P. mariana*	*P. tremuloides*
Drier montane boreal (DMB)		
Number of plots	24	28
Vascular plants	12.2^a (4.2)	16.7^b (2.7)
Woody plants	4.8^a (2.0)	4.8^a (1.5)
Herbaceous plants	7.4^a (3.2)	11.9^b (2.3)
Wetter montane boreal (WMB)		
Number of plots	67	60
Vascular plants	13.6^a (7.2)	20.3^b (4.4)
Woody plants	4.9^a (2.1)	6.6^b (1.9)
Herbaceous plants	8.7^a (5.9)	13.7^b (3.7)
Mild montane boreal (MMB)		
Number of plots	27	25
Vascular plants	22.1^a (6.8)	25.2^a (5.4)
Woody plants	6.5^a (2.2)	7.4^a (2.5)
Herbaceous plants	15.6^a (5.7)	17.8^a (3.8)

Table 4. Two-way ANOVA for species density (number of species per plot) by canopy dominant and climatic region in the 231-plot data set. *SS* = sum of squares; *MS* = mean square.

Source	*df*	*SS*	*MS*	*F*	*P*
Vascular plant density					
Canopy dominance type	1	1564.4	1564.4	49.91	< 0.001
Climatic region	2	2396.1	1198.0	38.22	< 0.001
Canopy dom. type × Climatic region	2	224.1	112.0	3.57	0.030
Error	225	7052.3	31.3		
Woody plant density					
Canopy dominance type	1	65.3	65.3	15.47	< 0.001
Climatic region	2	126.2	63.1	14.93	< 0.001
Canopy dom. type × Climatic region	2	33.3	16.7	3.94	0.021
Error	225	950.5	4.2		
Herbaceous plant density					
Canopy dominance type	1	990.3	990.3	47.25	< 0.001
Climatic region	2	1462.0	731.0	34.88	< 0.001
Canopy dom. type × Climatic region	2	121.5	60.7	2.90	0.057
Error	225	4715.9	21.0		

Canopy dominance type and climatic region had significant effects ($P < 0.001$) on species density, both of woody and herbaceous plants (Table 4). The interaction of canopy dominance type and climatic region was not or weakly significant ($0.021 < P < 0.057$; Table 4).

The 88-plot data set

Environmental differences between dominance types

Plots dominated by *P. tremuloides* differed significantly ($P \leq 0.001$) from *P. mariana* plots in 13 out of the 30 explanatory variables (App. 1). *P. tremuloides* plots occurred at lower elevations where temperatures were higher, and had more open canopies than *P. mariana* plots. The most striking differences were found in humus forms and their chemistry. For example, *P. tremuloides* plots had much higher pH, total N, mineralizable N, and extractable Ca, K and Mg than *P. mariana* plots. For mineral soils these properties were less different between the two canopy dominance types: only two out of eight variables were significantly different at the $P < 0.001$ level (App. 1). The canopy dominance types differed in humus form frequencies. The humus form profile of *P. tremuloides* plots was 25.9, 12.1, 1.7, 58.6, and 1.7 %, while the profile of *P. mariana* plots was 23.3, 6.7, 23.3, 23.3, and 23.3 % for Hemimors, Humimors, Mormoders, Leptomoders, and Mullmoders, respectively ($\chi^2 = 26.21$, $df = 4$, $P \leq 0.0001$).

Ordination

The eigenvalues of the first two DCA ordination axes were 0.498 and 0.347, respectively. Eigenvalues dropped considerably from axis 2 to axes 3 (0.203) and 4 (0.129), suggesting that the 88-plot data set contained two major compositional gradients. This was in agreement with the recommendation of a two-dimensional NMDS solution. The reliability of the main gradient structure identified by DCA and NMDS was confirmed by high pair-wise rank correlations between the first two axes of the DCA and NMDS ordinations (DCA1 and NMDS2: $\tau = -0.84$, $P < 0.0001$; DCA2 and NMDS1: $\tau = 0.54$, $P < 0.0001$). Both methods almost completely separated plots dominated by *P. tremuloides* from those dominated by *P. mariana* (Fig. 2); by DCA along the first as well as the second axes, by NMDS along the second axis (DCA axis 1: one-way ANOVA for canopy dominance type: $F_{1,86} = 94.083$, $P < 0.001$; DCA axis 2: one-way ANOVA for canopy dominance type: $F_{1,86} = 27.628$, $P < 0.001$). The DCA ordination was chosen for further interpretation of vegetation-environment relationships.

DCA axis 1 was significantly correlated with 16 out of the 30 explanatory variables at the $P < 0.001$ level (App. 1). Its strong correlations with pH ($\tau = -0.712$) and humus form nutrient status (e.g. calcium concentration, $\tau = -0.682$) led to the conclusion that the pattern of variation in species composition was associated primarily with variation in humus form properties. The axis was also moderately strongly correlated with mineral soil properties and elevation (App. 1). Thus, DCA axis 1 reflected compositional variation from lower-elevation sites with higher humus-layer pH and nutrient content to higher-elevation sites with lower pH and nutrient status.

DCA axis 2 was significantly correlated with nine explanatory variables ($P < 0.001$; App. 1), most strongly with canopy cover ($\tau = 0.475$) and the soil moisture index ($\tau = 0.473$). Mineral soil magnesium and nitrogen content and temperatures also varied along this gradient but less strongly (App. 1). This axis thus reflected variation in species composition from dry to moist sites and from open- to closed-canopy stands. Except for the Humimor group, which occurred in plots with relatively high DCA axis 1 scores within both stand types, all humus form types were well spread along DCA axis 1 (Fig. 2b) while no clear trend was observed along DCA axis 2.

Species density

Species density differed significantly between plots dominated by *P. tremuloides* and those by *P. mariana* (Table 5), in agreement with the results obtained for all 127 plots in the WMB region (Table 3). The mean ± 1 S.D. of the number of species was 6.6 ± 2.0 and 5.6 ± 1.9 for woody species in *P. tremuloides* and *P. mariana* stands, respectively, and 13.7 ± 3.7 and 10.2 ± 6.3 for herbaceous species, adding up to a highly significant difference in total vascular plant density between canopy dominance types (Table 5).

Total vascular plant density was significantly correlated with scores along the first DCA axis ($\tau = -0.485$, $P < 0.001$), indicating the existence of a significant relationship between species density and compositional variation. DCA axis 1 was not significantly correlated with woody species density ($\tau = -0.134$, $P = 0.082$), but was significantly correlated with herbaceous species density ($\tau = -0.493$, $P < 0.001$). No significant relationships between DCA axis 2 and species density were found (all $|\tau| < 0.1$, $P > 0.2$).

ANCOVA showed that the difference in herbaceous species density (and total vascular plant density) between stand types could mainly be explained by position along DCA axis 1, the main compositional gradient (Table 5). This difference was fully accounted for by positions along the two main compositional gradients. A weakly significant difference in woody species density between dominance types remained even after variation along gradients was removed (ANCOVA; Table 5).

Variation partitioning

All groups of explanatory variables contained at least one variable that independently explained a significant amount of variation in species composition ($P < 0.001$; Table 1). After simplification of results, ten intersections, including all five first-order intersections, explained significant amounts of variation ($P < 0.01$; Fig. 3).

The variation explained by tree-layer cover was mostly unshared with other variable groups. Some variation explained by topography was also explained by soil variables, but most of the variation in species composition explained by topography was not explained by any other group. A high proportion of the variation in species composition was uniquely explained by regional variables (15.6% of TVE) while 7.1% of TVE was explained jointly by the regional, mineral soil, humus form, and the canopy dominance variable groups (Fig. 3). This indicated that regional factors, e.g. those related to temperature, are important in explaining variation in understorey vegetation, notably through their effects on soil factors. The variation explained by humus form and mineral soil variables not shared with other variable groups was 6.2% of TVE. The large proportion of variation explained jointly by canopy dominance type and the regional, humus form, and mineral soil variable groups compared to the variation explained uniquely by dominance type indicated that canopy dominance (by either species) has a small direct effect on the understorey species composition while its indirect effect, through complex interactions with soil factors as influenced by regional factors, is comparatively larger.

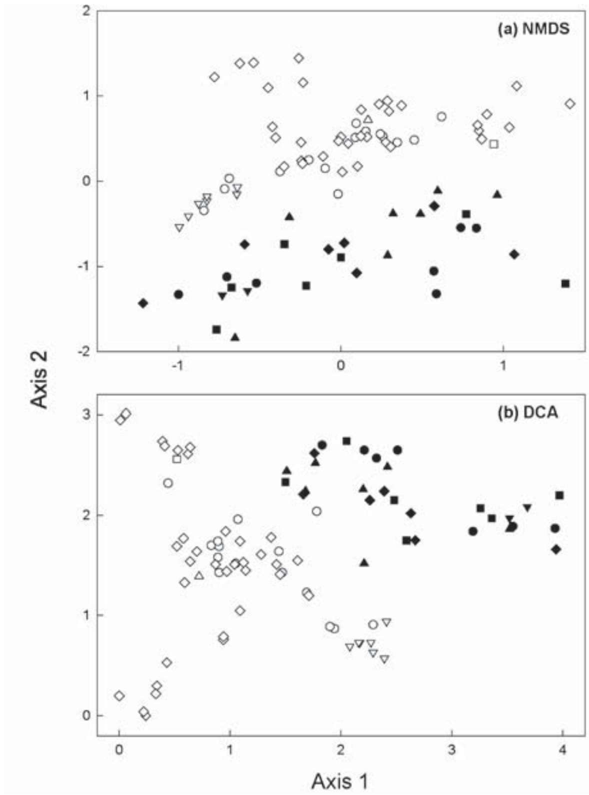

Fig. 2. Non-metric multidimensional scaling and Detrended Correspondence Analysis of the 88-plot data set with canopy dominance type; white = *Populus tremuloides*; black = *Picea mariana*; and humus form type plotted onto ordination spaces. Humus form types: ○, ● = Hemimor; ▽, ▼ = Humimor, ◇, ◆= Leptomoder; △, ▲ = Mormoder; □, ■ = Mullmoder.

Table 5. One-way ANOVA for zero-skewness transformed species density variables in the 88-plot data set, with respect to canopy dominance type (Can. dom.) followed by ANCOVA with DCA axes 1 and 2 plot scores as covariates. *SS* = sum of squares; *MS* = mean square; MS_{iv} = *MS* explained by independent variables; MS_{dr} = *MS* within dominance types (ANOVA; *df* = 86) or *MS* of residuals (ANCOVA; *df* = 84). Significant differences ($P \leq 0.001$) are in bold face

Analysis	Variables		ANOVA/ANCOVA				
	Dependent	Independent	Total SS	MS_{iv}	MS_{dr}	*F*	*P*
ANOVA	Vascular	Can. dom.	3.740	0.546	0.037	**14.688**	**< 0.001**
ANOVA	Woody	Can. dom.	4.637	0.287	0.051	5.672	0.019
ANOVA	Herbs	Can. dom.	3.504	0.409	0.036	11.378	0.001
ANCOVA	Vascular	DCA 1	3.740	0.731	0.023	**31.919**	**< 0.001**
		DCA 2		0.142		6.217	0.145
		Can. dom.		0.000		0.001	0.973
ANCOVA	Woody	DCA 1	4.637	0.021	0.051	0.418	0.526
		DCA 2		0.101		1.996	0.161
		Can. dom.		0.251		5.045	0.027
ANCOVA	Herbs	DCA 1	3.504	0.996	0.019	**52.506**	**< 0.001**
		DCA 2		0.092		4.917	0.030
		Can. dom.		0.028		1.471	0.229

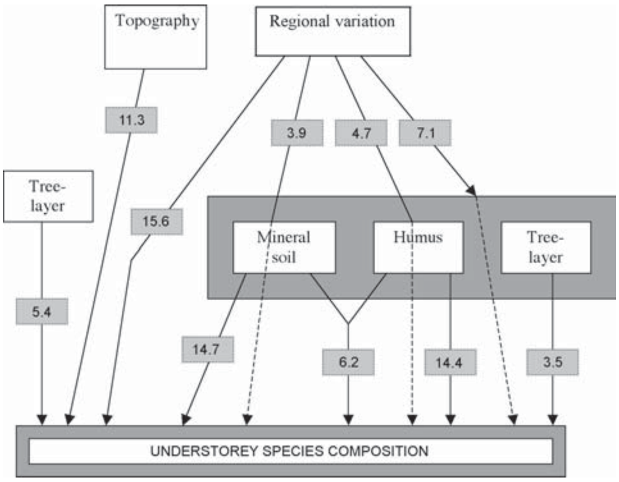

Fig. 3. Simplified path diagram for the partitioning of variation in species composition on six groups of explanatory variables. Only paths corresponding to partial intersections with amounts of variation (% of TVE, the total variation explained by all six groups) significant at $P < 0.01$ (after simplification) are shown.

Discussion

We demonstrated higher species density, particularly of herbaceous plants, in *Populus tremuloides* stands than in *Picea mariana* stands across all three climatic regions. This result contrasts with that of Légaré et al. (2001) who reported that understorey species density in boreal forests in eastern Canada does not vary significantly with canopy dominants, even under similar edaphic conditions: *P. tremuloides* stands have lower vascular plant species density than evergreen conifer stands (21.2 ± 5.45 species in *P. tremuloides* plots, 21.6 ± 4.13 in 100-m^2 plots dominated by *Picea glauca* and/or *Abies balsamea*, as compared to 24.4 ± 2.67 in *Pinus banksiana* plots. These differences may result from spatial scale differences: we recorded non-overstorey species in 400 1-m^2 plots, while Légaré et al. (2001) recorded all species, including overstorey tree species recruits, in ten 1-m^2 subplots in 100-m^2 plots. The differences may also be attributable to ecological differences between eastern and western North American stands with canopy dominants of comparable life strategies.

Ewald (2000), comparing stands dominated by *Fagus sylvatica* and *Picea abies* in Germany, also found that understorey species richness did not differ between canopy dominants. If, however, attention is restricted to vascular plants (excluding bryophyte species, which occur in significantly higher numbers in *P. abies* than in *F. sylvatica* stands), understorey species richness is higher in the deciduous broad-leaved than in the evergreen coniferous stands studied by Ewald (2000), in agreement with the results of our study.

Species density (richness) depends on the species involved as well as on ecological characteristics of the studied system. This may explain the apparently inconsistent relationship between species density in broad-leaved deciduous and evergreen conifer forests among regions, which differ in species composition. We find consistent differences in understorey composition between *P. mariana* and *P. tremuloides* stands within one region as well as across different climatic regions. Such a pattern may, however, result from a variety of scenarios in which the canopy dominant plays fundamentally different roles. In our first scenario, canopy dominance *results from* among-site differences in fundamental factors not affected by ecosystem processes, the so-called primary environmental factors (Dahl et al. 1967), as exemplified by topography, topographic soil moisture, climate, and the fundamental chemical and physical properties of the mineral soil. In this scenario, canopy dominance has no direct, modifying effect on the understorey species composition (and/or density). Our second scenario differs from the first in a strong role of secondary, ecosystem-dependent, processes (such as properties of the humus layer), in addition to the primary, in determination of canopy dominance while it agrees with scenario one in the lack of an independent effect of the canopy dominant. These two scenarios predict similar understorey species composition (and species density) of ecologically similar sites. Differences in the understorey species composition of *P. tremuloides* and *P. mariana* stands (88-plot data set) are related to differentiation along main environmental gradients. This study demonstrates strong environmental control over canopy dominance and understorey species composition. Forests dominated by *P. tremuloides* are generally less acid and richer in nutrients and occur at lower elevations than forests dominated by *P. mariana*, resulting in differentiation along the main compositional gradient (DCA axis 1). Similar differences in humus properties were found by Légaré et al. (2001). Furthermore, *P. mariana* forests generally occur on more strongly sloping sites with less unfavourable aspects and moister soils than those dominated by *P. tremuloides*, resulting in segregation along DCA axis 2.

Analyses by the variation partitioning approach demonstrate strong roles both of primary factors and secondary factors such as humus-layer properties, thus favouring the second over the first scenario. Our results are, however, not in complete accordance with predictions from scenario two: 1. The two dominance types overlap considerably along environmental gradients. 2. Canopy cover is strongly correlated with DCA axis 2 and explains a significant independent amount of variation in understorey species composition. 3. The partitioning of variation in species composition shows that stands with different canopy dominants in similar environmental conditions differ slightly but significantly in species composition, in agreement with the results of several previous studies (e.g. Host & Pregitzer 1992; Gilliam et al. 1995; Sagers & Lyon 1997; Légaré et al. 2001). These results call for a scenario in which differences in canopy dominance is both a result of environmental differentiation and a factor that plays a role independent of, and in addition to, the measured environmental factors. This role is both a direct physiological effect on the understorey and an indirect effect as a modifier of factors that directly affects species in the understorey.

Dominant canopy trees directly affect the understorey vegetation by litter shed and by modifying the microclimate near the ground, and indirectly via effects on humus-layer attributes such as humus form and nutrient concentrations. Stands dominated by *P. tremuloides* generally have a more open canopy than stands dominated by *P. mariana*. The effect of differences in canopy cover among dominance types is accentuated by the warmer and less humid understorey microclimate of *P. tremuloides* than of *P. mariana* dominated stands in the same climatic region since abundant solar radiation is transmitted to the understorey in spring and autumn when *P. tremuloides* is leafless (Shepperd & Jones 1985; Constabel & Lieffers 1996). *P. tremuloides* canopies also transmit more light than *P. mariana* canopies, especially in early and late stand development stages (Ross et al. 1986; Lieffers & Stadt 1994; Constabel & Lieffers 1996). A *P. tremuloides* stand with a leafless canopy provides for a greater snow accumulation and higher soil temperature than does a *P. mariana* stand. Indirect effects via the humus layer, demonstrated by variation partitioning to have a strong independent impact on understory species composition, are accentuated by differences in chemical composition and/or decomposition rates of broad-leaved and coniferous litter fall which may result in different soil biological processes and, hence, soil physical and/or chemical properties. In the boreal forest, litter decomposition and nutrient cycling in conifer-dominated stands is slow because of low soil temperature, high C:N ratio, or inhibitory effects of conifer litter on microbial activity (Prescott et al. 1989; Paré et al. 1993). *P. tremuloides* has a greater ability than its coniferous associates for soil nutrient uptake and to return nutrients in litter fall and root sloughage (Troth et al. 1976; Peterson & Peterson 1992; Paré et al. 1993). Rapidly growing *P. tremuloides* takes up large quantities of nutrients and stores them in woody tissue, particularly bole bark and bole wood (Pastor 1990). *P. tremuloides* functions as an efficient nutrient pump (Corns 1989), partly because *P. tremuloides* leaves have more nutrients than conifer needles (Stoeckeler 1961; Troth et al. 1976).

The difference between canopy dominance types in vascular plant species density can be explained by the plot positions along the main compositional gradients extracted by multivariate analyses, notably the higher level of nutrients in the humus layer of the *P. tremuloides*-dominated forest. Humus form is considered an essential component in determining ecological site quality because of its role in nutrient storage and cycling, and in influencing temperature and moisture conditions of soils (Sukachev & Dylis 1964). Since many understorey vascular plant species in boreal forests, particularly herbs, generally root in the humus layer (Ewald 2000), the characteristics of this layer in boreal forest co-determine understorey species composition and species density. Strong relationships between vascular plant species density and acidity and nutrient availability in the humus layer were demonstrated for European (Økland & Eilertsen 1993, 1996; T. Økland 1996) as well as North American boreal forests (Qian et al. 1997). More fine-grained variation in humus form may also contribute to higher species density in 400-m^2 plots in stands dominated by *P. tremuloides*. We find strong variation in humus form on ecologically similar sites. Although one type of humus form often dominates in a plant community, several major humus form types (e.g. Mor and Moder) may develop in a fine-grained pattern within one stand (Klinka et al. 1990; Qian & Klinka 1995). The *P. tremuloides* stands are often more diverse in humus form than the *P. mariana* stands.

The results of variance partitioning show that a small but significant amount of variation in species composition is exclusively attributable to canopy dominants, and that this variation is independent of the effect of canopy cover and also differs between stands dominated by *P. tremuloides* and those by *P. mariana*. In our study, this unique component of variation related to canopy dominants is proportionally lower than in the study by Légaré et al. (2001). One reason for this difference may be the extensive set of environmental variables used in our study. The more extensive this set is, the lower is the variation conceived as unexplained but that is actually due to unmeasured environmental factors (Økland & Eilertsen 1994), and the lower is the variation conceived as exclusively due to canopy dominants but that is actually shared with unmeasured environmental factors. We have discussed mechanisms related to the effect of canopy cover on the understorey vegetation, potentially involved in a *direct* effect of canopy dominants on understorey species composition of ecologically similar sites. We do, however, also observe a significant independent effect of the canopy dominant on understorey species composition. The mechanism for this is not clear. One can never rule out the possibility that yet unmeasured environmental variables may account for some of the variation conceived as exclusively due to canopy dominance, the occurrence of significant amounts of variation in species composition unshared with other groups of environmental variables is thus no proof for additional direct effects. However, the extensive set of variables recorded for each plot in our study reduces the probability for existence of unmeasured important factors.

Several biological mechanisms for a direct effect of canopy dominant on understorey species composition have been proposed. Ewald (2000) attributes the lower bryophyte richness in *Fagus sylvatica*-dominated stands than in *Picea abies*-dominated stands to the negative effects of deciduous litter on bryophyte survival (also see During & Verschuren 1988; R. Økland 1995). Similar effects have also been reported for vascular plants (Sydes & Grime 1981; T. Økland 1988), but are probably not applicable to rapidly decaying *P. tremuloides* litter.

There is no general agreement on how canopy dominants affect understorey vegetation. For example, Légaré et al. (2001) concluded that the canopy also exerts a certain control over the availability of nutrients in the soil and its pH. On the other hand, Ewald (2000) concluded that most of the variation in understorey species composition reflects site conditions irrespective of the present-day stand composition. Our results and interpretation fall in-between these two studies, pointing at a fundamental environmental control over canopy dominance and also opens for small but significant direct and indirect effects of the canopy dominant on understorey vegetation. Of additional importance for understanding relations between canopy dominance and understorey species composition are the dynamics of the tree layer, i.e. if canopy dominants alternate between generations or are stable over hundreds or thousands of years. In the latter case, the influence of the canopy dominants on local environmental conditions, notably humus layer chemical properties, are likely to become accentuated with time to the extent that significantly different understorey species compositions may be found under different canopy dominants. The history of the studied stands prior establishment of the present canopy dominants is not known and, accordingly, time scales in which differences between canopy dominants have arisen are unknown. However, the chronosequences studied by Paré et al. (1993) and Brais et al. (1995) suggest that less than one tree generation may be sufficient to bring a significant difference to humus layer chemistry and humus type. The rise of such differences may, however, be context-dependent as no significant differences in these respects are demonstrated by Ewald (2000) between sites dominated by *Fagus sylvatica* and *Picea abies*. Further studies that invoke long time scales are needed in order to assess if unique, direct effects of the dominant trees on the understorey generally occur.

The large relative amounts of variation in species composition explained jointly by canopy dominants, regional factors and soil variables were likely due to the influence of fundamental environmental factors on both understorey species composition and tree dominance. It may, however, also result from a long-term mutual interactive effect between the canopy dominants and important environmental factors, such as humus layer properties, soil moisture conditions, incident light that is influenced by the life form of the canopy trees (deciduous broad-leaved versus evergreen needle-leaved), and canopy cover (Mahendrappa & Kingston 1982; Beier et al. 1993; Koch & Matzner 1993; Messier et al. 1998). We suggest that both of these explanations are applicable to the observed patterns in our study. A considerable amount of variation in species composition explained jointly by regional variables as well as mineral soil and humus form properties, and canopy dominants suggested a fundamental effect of environmental factors. However, considerable differences found in humus form type and humus form properties but not in mineral soil properties between *P. mariana* and *P. tremuloides* stands may indicate that the environmental differences are accentuated by the influence of the canopy dominants. This influence is likely due to the more favourable chemical composition and/or rates of decomposition of broad-leaved deciduous versus evergreen coniferous litter, which influences the rates of soil biological processes (Sætre 1998, 1999), physical soil properties such as texture, humus form and moisture retention capacity (Green et al. 1993), and the acidity status and availability of essential elements from soils (e.g. Paré et al. 1993; Brais et al. 1995; Sætre et al. 1997; Ewald 2000; Légaré et al. 2001).

We conclude that differences in primary environmental factors and humus form properties, the latter accentuated by the canopy dominants themselves, are the most important causes of higher species density in *Populus tremuloides* stands than in *Picea mariana* stands, as well as differences in species composition among the two canopy dominance types. Furthermore, we demonstrate small but significant direct and indirect effects of the canopy dominant on understorey species composition. Further studies are required to understand the processes responsible for, and the time scales involved in, the differentiation of understorey species composition under different canopy dominants in boreal forests.

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