Classification and ecology of the mid-seral *Picea mariana* forests of British Columbia

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Abstract. We sampled vegetation and soils of, and classified mid-seral, even-aged, fire-origin, upland *Picea mariana* ecosystems in the Boreal White & Black Spruce and Sub-boreal Spruce zones of British Columbia, Canada. We applied multivariate and tabular methods to analyse and synthesize the data from 121 plots according to the methods of biogeoclimatic ecosystem classification. We delineated seven basic vegetation units and described their vegetation and environmental features. However, the delineated units could not be related to neither of the taxonomies proposed for the North American boreal forest communities. Although species-poor, the understorey vegetation in the sampled ecosystems provided for a sufficient floristic differentiation, which matched well the major edaphic differences between the units. The classification of mid-seral boreal ecosystems may be more useful that based on old-growth stands that are infrequent or lacking in the landscape due to wildfires.

Keywords: Biogeoclimatic ecosystem classification; Black spruce; Boreal forest; Edatopic grid; Vegetation-environment relationships.

Abbreviations: BC = British Columbia; NMDS = Non-metric multidimensional scaling; SMR = Soil moisture regime; SNR = Soil nutrient regime.

Nomenclature: Qian & Klinka (1998).

Introduction

Picea mariana is one of the principal species of the Canadian boreal forest. While it is one of the major timber crop species in eastern Canada, in British Columbia (BC) it is considered a non- or less desirable crop species, except on sites that are edaphically unsuitable for more desirable crop species, such as *Picea glauca* and *Pinus contorta*. From over 2000 reports on *Picea mariana* ecosystems published in Canada and the USA to date, only a few originated in the Province. A better understanding of the ecology and growth of *Picea mariana* is needed in anticipation of future demands for the timber resources of the boreal forest.

Wetland, *Picea mariana*-dominated ecosystems in BC have been investigated and classified by Revel (1972), Wali & Krajina (1973), and Annas (1974). More recently, the Ecological Program Staff of the BC Ministry of Forests presented a general overview of the Boreal Black & White Spruce (BWBS) and Sub-Boreal Spruce (SBS) zones (Meidinger & Pojar (1991) and site classification for these zones (e.g. DeLong et al. 1990; MacKinnon et al. 1990; Banner et al. 1993). More recently, two vegetation classifications of North American boreal forest communities were developed from existing and new data by Peinado et al. (1998) and Rivas-Martínez et al. (1999).

However, as much of the boreal forest has been fire-disturbed, upland, old-growth stands of *Picea mariana* are very infrequent, and there has been no investigation in younger, even-aged, mid-seral stands. Therefore, there is a need to develop a classification of mid-seral stands for further studies of *Picea mariana* ecosystems as a means to relate them to other studies in the North American boreal forest. A corollary was to determine the environmental uniformity of floristically delineated classes of ecosystems. We aimed to develop a classification that organizes ecosystems in a way that shows the greatest number of vegetation-environment relationships. Our objective was to produce ecologically distinct classes

of ecosystems that could be easily identified in the field using both floristic and environmental features and used as a framework for examining vegetation-environment relationships.

Methods

Study area

The study area encompassed nearly the entire native range of *Picea mariana* in BC extending from 54° to 60° N and 132° to 121° W. (Fig. 1). This area is included in the BWBS zone and the northern portion of the SBS zone of BC (Meidinger & Pojar 1991). Both zones are part of the Canadian Boreal Forest Region (Krajina 1969). The BWBS zone is influenced by a continental, montane boreal climate and subject to frequent outbreaks of arctic masses. Compared to the BWBS zone, the climate influencing the SBS zone is slightly less continental, with lower temperatures in summer, higher temperatures in winter, and a slightly longer growing season. Forest fires are frequent in both zones maintaining a large portion of the landscape in early and mid-seral stages (Meidinger & Pojar 1991).

The major tree species in the study area are *Picea mariana, Picea glauca, Picea engelmannii* × *P. glauca, Pinus contorta, Populus tremuloides, Populus balsamifera, Betula papyrifera*, and *Betula neoalaskana*. Abundance of *Picea mariana* increases with increasing latitude and with decreasing soil drainage. In mid-seral, upland ecosystems, *Picea mariana* may grow in mixtures with other tree species; typically with *Pinus contorta*; in ombrotrophic wetlands, *Picea mariana* predominates and may associate with *Larix laricina* (Viereck & Johnston 1990). Upland soils are primarily Luvisols, Podzols, Brunisols and Gleysols, while organic soils are associated with wetlands – bogs, fens, marshes, and swamps. More detailed information about the BWBS and SBS zones is given in Krajina (1969) and Meidinger & Pojar (1991).

Sampling

The study forests were located close to access roads branching from the Cassiar and Alaska Highways, around Tumbler Ridge, and north of Fort St. James. They were deliberately selected to obtain a wide range in climatic and soil moisture, nutrients, and aeration conditions. Suitable stands were typically found on sites that had an obvious, but unknown, history of wildfire. All selected ecosystems had a uniform canopy layer dominated by *Picea mariana*, occasionally with a minor proportion of *Picea glauca, Pinus contorta*, and *Populus tremuloides*.

In total 121 sample plots, each 20 m × 20 m (0.04 ha) in size, were located in naturally established, unmanaged, immature and early mature even-aged stands: trees were ≥ 37 yr but < 185 yr as measured at breast height; the age range of all sampled trees was < 20 yr in each stand (Smith 1986). Each sample plot was located to represent an ecosystem that was relatively uniform in stand structure, floristic composition, and site attributes (e.g., slope position, aspect, gradient, soils, and ground cover).

All plant species present within the plot were identified and their cover percentage was estimated. These cover values were converted in data tabulation to classes (+ to 9) of the Domin-Krajina scale of species significance (Mueller-Dombois & Ellenberg 1974). The plant nomenclature followed Qian & Klinka (1998). A soil pit was dug at each plot and soils were described and identified according to the Canadian Soil Classification System (Agriculture Canada Expert Committee on Soil Survey 1987). Humus samples were taken from each plot for a visual analysis and identification in the laboratory using the humus form classification of Green et al. (1993). The type of ground cover (forest floor, decaying wood, mineral soil, coarse fragments, and open water) was recorded. A more complete description of the field methods is given in Brooke et al. (1970) and Luttmerding et al. (1990).

Soil moisture and nutrient regimes (SMRs and SNRs) were estimated in the field by (1) a systematically guided evaluation of a selected number of topographic (slope aspect, gradient, and position) and soil morphological properties – humus form, rooting depth, soil texture, coarse fragment content, soil aeration, soil mineralogy, and the presence and depth of the growing-season water table (Green & Klinka 1994) – and (2) indicator plant analysis (Klinka et al. 1989). Field estimates of SNRs were substantiated by soil chemical analysis, while SMRs were only field-estimated and not directly measured.

Classification

Consistent with the biogeoclimatic ecosystem classification, (1) floristically uniform groups of the plots were required to be more or less distinct from other groups, and (2) to occupy a floristically defined segment of the edaphic and local climatic gradients. We used a computer-aided program, VTAB-Ecosystem Reporter, Revision 19907a (Emanuel 1999) to produce the tables required in the analysis and synthesis of vegetation data. The vegetation data were also submitted to non-metric multidimensional scaling (NMDS) analysis (McCune & Mefford 1997), and the analysis was run on percent cover of each recorded plant species.

We classified the sampled ecosystems into vegetation units at three categorical levels (subassociation, association, and alliance) applying the principles of the
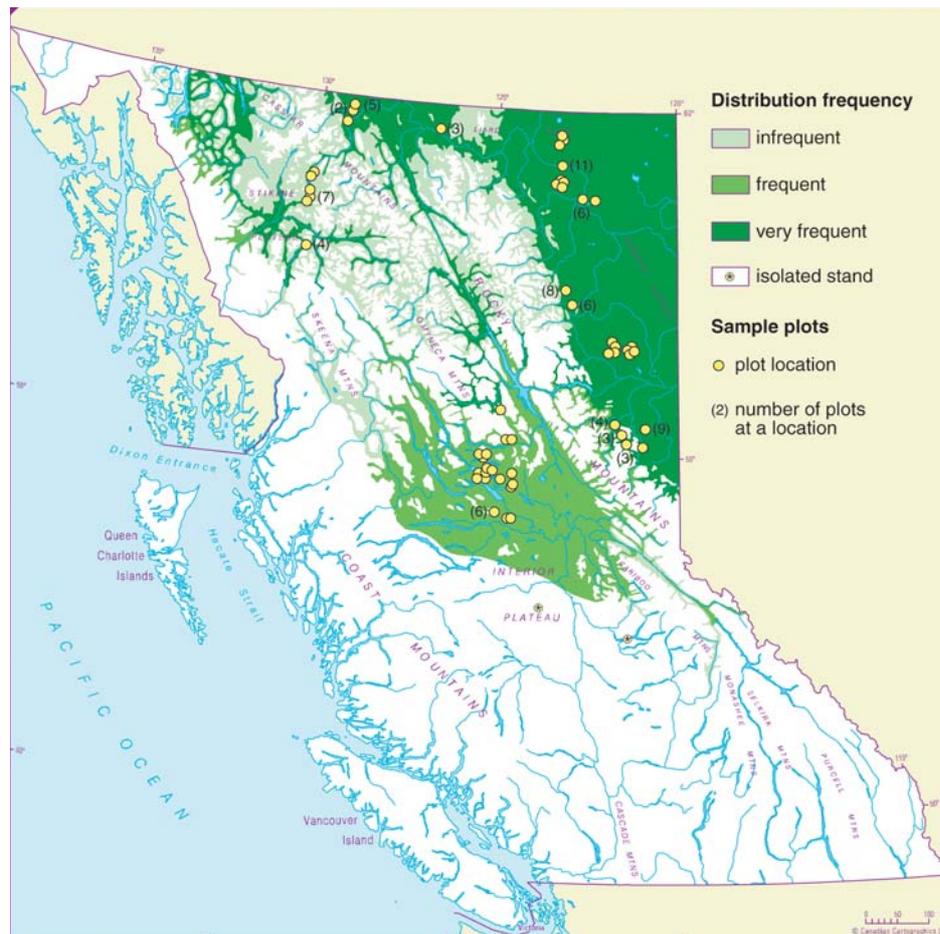
Fig. 1. The native range of *Picea mariana* in British Columbia and the general locations of sample plots.

Braun-Blanquet approach (Mueller-Dombois & Ellenberg 1974: 177-210; Westhoff & van der Maarel 1978: 287-399) but we deviated from this approach in several aspects that are described below.

There is no universally accepted methodology for, nor agreement upon, the required composition of the diagnostic combination of species for a particular category. We used the principle of relative differentiation that allows delineation of a unit by an exclusive diagnostic combination of species that must include at least one differential species or dominant-differential species. Differential species are those that may be associated with more than one vegetation unit in a hierarchy; presence class III (occurring in ≥ 40% of the plots of this unit) and at least two presence classes greater than in other units of the same hierarchical level and circumscription. Dominant-differential species are those species that may be associated with more than one vegetation unit in a hierarchy; presence class III, mean species significance 5 (≥ 10% cover) and two or more species significance classes greater than in other units of the

same hierarchical level and circumscription. However, one unit that represents the central (typic) concept of a higher circumscribing unit can be recognized without a diagnostic combination of species. The use of important companion species, which do not meet the criteria for a differential or dominant-differential species but show affinity to a particular unit, is optional (Pojar et al. 1987: 131-132).

The following four analytical steps were used to synthesize the vegetation data:

1. Plots were stratified into floristically similar groups using TWINSPAN (Hill 1979).

2. For each of the groups obtained in step 1, a provisional plot table was produced and examined for within-group similarities and differences. A provisional differentiated summary table was used to examine affinities and differences between groups.

3. Provisional environmental plot tables for all plots within each group were used to determine whether the floristically similar plots were also similar in environmental characteristics.

Steps 2 and 3 were repeated iteratively in a process of successive approximation (Poore 1962), in which the production of revised vegetation and environmental tables continued until there were no more plot re-assignments and group mergers.

4. A tentative hierarchy of groups was then proposed, where each group was considered to be either an association or a subassociation depending on its relationship to the hierarchy. A preliminary diagnostic table showing the diagnostic combination of species for every group was produced. Step 4 was repeated until exclusive diagnostic combinations of species were obtained for each group of the hierarchy.

The full relevé table is available upon request from the senior author of this paper. We used one, two but no more than three plain scientific names without suffixes for naming vegetation units as proposed by Rejmánek (1997) (see also Klinka et al. 1996). Plant alliances and associations were named using the generic and specific names of two dominant species from the diagnostic combination of species for that association. Plant subassociations were named by adding a colon (:) to the association name, followed either by the term 'typic' or the name of one diagnostic species. All units based on the synthesis of <10 sample plots were considered tentative.

Similarity and life-form spectral analyses

Using the VTAB, we compared floristic similarities between each pair of vegetation units using Sørenson's index based on species cover (Qian et al. 1997).

Complementary to tabular analysis, we carried out a VTAB-assisted 'spectral analysis' (Mueller-Dombois & Ellenberg 1974: 315-319). The spectral analysis was performed on life forms (coniferous trees, broad-leaved trees, evergreen shrubs, deciduous shrubs, ferns, graminoids, herbs, mosses, liverworts, lichens, and dwarf woody plants). A spectrum was constructed for each vegetation unit, representing the relative frequency of each life form in that unit. Relative frequencies were calculated using Eq. 1 (Klinka et al. 1996). The plots were not standardized, i.e. plots with a greater total vegetation cover contributed relatively more to the spectrum of the vegetation unit.

$$F_j = \frac{\sum_{i=1}^{n} C_i}{\sum_{j=1}^{m} \sum_{i=1}^{n} C_{ij}} , \qquad (1)$$

where F_j = the relative frequency (%) of species group j ($j = 1, 2, 3 \ldots m$) for life form ($m = 12$), and C_i = midpoint percent cover value of species i ($i = 1, 2, 3 \ldots n$).

Results and Discussion

All 121 sample plots were classified into a hierarchy that includes four subassociations, five associations, and two alliances (Table 1). These units were delineated according to floristic differences that are summarized in diagnostic combinations of species (Table 2). The edaphic individuality of seven basic units (associations or subassociations) is depicted on the edatopic grid (Fig. 2).

All distinguished units belong to the 'Picea glauca & mariana' order (Krajina 1969) that represents montane boreal ecosystems of BC. He proposed Abies lasiocarpa, Larix laricina, Picea glauca, P. mariana, Pinus banksiana, P. contorta, and Populus tremuloides as the characteristics species of this order. All these species are present in our data, except for Pinus banksiana whose native range is outside the study area (Rudolph & Laidly 1990). Peinado et al. (1998) recognized this order (Piceetalia glauco–marianae); however, according to Rivas-Martínez at al. (1999) our units would likely be treated as a part of the Gaultherio – Piceetalia (the Ledo decumbentis – Piceion marianae).

In addition to the constant occurrence of Picea mariana, many other species, such as Cornus canadensis, Geocaulon lividum, Hylocomium splendens, Ledum groenlandicum, Linnaea borealis, Peltigera aphthosa, Pinus contorta, Pleurozium schreberi, Ptilium crista-castrensis, and Rosa acicularis occurred in all or nearly all units. This resulted in the weak floristic differentiation (Table 2, Fig. 3). Some other species that had

Table 1. Synopsis of vegetation units delineated in mid-seral, upland, Picea mariana forests indicating levels of generalization and relationships. The rows containing the names of plant associations are printed in bold. Numerical codes indicate the position of a unit in the hierarchy; the same codes are used in the diagnostic table (Table 2). An asterisk indicates an insufficiently sampled unit (< 10 plots).

Code	Alliance / Association / Subassociation
100	*Picea mariana – Vaccinium vitis-idaea*
110	**Picea mariana – Cladina stellaris*** (5 plots)
120	**Picea mariana – Vaccinium vitis-idaea** (25 plots)
130	**Picea mariana – Equisetum sylvaticum**
131	*Picea mariana – Equisetum sylvaticum: typic* (34 plots)
132	*Picea mariana – Equisetum sylvaticum: Larix laricina* (13 plots)
200	*Picea glauca – Picea mariana – Lonicera involucrate*
210	**Picea glauca – Picea mariana – Viburnum edule**
211	*Picea glauca – Picea mariana – Viburnum edule: Shepherdia canadensis* (13 plots)
212	*Picea glauca – Picea mariana – Viburnum edule: Mitella nuda* (28 plots)
220	**Picea glauca – Picea mariana – Equisetum pratense*** (3 plots)

marginal differential values were used only as important companions, e.g. *Empetrum nigrum* – an important companion for the *Picea mariana – Vaccinium vitis-idaea* alliance (100) (Table 2).

We considered two distinct groups to be alliances: *Picea mariana – Vaccinium vitis-idaea*, and *Picea glauca-Picea mariana – Lonicera involucrata*. The former featured a high presence of ericaceous shrubs and was associated with nutrient-poor soils, the latter featured a higher presence of *Picea glauca*, deciduous shrubs, and herbs, and was associated with nutrient-medium and -rich soils (Table 2, Fig. 2).

The *Picea mariana – Vaccinium vitis-idaea* alliance includes three associations, which are, in order of increasing soil moisture: *Picea mariana – Cladina stellaris* (110), *Picea mariana – Vaccinium vitis-idaea* (120), and *Picea mariana – Equisetum sylvaticum* (130) (Table 1, Fig. 2). Of all distinguished units, the *Picea mariana – Vaccinium vitis-idaea* (120) association, which is related to slightly dry and nutrient-poor sites, is most poorly differentiated but most widespread in the BWBS zone (Table 2).

Our *Picea mariana – Cladina stellaris* (110) association, which was originally named by Wali & Krajina (1973) as '*Cladonio (gracilis) – Arctostaphylos (uva-ursi) – Vaccinium (myrtilloides) – Pinetum contortae*', is akin to the *Arctostaphylo uvae-ursi – Pinetum latifoliae* of Peinado et al. (1998) and somewhat related to the *Pulsatillo multifidae – Pinetum latifoliae* of Rivas-Martínez et al. (1999). Our *Picea mariana – Vaccinium vitis-idaea* (120) association could not be aligned with any association of the two systems; however, the *Picea mariana – Equisetum sylvaticum* (130) association had a weak affinity to the *Piceetum glauco – marianae*, and the *Picea mariana – Equisetum sylvaticum*: *Larix laricina* (132) subassociation had some affinity to the *Sphagno – Piceetum marianae* of Rivas-Martínez et al. (1999).

Nearly all communities of the *Picea glauca – Picea mariana – Lonicera involucrata* (200) alliance were influenced by a fluctuating growing-season water table, which is typically found on flat terrain associated with fine-textured soils. This alliance includes two associations which are, in order of increasing soil moisture: *Picea glauca – Picea mariana – Viburnum edule* (210) and *Picea glauca – Picea mariana – Equisetum pratense* (220) (Table 1, Fig. 2). The *Shepherdia canadensis* (211) and *Mitella nuda* (212) subassociations signify differences in local climate, with the former occupying warmer sites than the latter. Communities of the *Picea glauca – Picea mariana – Equisetum pratense* (220) association occur on nutrient-medium and -rich organic soils.

The only edaphically richer unit that could be aligned to one of the two syntaxonomies was the *Picea glauca –*
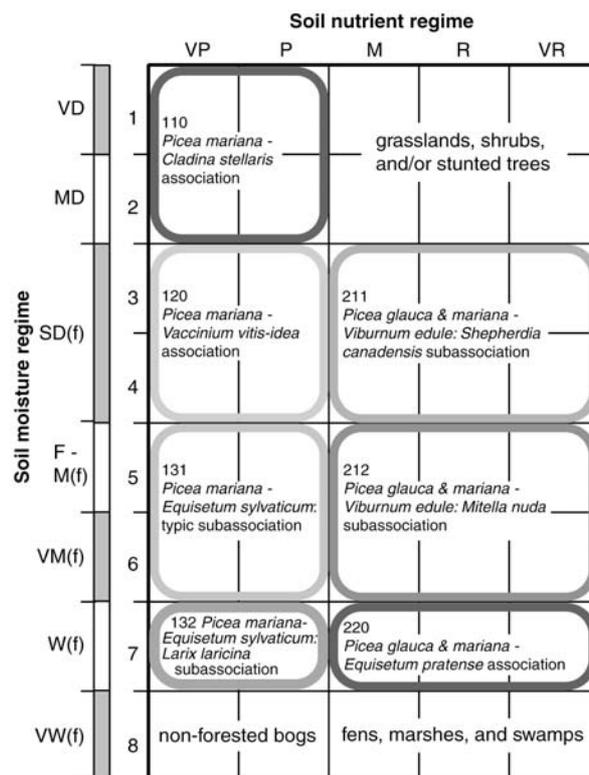
Fig. 2. Edatopic grid showing the relationships of the eight basic vegetation units to soil moisture regimes (SMRs) and soil nutrient regimes (SNRs). Numerical codes for the vegetation units as in Table 1. Abbreviations for SMRs are: VD = very dry; MD = moderately dry; SD = slightly dry;F = fresh; M = moist; VM = very moist; W = wet; f = fluctuating water table. Abbreviations for SNRs are: VP very poor, P = poor, M = medium, R = rich, VR = very rich.

Fig. 3. The distribution pattern of 121 sample plots along the first three axes of a Non-Metric Multidimensional Scaling.

Table 2. Diagnostic combinations of species for the vegetation units delineated in mid-seral, upland, *Picea mariana* forests. The diagnostic combinat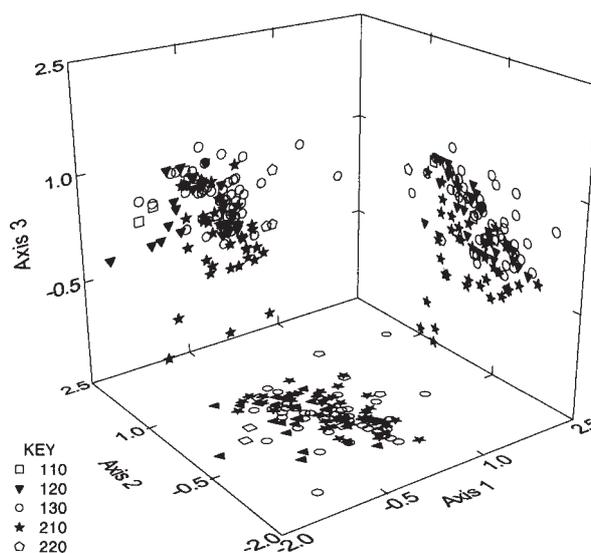ion of species for each vegetation unit is shaded in gray. Species presence classes are based on percent frequency: I = 1-20%; II = 21-40%; III = 41-60%; IV = 61-80%; V = 81-100%. Presence values ≥ III are printed in bold. An asterisk indicates an insufficiently sampled unit (< 10 plots). Species diagnostic values: dd = dominant differential, d = differential, ic = important companion (Pojar et al. 1987). Species significance classes and the corresponding mid-point and range (in parentheses) of cover: t = 0.005 (0.001-0.009); h = 0.05 (0.01-0.09); + = 0.2 (0.1-0.29); 1 = 0.4 (0.30-0.49); 2 = 0.75 (0.5-0.9); 3 = 1.5 (1-1.9); 4 = 3.5 (2.0-4.9); 5 = 7.5 (5.0-9.9); 6 = 15 (10.0-19.9); 7 = 35 (20.0-49.9); 8 = 60 (50.0-69.9); 9 = 85 (70-100). The mean species significance was computed using only relevés where the species was present.

Vegetation unit code		110		120		131		132		211		212		220	
Number of plots		5		25		34		13		13		28		3	
Species	**Diagnostic value**	**Species presence and species significance**													
100 *Picea mariana – Vaccinium vitis-idaea* alliance															
Dicranella palustris	(ic)	II	3	II	h	I	+	**III**	+	I	h	I	+		
Empetrum nigrum	(ic)	II	4	**III**	3	II	2	II	2			I	h		
Peltigera membranacea	(ic)	**III**	4	**III**	2	**III**	+	I	h	I	1	II	+		
Vaccinium scoparium	(ic)	II	2	II	2	I	3	I	h			I	+		
Vaccinium vitis-idaea	(d)	**V**	5	**IV**	5	**V**	5	**V**	4	I	h	**III**	3	II	h
Vaccinium uliginosum	(ic)	I	1	I	h	I	+	II	2						
110 *Picea mariana – Cladina stellaris* association*															
Arctostaphylos uva-ursi	(ic)	II	4			I	+								
Cladina stellaris	(d)	**V**	6	**III**	4	II	+	II	+	I	2	I	h	II	h
Cladonia ecmocyna	(ic)	**III**	+	II	h	I	h	I	h	I	h	I	h	II	h
Nephroma arcticum	(ic)	II	h	I	h										
Stereocaulon paschale	(ic)	II	5	I	h										
120 *Picea mariana – Vaccinium vitis-idaea* association															
Orthilia secunda	(ic)			**III**	+	II	h	I	h	II	h	**III**	+	**IV**	+
130 *Picea mariana – Equisetum sylvaticum* association															
Equisetum sylvaticum	(d)			I	h	**III**	3	**IV**	4	II	+	II	h	II	5
131 *Picea mariana – Equisetum sylvaticum*: typic subassociation															
Peltigera membranacea	(d)	**III**	4	**III**	2	**III**	+	I	h	I	1	II	+		
Pinus contorta	(dd)	**V**	7	**IV**	7	**III**	6	II	4	**III**	6	**III**	5		
132 *Picea mariana – Equisetum sylvaticum: Larix laricina* subassociation															
Aulacomnium palustre	(d)	I	2	I	+	II	1	**IV**	4			I	+	**IV**	5
Dicranella palustris	(d)	II	3	II	h	I	+	**III**	+	I	h	I	+		
Larix laricina	(d)					I	4	**III**	5	I	+	I	4	II	h
Rubus chamaemorus	(d)					I	+	**III**	4			I	t		
Rubus pedatus	(d)			I	h	I	h	**III**	1			II	3	II	+
200 *Picea glauca – Picea mariana-Lonicera involucrata* alliance															
Arnica cordifolia	(ic)			II	+	I	h			**III**	1	II	+	II	h
Aster ciliolatus	(ic)							I	h	**III**	2	II	h	II	h
Delphinium glaucum	(ic)			I	t	I	t	I	h	I	h	II	h	II	+
Heracleum maximum	(ic)									I	+	I	h	II	2
Lonicera involucrata	(d)			II	h	I	h	I	3	**III**	2	**IV**	4	**V**	4
Osmorhiza berteroi	(ic)			I	t	I	h			**III**	h	II	h	II	+
Picea glauca	(d)	II	4	II	5	II	4	I	4	**V**	6	**IV**	7	**IV**	6
Rosa acicularis	(d)	**III**	+	**III**	2	**III**	2	**III**	2	**V**	2	**V**	2	**IV**	4
Ribes lacustre	(ic)			I	h	I	h	I	h	II	h	**III**	1	II	+
Rubus pubescens	(ic)			I	h	I	+			**III**	3	**III**	2	**IV**	2
210 *Picea glauca – Picea mariana – Viburnum edule* association															
Abies lasiocarpa	(ic)			II	4	I	3	I	4	**III**	4	II	4		
Actaea rubra	(ic)							I	h	II	1	II	+		
Amelanchier alnifolia	(ic)									II	2	I	h		
Epilobium angustifolium	(d)	I	h	II	+	II	2	II	h	**V**	2	**IV**	2	II	+
Fragaria virginiana	(ic)					I	h	I	h	**III**	+	II	h		
Galium boreale	(ic)			I	h	I	h	I	+	**III**	+	II	h		
Galium triflorum	(ic)									II	h	II	+		
Pinus contorta	(d)	**V**	7	**IV**	7	**III**	6	II	4	**III**	6	**III**	5		
Populus tremuloides	(d)			I	h	I	1	I	3	**III**	7	**III**	5		
Viburnum edule	(d)			II	h	I	h	I	2	**IV**	3	**IV**	2		

Table 2. (*cont.*)

Vegetation unit code	Diagnostic value[1]	110		120		131		132		211		212		220	
Number of plots		5		25		34		13		13		28		3	
Species							Species presence and species significance								
211 *Picea glauca-Picea mariana-Viburnum edule: Shepherdia canadensis* subassociation															
Geocaulon lividum	(d)	II	1	**III**	2	II	+	II	h	**IV**	3	II	h		
Maianthemum racemosum	(d)			I	t					**III**	+	I	+		
Populus tremuloides	(dd)			I	h	I	1	I	3	**III**	7	**III**	5		
Shepherdia canadensis	(d)	I	h	II	3	I	+	I	+	**IV**	4	II	2		
212 *Picea glauca-Picea mariana-Viburnum edule: Mitella nuda* subassociation															
Achillea millefolium	(d)			I	h	I	h	I	h	I	h	**III**	h		
Mertensia paniculata	(d)	I	+	II	h	II	+	I	+	II	+	**IV**	1	V	3
Mitella nuda	(d)			I	h	II	h	I	h	II	h	**V**	1	V	1
Vaccinium vitis-idaea	(d)	**V**	5	**IV**	5	**V**	5	**V**	4	I	h	**III**	3	II	h
220 *Picea glauca-Picea mariana-Equisetum pratense* association*															
Angelica genuflexa	(d)									I	h			**V**	3
Aulacomnium palustre	(d)	I	2	I	+	II	1	**IV**	4			I	+	**IV**	5
Carex disperma	(d)			I	t	I	h	II	1			I	+	**IV**	5
Disporum hookeri	(d)									I	h	I	h	**IV**	+
Equisetum pratense	(d)			I	t	II	+	II	2	I	h	II	+	**V**	7
Equisetum scirpoides	(d)			I	h	II	+	II	h	I	h	II	2	**IV**	1
Geum macrophyllum	(d)													**IV**	3
Impatiens noli-tangere	(ic)													II	h
Listera cordata	(d)			I	t	I	h	I	h			II	h	**IV**	+
Moneses uniflora	(d)	I	h	I	h	I	h	I	h			II	h	**IV**	+
Oxycoccus oxycoccos	(d)			I	h	I	+	I	3			I	+	**IV**	+
Parnassia palustris	(ic)					I	t							II	h
Plagiochila aspleniformis	(ic)							I	h					II	+
Ranunculus eschscholtzii	(ic)													II	h
Rhizomnium glabrescens	(d)							II	2			I	t	**IV**	4
Ribes triste	(d)			I	h	I	h	I	h	I	h	II	+	**IV**	+
Salix glauca	(d)			I	+	I	2	I	2			I	2	**IV**	3
Senecio triangularis	(d)									I	h			**IV**	+
Sphagnum girgensohnii	(d)					II	4	I	4			I	t	**IV**	6

Picea mariana – Equisetum pratense (220) association which showed a weak relationships to the *Corno canadensis – Piceetum marianae* of Peinado et al. (1998), originally named '*Sphagno (nemorei) – Pleurozio (schreberi) – Ptilio (crista-castrensis) – Hylocomio (splendentis) – Corno (canadensis) – Piceetum marianae*' (Wali & Krajina (1973).

The floristic affinities of the distinguished units are corroborated by scaling and similarity indices (Fig. 3). Despite an observable separation between the *Picea mariana – Vaccinium vitis-idaea* (120) and *Picea glauca – Picea mariana – Viburnum edule* (210) associations along the first and third axes, the NMDS showed a considerable overlap between study stands in the three-dimensional ordination space (Fig. 3). This pattern gives a credible demonstration that the floristic differences among vegetation units are subtle, and that the development of understorey vegetation is influenced by the similarity in light and climatic conditions imposed by *Picea mariana*.

The most dissimilar units were the *Picea mariana – Cladina stellaris* (110) and *Picea glauca – Picea mariana – Equisetum pratense* (220) associations – two units with contrasting edaphic properties, the former drier and poorer, the latter wetter and richer relative to the other units. All other units had relatively high similarities to each other according to cover index. The two most similar pairs were: (1) the *Picea mariana – Vaccinium vitis-idaea* (120) association and the *Picea mariana – Equisetum sylvaticum*: typic (131) subassociation, and (2) the *Picea mariana – Equisetum sylvaticum*: typic (131) subassociation and the *Picea glauca – Picea mariana – Viburnum edule*: *Mitella nuda* (212) subassociation, with the units of each of these two pairs adjacent to each other on regional soil moisture or soil nutrient gradients.

Floristic affinities were also portrayed by the spectra presenting the life form profile for each vegetation unit (Fig. 4). All units had similar profiles, with coniferous trees and mosses representing over 65% of each spectrum.
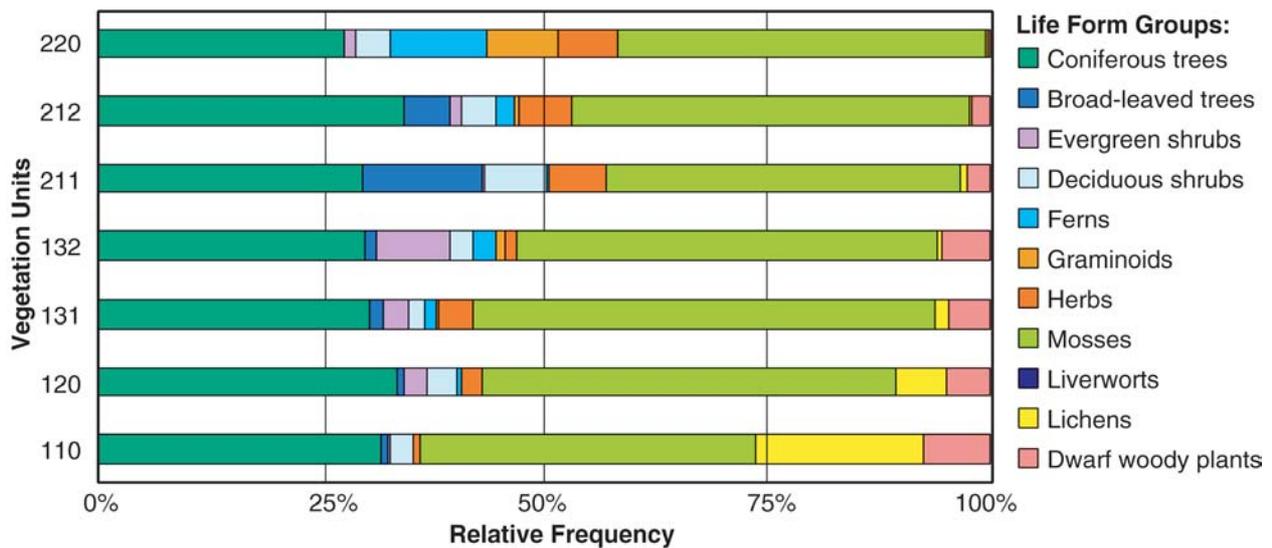
Fig. 4. Life form spectra of the seven basic vegetation units delineated in mid-seral, upland, *Picea mariana* forests. Codes for vegetation units as in Table 1.

While the proportion of coniferous trees and mosses was relatively consistent, the relative frequency of other life form groups varied from unit to unit reflecting the variation in edaphic conditions.

Broad-leaved trees (predominantly *Populus tremuloides*) had the highest relative frequency (5 to 10%) on nutrient-rich sites (*Picea glauca – Picea mariana – Viburnum edule* (210) association) (Fig. 2 and 4). Regardless of a low proportion, evergreen shrubs (predominantly *Ledum groenlandicum*) were characteristic of nutrient-poor sites (*Picea mariana – Vaccinium vitis-idaea* (120) and the *Picea mariana – Equisetum sylvaticum* (130) associations). As expected, the spectra for the *Picea mariana – Equisetum sylvaticum* (130) and *Picea glauca – Picea mariana – Equisetum pratense* (220) associations had a modest proportion of ferns and allies (predominantly *Equisetum* spp.). Herbs had a relatively high frequency (5 to 20%) on nutrient-rich sites (*Picea glauca – Picea mariana – Viburnum edule* (210) and *Picea glauca – Picea mariana – Equisetum pratense* (220) associations). Lichens were most abundant on water-deficient sites (*Picea mariana – Cladina stellaris* (110) association). Dwarf woody plants occurred with a low relative frequency (generally < 10%) and were most characteristic of nutrient nitrogen-poor sites (*Picea mariana – Vaccinium vitis-idaea* (100) alliance).

We were not successful relating our hierarchy to the two competing, and in fact, conflicting syntaxonomies for the North American boreal forest communities (Peinado et al. 1998; Rivas-Martínez et al. 1999). We suggest the following reasons: (1) our study stands were immature, mid-seral communities compared to late-seral communities synthesized in the syntaxonomies, (2) different hierarchies of the two syntaxonomies, and (3) differences in the classification methodology between the Braun-Blanquet approach and biogeoclimatic ecosystem classification.

One of the premises of plant ecology is that there are predictable, if inexact, relationships between vegetation patterns and environmental gradients. These relationships can be used to infer certain environmental conditions from the presence of a plant community or, conversely, to predict the presence or development of that plant community given these environmental conditions. The most influential, primary environmental factors directly affecting vegetation that can be used to predict its pattern in the landscape are climatic and edaphic (soil moisture, soil nutrients, and aeration). The other, secondary environmental factors, which integrated effects determine the primary factors, include aspect, slope gradient, slope position, parent material, soil texture, drainage patterns and many others. In this study, there is almost 1 : 1 correspondence between vegetation units and their environments (habitats) (Fig. 2). This nearly perfect correspondence was attributed to (1) very similar stand characteristics and stand development stage, and (2) vegetation units, each with a nearly exclusive range of soil moisture and nutrient regimes.

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