Comparison of the understory vegetation in boreal forest types of southwest Quebec

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Abstract: Variation in canopy composition can influence ecosystem processes, such as nutrient cycling and light transmittance, even when environmental soil conditions are similar. To determine whether forest cover type influences species composition of the understory vegetation (herbs and shrubs), the composition of this layer was studied on two different surface deposits, clay and till, and under four different forest cover types dominated, respectively, by *Populus tremuloïdes* Michx. (aspen), *Betula papyrifera* Marsh. (white birch), *Pinus banksiana* Lamb. (jack pine), and *Picea glauca* (Moench) Voss – *Abies balsamea* (L.) Mill. (spruce–fir) over similar environmental conditions. Detrended correspondence analysis and analysis of variance performed on the ordination scores revealed that understory plant composition was highly affected by surface deposit and forest cover. The gradient observed in the correspondence analysis proceeds from aspen, white birch, spruce–fir, to jack pine. Indicator species were identified for each surface deposit and cover type, and most of them were associated with either jack pine or aspen. The richness, evenness, and diversity of the understory vegetation did not vary between cover types, but were affected by surface deposit. By controlling ecosystem processes such as light transmittance and nutrient cycling, forest cover influences understory composition.

Key words: cover, understory, composition, boreal forest, environmental condition.

Résumé : La composition du peuplement peut affecter les processus écosystémiques, tels que le cycle des éléments nutritifs et la transmission lumineuse, malgré la présence de conditions environnementales similaires. Afin de vérifier si le couvert arborescent influence la composition de la strate de sous-bois, des relevés de la végétation herbacée et arbustive ont été effectués dans des conditions environnementales détendancées similaires, incluant deux dépôts de surface différents, till et argile, et quatre couverts forestiers dominés respectivement par les *Populus tremuloïdes* Michx. (peuplier faux-tremble), *Betula papyrifera* Marsh. (bouleau blanc), *Pinus banksiana* Lamb. (pin gris) et *Picea glauca* (Moench) Voss et *Abies balsamea* (L.) Mill. (épinette–sapin). L'analyse des correspondances détendancées et l'analyse de variance effectuées sur les coordonnées des axes de l'ordination révèlent un effet du dépôt de surface et du couvert arborescent. Le gradient observé en analyse des correspondances va du peuplier faux-tremble, bouleau blanc, mélange de conifères, au pin gris. Des espèces indicatrices ont été identifiées pour chacun des dépôts de surface et couverts forestiers, et la majorité d'entre-elles étaient associées soit au pin gris soit au peuplier faux-tremble. La richesse, l'équitabilité et la diversité de la strate de sous-bois ne varient pas en fonction du couvert forestier, mais sont significativement affectées par le dépôt de surface. Les différents processus écosystémiques, tels que la transmission de la lumière et le cycle des éléments nutritifs, semblent expliquer l'influence du couvert forestier sur la composition de la strate de sous-bois.

Mots clés : couvert, sous-bois, composition, forêt boréale, condition environnementale.

Introduction

The mixed boreal forest of eastern Canada is an ecosystem in which ecological processes are controlled by disturbances, such as fire (Rowe 1961; Heinselman 1981; Bergeron 1991) and spruce budworm (*Choristoneura fumiferana*) outbreaks (Bergeron et al. 1995). These disturbances create a mosaic-like pattern in the forest, characterized by a large variability in species composition of the forest canopy. Following fire, overstory composition varies mainly with ambient soil conditions, fire severity, and stand composition before the disturbance (Carleton and Maycock 1978; Bergeron and Bouchard 1983). The mixed boreal forest is characterized by the presence of several different successional pathways (Bergeron and Dubuc 1989). Aspen (*Populus tremuloïdes* Michx.), white birch (*Betula papyrifera* Marsh.), and jack pine (*Pinus banksiana* Lamb.) are the three main postfire tree species. They are gradually replaced by coniferous species such as balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and white cedar (*Thuja occidentalis L.*), as the stand reaches a conifer-dominated stage (Bergeron and Dubuc 1989; Bergeron 2000).

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Table 1. Number of sampling plots and mean basal area of four forest covers types.

	Aspen	White birch	Spruce–fir	Jack pine
Average basal area (m^2/ha)				
White birch	1.50	28.00	4.39	2.08
Spruce–fir	1.51	2.30	23.46	0.93
Aspen	44.76	0.95	1.76	0.00
Jack pine	0.16	0.00	0.43	36.55
Number of plots				
Clay	16.00	11.00	12.00	4.00
Till	16.00	16.00	15.00	4.00
Total	32.00	27.00	27.00	8.00

Table 2. Results of analysis of variance performed on ordination scores from correspondence analysis.

Source of variation	df	SS	*F* ratio
Axis 1 (R^2 = 0.62)			
	7[a]	13.49	20.37***
	86[b]	8.13	
Surface deposit	1	9.18	97.06***
Cover type	3	2.48	8.76***
Interaction	3	0.29	1.04***
Axis 2 (R^2 = 0.26)			
	7[a]	2.98	4.27***
	86[b]	8.57	
Surface deposit	1	0.29	2.93***
Cover type	3	1.19	3.99***
Interaction	3	0.73	2.43***

Note: df, degrees of freedom; SS, sum of squares.

[a] model df.

[b] error df.

***$P < 0.001$.

Table 3. Richness, evenness, and Shannon's diversity index for each cover type and surface deposit.

	Richness	Evenness	Shannon's diversity index
Aspen	21.22±5.45	0.67±0.09	1.98±0.34
White birch	20.37±4.13	0.66±0.11	1.94±0.39
Spruce–fir	21.56±5.83	0.71±0.08	2.11±0.37
Jack pine	24.38±2.67	0.72±0.10	2.28±0.35
Clay	22.16±4.88	0.65±0.11	2.02±0.42
Till	18.80±4.77	0.70±0.08	2.05±0.33

Note: Values given are mean ± SD.

Table 4. Analysis of variance performed on richness, evenness, and Shannon's diversity index.

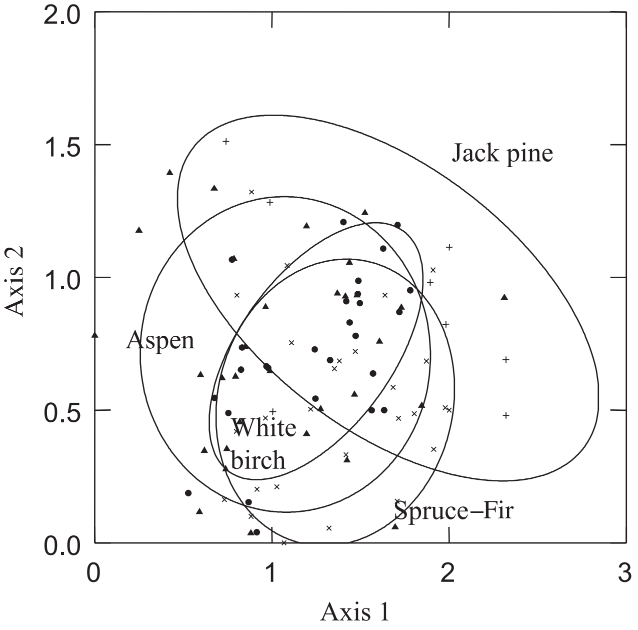
Variables	Source	R^2	$p > F$
Full model			
Richness	Model	0.21	0.0042
	Surface deposit		0.0124
	Cover type		0.1925
	Interaction		0.0864
Evenness	Model	0.12	0.1134
	Surface deposit		0.0328
	Cover type		0.1004
	Interaction		0.9872
Shannon's diversity index	Model	0.11	0.1481
	Surface deposit		0.5336
	Cover type		0.0466
	Interaction		0.3070
Model without interaction and cover type terms			
Richness	Model	0.11	0.0011
	Surface deposit		0.0011
Evenness	Model	0.06	0.0204
	Surface deposit		0.0204

Understory composition is also influenced by fire regime and has been analysed extensively (Ahlgren 1960; Carleton and Maycock 1978; Archibold 1979; De Grandpré et al. 1993). Distribution of understory species is generally associated with gradients in fertility and humidity. In their study of the southern boreal forest, Bergeron and Bouchard (1983) mention that the composition of the understory varies with surface deposits and drainage. Carleton and Maycock (1980) identify two major gradients explaining understory composition in boreal forests of the Clay Belt region of Ontario: (*i*) a moisture and nutrient concentration gradient mainly related to exchangeable calcium and magnesium in alluvial and clay deposits and (*ii*) a general fertility–productivity gradient related to organic matter depth and canopy type as defined by basal area and the proportion of coniferous species in the stand. Close association between overstory and understory species has been reported by many authors and attributed to the similar response of understory species to environmental gradients (Carleton and Maycock 1981; Gagnon and Bradfield 1986; Host and Pregitzer 1992; Gilliam et al. 1995; Sagers and Lyon 1997). However, few studies have observed a direct relationship between species composition of the overstory and the understory layer.

Cover types may influence ecosystem processes such as nutrient cycling and light transmittance directly. Numerous studies have shown that species composition of the canopy influences the availability of nutrients in the soil (Pastor et al. 1984; Xiao et al. 1991; Paré et al. 1993; Brais et al. 1995). Aspen, a species with high nutrient requirements, enhances biogeochemical fluxes of nutrients (Paré and Bergeron 1996), while jack pine, with its low nutrient requirements, is often found in nutrient-poor ecosystems. Forest cover also influences the transmittance of light through the canopy (Anderson et al. 1969; Messier et al. 1998). Light and soil nutrient availability, as well as soil pH, are influenced by forest cover and may affect the presence and growth of understory species. In the southwestern portion of the boreal forest of Quebec, many different successional pathways can be found on similar edaphic conditions, thus offering an opportunity to examine the effect of forest cover type on understory composition.

Our general hypothesis is that over uniform edaphic conditions, the forest cover type influences the richness, evenness, diversity, and composition of the understory layer. By comparing the composition of understory vegetation beneath different cover types with similar edaphic conditions, we should be able to identify relationships between understory and overstory species and thus demonstrate that the forest stand creates conditions that directly control the understory composition. Our main objectives are (*i*) to show the influence of forest cover type on understory composition and di-

Fig. 1. Ordination resulting from correspondence analysis of 10 × 10 m sample plots, on clay and till, for four forest cover types : +, jack pine; ▲, aspen; ×, spruce–fir; •, white birch. The ellipses contain 70% of the sample plots for each cover type. $N = 94$.



versity and (*ii*) to discuss the possible relationships between cover types, environmental variables, and understory composition. Direct effects of forest cover on understory composition may have important consequences on the development of strategies to maintain ecological processes and species diversity in managed boreal ecosystems.

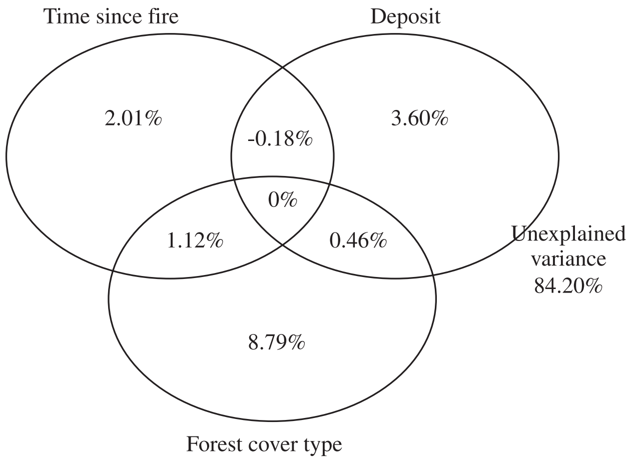
Materials and methods

Study area

The study area is located around Lake Duparquet, in northwestern Quebec (48°30′N, 79°20′W). This area is part of the western balsam fir – paper birch (*Abies balsamea* – *Betula papyrifera*) bioclimatic domain (Grondin 1996). This domain extends over the Clay Belt region of Quebec and Ontario, a major physiographic region resulting from the deposits left by the proglacial lakes Barlow and Ojibway at the time of their maximum expanse, in the post-Wisconsinian (Vincent and Hardy 1977). The closest weather station to the study area is located at La Sarre, 35 km north of Lake Duparquet. The average annual temperature is 0.8°C, daily mean temperature is –17.9°C for January and 16.8°C for July, and the average annual precipitation totals 856.8 mm (Environment Canada 1993).

The composition of the vegetation in the area studied varies along a successional gradient described by Bergeron and Dubuc (1989). By dendrochronological analysis, Bergeron (1991) and Dansereau and Bergeron (1993) determined that present stands originated from fires that took place 34 to 281 years ago. In the early stages of succession, paper birch, aspen, or jack pine dominate the forest. If stands are not subjected to any major disturbances, they become dominated by balsam fir and white cedar. However, several different successional pathways are possible, and in some cases fir and spruce return immediately after a fire (Bergeron and Dubuc 1989). A severe spruce budworm outbreak occurred from 1970 to 1987, causing most of the mature balsam fir in the region to die off (Morin et al. 1993). The cover type and the age of the stand also affect certain soil properties (Paré et al. 1993; Longpré et al. 1994; Brais et al. 1995; Paré and Bergeron 1996).

Fig. 2. Partitioning of the understory vegetation data set variance using forest cover types, time since fire, and deposit as subsets of explanatory variables. $N = 94$.



Sampling design

A total of 94 sample plots, each measuring 10 × 10 m, were selected on sites with similar conditions (slope and drainage). The small size of these plots enabled us to avoid areas that had been disturbed by spruce budworm. Plots were located over two types of surface deposits: mesic clay and mesic till. A plot was assigned to one each of four categories of forest cover type (aspen, white birch, jack pine, and spruce–fir (balsam fir, white spruce, white cedar)) when the corresponding species or group of species exceeded 75% of the total basal area of the stand (Table 1). These stands originated from fires that took place in 1870, 1916, 1919, 1923, 1944, and 1964. In all stands, dominant trees originated after fire, except for the aspen stand of 1870, which is a second cohort of aspen (Bergeron 2000). The species and surface deposits selected represent the dominant species and soils of the region (Bergeron et al. 1983). The types of forest cover involved in the sampling plan were selected on the basis of their effects on ecosystem processes such as nutrient cycling and light transmittance.

Understory vegetation and soil sampling and analyses

Between the last week of June and the first week of August in 1998, 10 randomly distributed subplots, measuring 1 × 1 m, were sampled within each plot, for a total of 940 subplots. Percent cover of each species in each subplot was estimated; nomenclature follows Marie-Victorin (1995). Two soil horizons were sampled: four samples of the FH layer and four samples of the first 10 cm of the mineral soil (Ae horizon and the top of the B horizon) in each plot. The four samples were pooled by horizon, air dried, and ground. Forest floor pH was analyzed in distilled water (McKeague 1977). Mineral N (NH_4 and NO_3) was extracted with 2 M KCl and analyzed by flow injection analysis (Tecator FIA Star 5020, Foss Tecator, Höganäs, Sweden). Exchangeable calcium, magnesium, and potassium in the forest floor were extracted with 0.1 M $BaCl_2$ and determined by atomic absorption (Hendershot et al. 1993). Available phosphorus was extracted with the Bray II method (McKeague 1977) and analysed spectrophotometrically. Soil texture was determined by granulometric analysis (McKeague 1977).

Light sampling

Photosynthetic photon flux density (PPFD) at the forest floor level and at 50 cm above the forest floor was measured at eight systematically located points in each plot using a LAI-2000 plant canopy analyzer (LI-COR Inc., Lincoln, Nebr.). Simultaneously, reference measures corresponding to full light were taken every

Table 5. Indicator values and significance levels of understory species for each cover type.

	Cover type				
Understory species	Aspen	Birch	Spruce–fir	Pine	*p*
Coptis groenlandica (Oeder) Fern.	1	4	6	62	0.0001
Lycopodium annotinum L.	1	0	0	61	0.0001
Cornus canadensis L.	3	9	17	60	0.0001
Gaultheria hispidula (L.) Mühl.	0	0	0	50	0.0001
Sorbus americana Marsh.	1	8	2	36	0.01
Betula papyrifera Marsh.	1	16	2	33	0.034
Pteridium aquilinum (L.) Kuhn	7	4	1	32	0.017
Oxalis montana Raf.	0	0	1	32	0.005
Picea mariana (Mill.)	0	0	0	32	0.003
Picea glauca (Moench) Voss	1	0	2	31	0.022
Vaccinium angustifolium Ait.	1	5	15	30	0.04
Dryopteris spinulosa (O.F. Muell.) Watt	2	1	1	28	0.033
Lycopodium lucidulum Michx.	0	0	0	25	0.007
Lycopodium clavatum L.	1	5	3	24	0.047
Alnus crispa (Ait.) Pursh	0	1	0	23	0.007
Aralia nudicaulis L.	38	26	20	15	0.018
Corylus cornuta Marsh.	43	15	9	8	0.01
Galium triflorum Michx.	34	3	1	0	0.011
Prunus spp.[a]	18	0	0	0	0.05
Trillium cernuum L.	16	0	0	0	0.052

[a] *Prunus pensylvanica* L. and *Prunus virginiana* L.

15 s in an open field near the study stand. Light measured at the floor level and 50 cm above the forest floor was associated to the appropriate reference measure by C-2000 software (LI-COR), from which the light ratio transmitted at each level was calculated.

Statistical analyses

To obtain an integrated representation of understory composition, we performed detrended correspondence analysis (DCA; Hill and Gauch 1980) on the mean percent cover of each species in each 100-m^2 plot. The broken stick method was used to ensure that DCA axes were significant (Frontier 1976). The ordination scores obtained from the DCA were subjected to an analysis of variance (general linear model) to determine whether the effects of forest cover and surface deposits were significant. Richness, evenness, and Shannon's diversity index (Scherrer 1984) were calculated on the mean percent cover of each species in each 100-m^2 plot. Richness and Shannon's index were subjected to an analysis of variance (general linear model). An analysis of variance on rank of evenness was performed to test the effect of cover, deposit, and interaction. An effect of deposit was detected but with a nonsignificant general model, and for increased degrees of freedom another analysis was performed, including only the effect of deposit. In the literature, time elapsed since fire is recognized to affect understory composition (Ahlgren 1960; De Grandpré et al. 1993). However, the influence of time since last fire on understory composition could not be tested because the jack pine stands of our study all originated after the same fire. To ensure that the influence of cover type on understory composition is independent of the influence of both the time since fire and the effect of deposit, we conducted variation partitioning analysis (Bocard et al. 1992). The cover type data set consisted of the absolute basal area of aspen, white birch, jack pine, and the sum of absolute basal area of fir, white spruce, and white cedar. The absolute basal area of each species was determined by summing the basal area of each stem of the mentioned species. The time since last fire was the stand age, and the surface deposit is represented by percent clay of the mineral soil.

Using the method of Dufrene and Legendre (1997), we calculated the indicator value and level of significance of understory species for cover type and surface deposit. The indicator value was obtained using the relative abundance and the relative frequency. The indicator values are between 0 and 100, where 100 is given to a species exclusively found in all plots of a single cover type. The indicator value of each species was calculated from the mean cover of each species present in each plot, the significance of which was tested by permutations (Edgington 1987).

To test the effect of forest cover type and surface deposit on environmental variables, analyses of variance were performed on ranked data of pH and available nutrients (Ca, Mg, K, P, NO_3, NH_4) from the humus layer, available light at the forest floor level and 50 cm above the forest floor, total basal area, and stand height. The total basal area was determined by summing the basal area of each stem in the stand, and stand height was determined by averaging the heights of all stems in a stand. Tukey's multiple comparison tests were performed on the rank of each variable found significantly affected by forest cover type. DCA was performed using a FORTRAN program for canonical community ordination (ter Braak 1988); all other analyses were performed using SAS software (SAS Institute Inc. 1985) except for the indicator value calculated by PC-ORD software (MjM Software 1997).

Results

Effect of canopy composition

The eigenvalues for the two first axes of the correspondence analysis performed at the stand level were 0.20 and 0.11, respectively; these two axes are significant according to the "broken stick" method (Fig. 1; Frontier 1976). The analysis of variance performed on ordination scores revealed that the composition of the understory varies significantly with the cover type along axis 1 and axis 2 (Table 2). The type of surface deposit has a significant effect on composition along axis 1, while the interaction between cover type and deposit is not significant along either of the two axes (Table 2). The measure of determination (R^2) between the

Table 6. Indicator values and significance levels of species for surface deposit.

	Surface deposit		
Understory species	Clay	Till	*p*
Mitella nuda L.	76	0	0.0001
Rubus pubescens Raf.	68	1	0.0001
Aster macrophyllus L.	59	33	0.011
Acer spicatum Lam.	56	38	0.041
Virburnum edule (Michx.) Raf.	44	7	0.003
Galium triflorum Michx.	44	0	0.0001
Rosa acicularis Lindl.	43	0	0.0001
Lonicera candensis Bartr.	42	10	0.011
Pyrola asarifolia Michx.	38	0	0.0001
Ribes glandulosum Grauer	35	2	0.0001
Clintonia borealis (Ait.) Raf.	35	58	0.016
Ribes lacustre (Pers.) Poir.	32	0	0.0001
Ribes triste Pallas	28	6	0.044
Athyrium filix-femina (L.) Roth	28	0	0.0001
Mertensia paniculata (Ait.) G. Don	25	0	0.0001
Dryopteris spinulosa (O.F. Muell.)	25	1	0.015
Pyrola elliptica Nutt.	24	2	0.038
Actaea rubra (Ait.) Willd.	23	3	0.019
Dryopteris disjuncta (Ledeb.) Morton	19	1	0.029
Rubus idaeus L.	19	0	0.0001
Maianthemum canadense Desf.	15	82	0.0001
Cornus stolonifera Michx.	15	0	0.024
Diervilla lonicera Mill.	9	54	0.0001
Circaea alpina L.	9	0	0.041
Sorbus americana Marsh.	3	27	0.047
Vaccinium angustifolium Ait.	2	42	0.0001
Pteridium aquilinum (L.) Kuhn	2	29	0.008
Vaccinium myrtilloides Michx.	1	44	0.0001
Lycopodium obscurum L.	0	68	0.0001
Lycopodium clavatum L.	0	32	0.002
Viburnum cassinoides L.	0	13	0.044

cover type and plot ordination scores is 0.62 for axis 1 and 0.26 for axis 2. Together, all explanatory variables in the variance partitioning analysis accounted for 15.80% of the variance in the understory vegetation data set (Fig. 2). Forest cover type alone accounted for 8.79%, and time since last fire and deposit accounted for, respectively, 2.01% and 3.60% of the variance in the data set.

Richness, evenness, diversity, and indicator values

The results of the analyses of variance (general linear model) indicate that richness, evenness, and diversity of the understory do not vary significantly with cover type (Tables 3 and 4). However, understory richness and evenness were affected by surface deposit. The majority of species showing a high indicator value are associated with either jack pine or aspen. *Trillium cernuum*, *Galium triflorum*, *Corylus cornuta*, and *Prunus* sp. are strongly associated with aspen stands, and the highest indicator values for jack pine stands are obtained by *Gaultheria hispidula*, *Coptis groenlandica*, *Cornus canadensis*, and *Oxalis montana* (Table 5). Several species, such as *Mitella nuda*, *Rubus pubescens*, and *Galium triflorum*, are associated with clay deposits and two species, *Diervilla lonicera* and *Maïanthemum canadense*, are associated with till deposit (Table 6).

Humus pH, exchangeable calcium and magnesium, and available nitrate and phosphorus are affected by cover type (Table 7). According to the Tukey's multiple comparison test, exchangeable calcium and pH were higher in aspen stands than in jack pine stands, and available nitrate and phosphorus were higher in jack pine stands than the other cover types (Fig. 3). There is no difference in exchangeable magnesium among cover types. Total basal area and stand height were significantly affected by cover type (Table 8). Total basal area in aspen stands was higher than that in birch and spruce–fir stands. The heights of aspen and jack pine were significantly greater than those of birch and spruce–fir (Fig. 4). At the forest floor level and at 50 cm above the forest floor, percent PPFD did not change significantly with cover type (results not shown). Surface deposit affected pH and available calcium and magnesium, which were higher on clay deposits (Table 9).

Discussion

Even over similar edaphic conditions, there is a change in understory composition among forest cover types. However, richness, evenness, and diversity do not vary significantly with forest composition. Our work is consistent with that of Saetre et al. (1997), who showed that forest cover type influences understory composition but not richness in Norway spruce (*Picea abies* (L.) Karst.) forests of Sweden. Environmental conditions controlled by forest cover may affect understory composition, but not diversity. Soil texture influences richness, evenness, and understory composition but not diversity. Thus, the influence of soil texture on the number of species is compensated for by the variation in species abundance. On clay, richness is higher though diversity did not increase, suggesting that the understory is composed of a few aggressive species, which dominate others.

Aspen and jack pine stands have shown the greatest variation in understory composition and, accordingly, the majority of indicator species are associated with one or both. Indicator species associated with aspen occur on mesotrophic soil, while indicator species of jack pine are linked, in general, to poor soils. In fact, only jack pine is associated with evergreen ericaceous species such as *Coptis groenlandica* and *Gaultheria hispidula*; evergreens are most prominent on infertile soils (Monk 1966; Small 1972; Al-Mufti et al. 1977). *Gaultheria hispidula* is also associated with poorly decomposed humus (Bergeron and Bouchard 1983). Soil acidity, which is the result of complex and interacting biogeochemical processes, seems to be an important factor in explaining the cover type effect on understory composition: *Coptis groenlandica*, *Cornus Canadensis*, *Gaultheria hispidula*, *Oxalis Montana*, and *Dryopteris spinulosa*, all of which are common on acidic humus soils (Siccama et al. 1970; Glaser et al. 1990). *Gallium triflorum*, which is associated with aspen is generally considered a nutrient-demanding species and is also more common on clay soils. Since such soils constitute a major reserve of nutrients, and of calcium in particular, this result suggests that the understory species associated with aspen have a high demand for calcium, or nutrients in general. Moreover,

Table 7. Average soil and light variables for cover types on clay and till deposits.

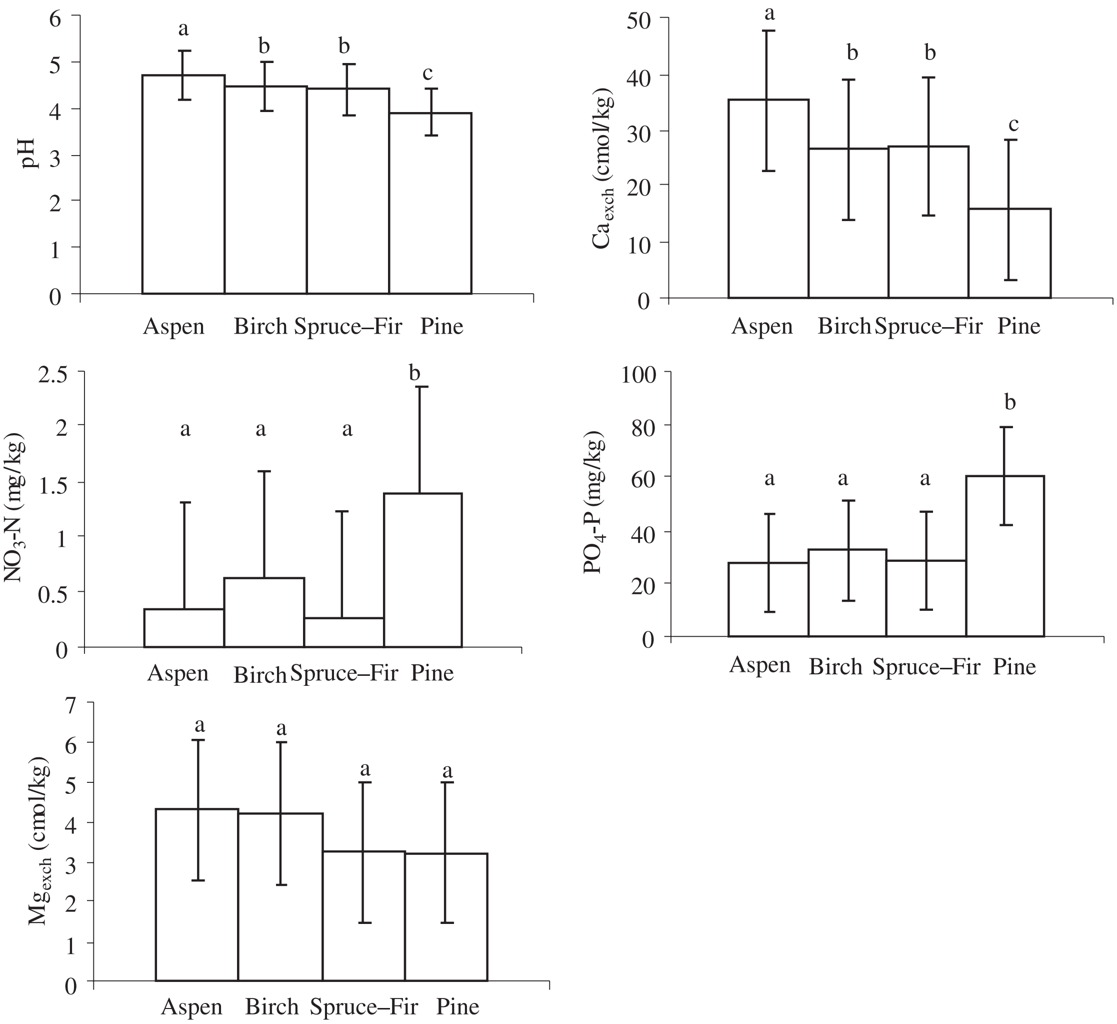
Deposit	Soil and light variables[a]	Aspen	White birch	Spruce–fir	Jack pine
Clay					
Light	% PPFD at 50 cm above forest floor	6.44±3.90	4.91±3.48	4.08±2.46	4.92±1.19
	% PPFD at 0 cm above forest floor	4.56±2.55	3.94±2.51	3.57±2.11	3.76±0.91
Humus	$\mathrm{Ca_{exch}}$ (cmol/kg)	43.44±12.00	33.90±10.73	33.99±11.52	18.97±3.40
	$\mathrm{K_{exch}}$ (cmol/kg)	3.27±1.15	3.80±1.13	3.18±0.68	3.10±0.50
	$\mathrm{Mg_{exch}}$ (cmol/kg)	5.34±2.15	5.15±1.75	3.92±1.35	3.93±0.51
	Available $\mathrm{NH_4}$-N (mg/kg)	163.33±198.20	117.65±197.79	68.82±113.16	196.05±105.56
	Available $\mathrm{NO_3}$-N (mg/kg)	0.44±0.61	0.90±2.35	0.18±0.46	1.53±0.10
	Available $\mathrm{PO_4}$-P (mg/kg)	29.66±13.23	28.73±17.67	30.35±16.88	61.20±16.82
	pH (water)	5.10±0.3	4.90±0.4	4.60±0.50	4.20±0.10
Mineral	$\mathrm{Ca_{exch}}$ (cmol/kg)	012.82±9.69	7.94±7.33	7.98±4.94	4.02±2.08
	$\mathrm{K_{exch}}$ (cmol/kg)	0.57±0.29	0.54±0.30	0.50±0.23	0.73±0.08
	$\mathrm{Mg_{exch}}$ (cmol/kg)	2.69±1.98	1.75±0.67	1.73±0.94	1.56±0.87
	Available $\mathrm{NH_4}$-N (mg/kg)	20.05±23.81	13.88±28.47	7.00±9.65	5.68±2.59
	Available $\mathrm{NO_3}$-N (mg/kg)	0.32±0.50	0.15±0.30	0.06±0.09	0.33±0.05
	Available $\mathrm{PO_4}$-P (mg/kg)	7.92±4.06	7.97±4.32	9.19±5.49	23.28±15.33
	pH (water)	4.50±0.5	4.10±0.30	4.10±0.30	4.60±0.10
Till					
Light	% PPFD at 50 cm above forest floor	6.38±3.03	5.79±3.01	4.92±2.92	7.88±0.82
	% PPFD at 0 cm above forest floor	4.76±2.20	4.73±2.43	4.20±2.37	6.25±0.36
Humus	$\mathrm{Ca_{exch}}$ (cmol/kg)	26.71±8.51	21.79±7.44	21.72±6.15	12.82±2.60
	$\mathrm{K_{exch}}$ (cmol/kg)	3.11±0.79	3.11±0.68	2.66±0.87	2.53±0.23
	$\mathrm{Mg_{exch}}$ (cmol/kg)	3.26±1.34	3.53±1.59	2.69±0.99	2.46±0.12
	Available $\mathrm{NH_4}$-N (mg/kg)	238.52±329.54	393.56±620.97	110.41±162.31	155.83±063.93
	Available $\mathrm{NO_3}$-N (mg/kg)	0.24±0.34	0.43±0.71	0.30±0.48	1.25±0.06
	Available $\mathrm{PO_4}$-P (mg/kg)	25.76±14.49	34.55±21.17	26.75±17.49	59.03±4.29
	pH (water)	4.40±0.4	4.20±0.40	4.20±0.4	3.60±0.10
Mineral	$\mathrm{Ca_{exch}}$ (cmol/kg)	1.48±1.18	1.81±2.39	0.79±0.58	1.06±0.85
	$\mathrm{K_{exch}}$ (cmol/kg)	0.14±0.07	0.14±0.10	0.11±0.04	0.52±0.10
	$\mathrm{Mg_{exch}}$ (cmol/kg)	0.32±0.22	0.36±0.30	0.22±0.11	0.30±0.20
	Available $\mathrm{NH_4}$-N (mg/kg)	18.49±25.33	15.99±24.64	6.02±7.82	4.50±3.56
	Available $\mathrm{NO_3}$-N (mg/kg)	0.12±0.24	0.04±0.08	0.09±0.14	0.33±0.05
	Available $\mathrm{PO_4}$-P (mg/kg)	4.26±2.74	8.08±5.49	7.41±5.78	27.60±012.49
	pH (water)	3.90±0.3	4.00±0.20	3.90±0.20	4.00±0.30

[a] $\mathrm{Ca_{exch}}$, $\mathrm{K_{exch}}$, $\mathrm{Mg_{exch}}$, exchangeable Ca, K, and Mg, respectively.

Trillium cernuum and *Corylus cornuta* are common in nutrient-rich habitats (Carleton 1979; Brumelis and Carleton 1989). It is important to stress, however, that only a few species are restricted to a specific forest composition, suggesting that the observed differences in understory composition are mainly due to variation in species abundance.

The gradient of forest cover observed, from aspen to jack pine, separates the understory composition of coniferous and deciduous stands. Coniferous tree species are known to immobilize nutrients at a higher rate than deciduous species. At both ends of the forest composition gradient, aspen and jack pine stands differed significantly for humus layer pH and exchangeable calcium and magnesium (Paré et al. 1993; Brais et al. 1995; Paré and Bergeron 1996), suggesting that forest cover affects understory composition through its influence on nutrient availability. However, available phosphorus and nitrate were higher in jack pine stands, which represent the poorest sites. A separate study, conducted in the same area as ours, found that low concentrations of soil nitrate were associated with aspen and white birch soils (Brais et al. 1995). However, a study by Ste-Marie and Paré (1999) indicated that potential net nitrification and pH were very high in aspen soil and low in jack pine stands. These contradictory results can be explained by a higher nitrate demand in aspen and birch stands (Nadelhoffer et al. 1984) as well as in spruce–fir stands, which contain a greater proportion of deciduous tree species when compared with jack pine stands (Ste-Marie and Paré 1999). Higher availability of phosphorus in jack pine stands could also be explained by the greater uptake of this nutrient in other cover types. Perala and Alban (1982) showed that less phosphorus was contained in leaves, branches, boles, and litter-fall for jack pine than for aspen, while greater amounts of phosphorus were found in the forest floor of jack pine than aspen stands. However, Xiao et al. (1991) found that phosphorus was lower in the humus layer of coniferous stands. It is possible that by influencing nutri-

Fig. 3. Multiple comparisons of organic soil property means among forest cover types, $N = 94$. Histograms with same letter (*a* or *b*) are not significantly different according to Tukey's test. Bars = standard deviation.



ent cycling, understory vegetation creates a positive feedback mechanism, accentuating the influence of forest cover on understory composition.

To a lesser extent, understory composition of spruce–fir stands was different from other stands. In the southwestern boreal forest, available light above understory vegetation is lower in late-successional (spruce–fir) stands than in early-successional stands such as aspen, white birch, and jack pine (Messier et al. 1998). Moreover, stand height and total basal area, affected by forest composition, can create different light conditions, which affect understory species (Messier et al. 1998). However, in the present study, light availability in the herb layer was not affected by forest composition and no indicator species were related to spruce–fir stands. Light quality and soil moisture are also affected by stand composition (Federer and Tanner 1966; Anderson et al. 1969; Tasker and Smith 1977) and could be important, but these variables were not measured in our study. The competition for water and nutrients between the understory layer and late-successional trees could account for different understory composition in the spruce–fir stand because the fine roots of late-successional trees such as balsam fir and white spruce are located at more superficial levels of the soil than those of aspen and white birch stands (Grier et al. 1981; Gale and Grigal 1987; Finér et al. 1997).

Conclusions

There is an obvious relationship between the understory and overstory layer. However, the great variability and overlap in the results show no strong species association. Forest cover affects understory species habitat and thus could facilitate the survival of a heterogeneous group of understory species. Even if understory diversity is unaffected by stand composition, some species are related to a specific stand composition, suggesting that the loss of a forest cover type will be associated with a loss of understory species. For this reason, this study supports the conservation of a diversity of stand compositions at the landscape level. The canopy also exerts a certain control over the quality of the site, that is, on the availability of nutrients in the forest soil, its pH, and the forms of nitrogen available. The forest management favouring coniferous species could induce a change in nutrient availability and understory composition and, with time, provoke a reduction of biological diversity and even a decrease in productivity.

Table 8. Effect of surface deposit and forest cover type on the rank of environmental variables.

Environmental variable	Source	R^2	$p > F$
pH	Model	0.55	<0.0001
	Surface deposit		<0.0001
	Cover type		<0.0001
	Interaction		0.3875
Ca_{exch}	Model	0.51	<0.0001
	Surface deposit		<0.0001
	Cover type		<0.0001
	Interaction		0.8186
Mg_{exch}	Model	0.3	<0.0001
	Surface deposit		<0.0001
	Cover type		0.0282
	Interaction		0.9371
K_{exch}	Model	0.14	0.0712
	Surface deposit		0.0259
	Cover type		0.0718
	Interaction		0.6591
Available NO_3-N	Model	0.22	0.0029
	Surface deposit		0.8676
	Cover type		<0.0001
	Interaction		0.7015
Available PO_4-P	Model	0.2	0.0113
	Surface deposit		0.6590
	Cover type		0.0012
	Interaction		0.6861
Total basal area	Model	0.3	<0.0001
	Surface deposit		0.3879
	Cover type		<0.0001
	Interaction		0.9452
Stand height	Model	0.39	<0.0001
	Surface deposit		0.0623
	Cover type		<0.0001
	Interaction		0.8172

Table 9. Means of environmental variables affected by surface deposit.

Variables	Clay	Till
pH (water)	4.8±0.5	4.2±0.4
Ca_{exch} (cmol/kg)	36.14±12.91	22.61±7.93
Mg_{exch} (cmol/kg)	4.76±1.82	3.11±1.31

From a forest management point of view, our results suggest that similar site types (as defined by constant edaphic conditions) may not be the best predictors of productivity and that a combination of both site types and stand types is needed. Alternatively, when the canopy has been removed, indicator understory species might be used to assess site quality.

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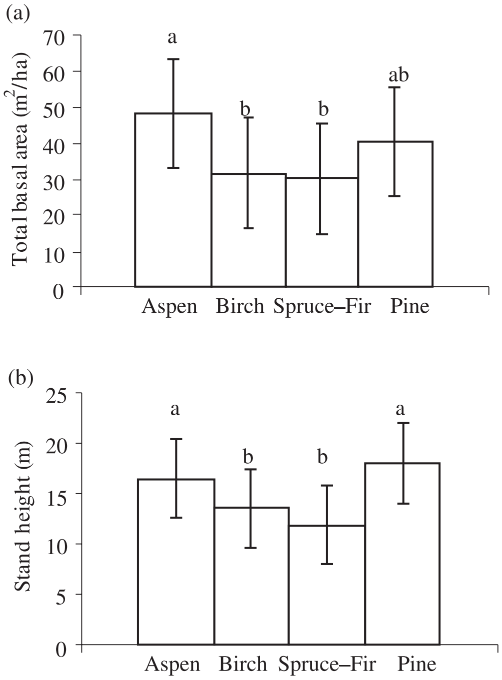
Fig. 4. Multiple comparison of stand structure property means among forest cover types, N = 94. Histograms with same letter are not significantly different according to Tukey's test. Bars = standard deviation.



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