Scale-dependent environmental controls over species composition in Alaskan black spruce communities

T.N. Hollingsworth, M.D. Walker, F.S. Chapin III, and A.L. Parsons

Abstract: The boreal forest is the second largest terrestrial biome, and the black spruce (*Picea mariana* (Mill.) BSP) forest type occupies a large extent of boreal North America. Black spruce communities occur in a variety of environmental conditions and are especially important in the context of climate change because of underlain permafrost in much of the northern black spruce forests, as well as their adaptation to fire disturbance. We used a classification and ordination approach to describe and name Alaskan black spruce communities and relate them to key environmental variables. We analyzed the relationship of species richness with topographic position and with soil pH using both univariate and multivariate analyses of variance. We also explored the variability in structural, physical, and soil characteristics. We described three black spruce community types and five subtypes based purely on floristic composition. Paludification and topography were the most important gradients explaining species composition for the Fairbanks region (61% variance explained). However, at the scale of interior Alaska, pH, drainage, and productivity were the strongest environmental gradients (81% variance explained). We conclude that species composition of mature black spruce forests in interior Alaska results from the complex interaction of landscape and fire history, soil pH, paludification, permafrost, and topographic position.

Résumé : La forêt boréale est le deuxième plus grand biome terrestre, et la pessière à épinette noire (*Picea mariana* (Mill.) BSP) occupe une grande partie de la forêt boréale en Amérique du Nord. Les pessières à épinette noire se développent dans une multitude de conditions environnementales et sont particulièrement importantes dans le contexte des changements climatiques à cause du pergélisol qui est sous-jacent dans la plupart des forêts nordiques d'épinette noire mais aussi à cause de leur adaptation aux perturbations causées par le feu. Les auteurs ont utilisé une approche de classification et d'ordination pour décrire et nommer les pessières à épinette noire de l'Alaska et les relier à des variables environnementales clefs. Ils ont analysé la relation entre la richesse en espèces et la position topographique ainsi que le pH du sol à l'aide de l'analyse de variance multivariée et de l'analyse de variance. Ils ont aussi examiné la variabilité des caractéristiques physiques et structurales du sol. Ils ont décrit trois types de pessières à épinette noire et cinq sous-types uniquement sur la base de la composition floristique. La tourbification et la topographie sont les deux plus importants gradients qui expliquent la composition en espèces pour la région de Fairbanks (61 % de la variance expliquée). Cependant, à l'échelle de l'intérieur de l'Alaska, le pH, le drainage et la productivité sont les gradients environnementaux les plus significatifs (81 % de la variance expliquée). Ils arrivent à la conclusion que la composition en espèces des forêts mature d'épinette noire de l'intérieur de l'Alaska est le résultat de l'interaction complexe entre le paysage, l'historique des feux, le pH du sol, la tourbification, le pergélisol et la position topographique.

[Traduit par la Rédaction]

Introduction

Over the last two decades, it has become increasingly clear that species' distribution along environmental gradients is scale dependent (Allen and Hoekstra 1990; Levin 1992). Many community and landscape studies have linked species responses to environmental gradients at fine spatial or temporal scales (Tilman 1993; Raisa 1999) or at broad spatial and temporal scales (Currie and Paquin 1987; Latham and Ricklefs 1993), yet few studies have investigated community patterns across multiple scales of space or time (e.g., Reed et al. 1993; Fridley et al. 2005).

Soil temperature and moisture, which are controlled primarily by topography and successional status, have been de-

Received 15 September 2005. Accepted 2 March 2006. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 14 June 2006.

T.N. Hollingsworth[1] and M.D. Walker. USDA Forest Service, Pacific Northwest Research Station, Boreal Ecology Cooperative Research Unit, P.O. Box 756780, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
F.S. Chapin III. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
A.L. Parsons. School of Natural Resources Management and Agricultural Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

[1] Corresponding author (e-mail: thollingsworth@fs.fed.us).

Can. J. For. Res. **36**: 1781–1796 (2006) doi:10.1139/X06-061

scribed by many as the primary drivers of plant community composition in the boreal forest of interior Alaska (Van Cleve 1983; Yarie 1983; Van Cleve et al. 1990). However, to the north of the boreal forest in the Alaskan arctic, broad-scale patterns are related primarily to soil pH as governed by landscape age (Walker and Everett 1991; Walker et al. 1994). Although the species composition of the boreal forest understory broadly overlaps with the arctic tundra to the north, the interaction between mineral soil pH and Alaskan boreal community composition has never been studied. This raises questions about whether boreal forest and tundra are controlled by fundamentally different environmental gradients and whether the controls over community composition in the boreal forest might be regionally variable and therefore scale dependent. This is the first study in Alaskan boreal forest to address these questions.

The boreal forest covers approximately 6.7 $\times 10^6$ km^2 across North America and Eurasia (Scott 1995), making it the second largest terrestrial biome on earth (Whittaker 1975). Although the boreal forest is the largest biome in North America, its diversity is one of the lowest, causing the vegetation to seem homogeneous or simple in its patterns. This apparent simplicity may facilitate the recognition of key underlying determinants of community composition. The most widespread forest type of the Alaskan and western Canadian boreal forest is dominated by black spruce (*Picea mariana* (Mill.) BSP) (Viereck et al. 1992) and covers approximately 44% of the interior Alaskan landscape (Van Cleve 1983). Black spruce communities are particularly important in the context of global climate change in part because of the large amount of carbon stored in their soils, the prevalence of permafrost, and the tight link between the black spruce forest type and fire disturbance (e.g., Van Cleve et al. 1990; Johnstone and Kasischke 2005; Vogel et al. 2005).

The phytosociological approach, defined as the delineation of different vegetation and plant communities, has a long history of use in the boreal regions of Europe, Asia, and Russia (Ellenberg 1988; Korotkov et al. 1991; Dierbenik 1996). In addition, there has been some work done on the phytosociology of boreal forests in Canada (e.g., Orloci and Stanek 1979; Foster 1984; Peinado et al. 1998). These Canadian vegetation classifications range from large landscape- and regional-scale studies (La Roi 1967; La Roi and Stringer 1975; Peinado et al. 1998) to site-specific studies (La Roi 1991; Timoney et al. 1993). For example, Foster (1984) classified the black spruce communities of Labrador into five major assemblages indicative of fire history and soil drainage.

The current classifications of Alaskan boreal forest communities however, are based on a combination of physiognomic and floristic data, with physiognomy being a primary element of the classification (e.g., Viereck et al. 1992; Brown and Smith 2000). For example, the Alaska vegetation classification (Viereck et al. 1992) divides black spruce communities dominated by dense, tall trees from those dominated by sparse shrubby trees, regardless of understory vegetation. However, many ecosystem processes in the boreal black spruce forest type such as nutrient cycling, soil carbon storage, and fire regime are more tightly associated with species composition than with stand structure (Flanagan and Van Cleve 1983; Driscoll et al. 1999; Bisbee et al. 2001). Therefore, previous vegetation classifications of the boreal region of Alaska may be insensitive to key relationships between species distribution and environment that have important functional consequences. Despite the extensive distribution and range of topographic conditions occupied by black spruce forests, there have been no detailed floristic surveys of this ecosystem type in boreal Alaska, which is the first step towards understanding the relationships between black spruce vegetation communities and the environment across the region and linking this region with the rest of the North American boreal forest.

This paper has three objectives: (*i*) to generate the first floristic-based classification for the black spruce communities of Alaska; (*ii*) to examine both species composition and diversity along topographic (uplands versus lowlands) and pH (acidic versus nonacidic) gradients; and (*iii*) to explore the range of variability in black spruce stand structure and physical attributes associated with the forest type.

Methods

Study area

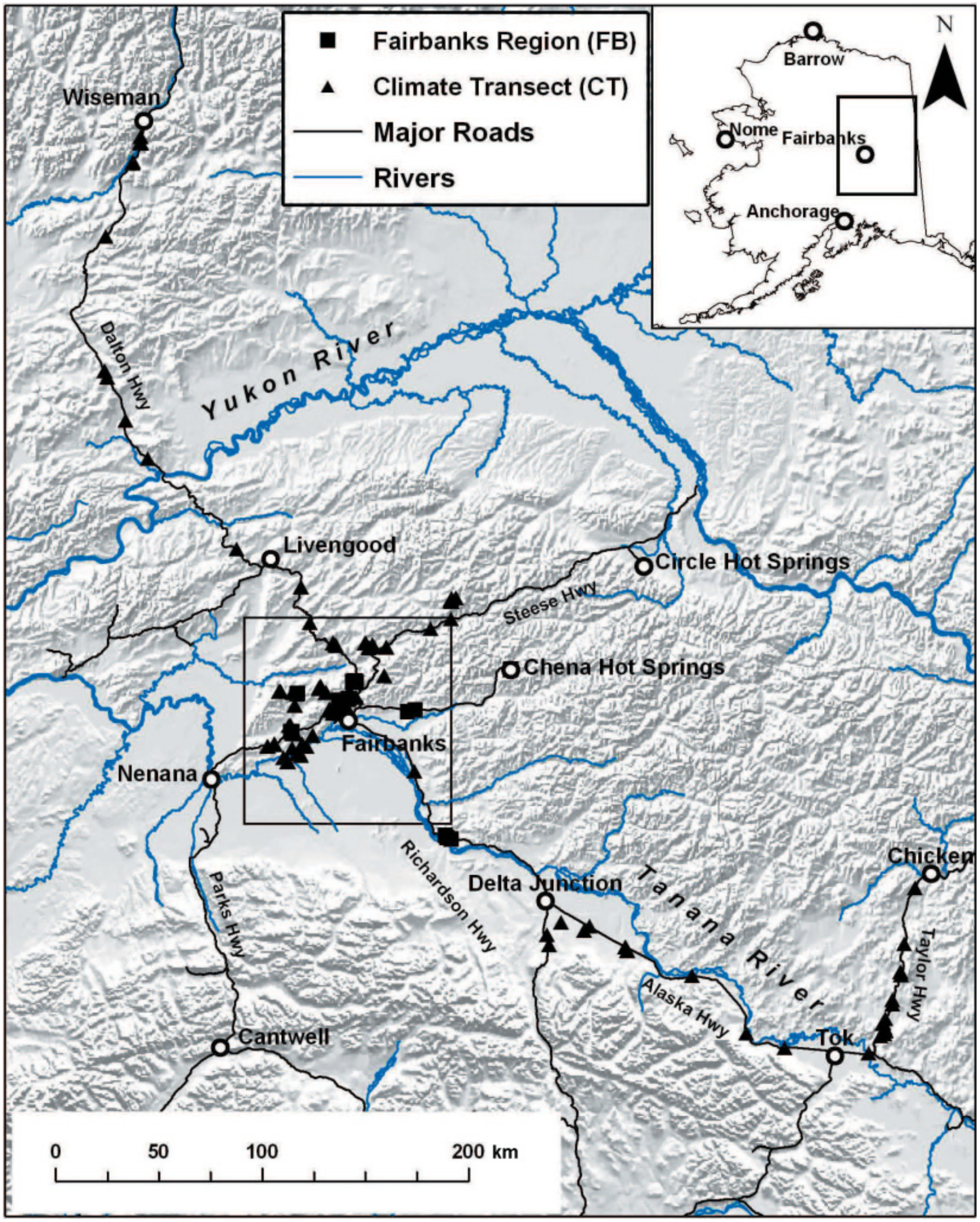
The study area is bounded by the Alaska Range (~63°N) to the south, the Brooks Range (~67°N) to the north (where black spruce reaches its northern limit), the Dalton Highway (~150°W) to the west and the Alaskan–Canadian border (~142°W) to the east. This 250 000 km^2 area is an intermontane plateau dissected by the Yukon, Tanana, and Kuskokwim River valleys (Hultén 1968). It is characterized by small mountain ranges and associated gently sloping uplands, large areas of flat lowlands, and braided rivers with broad floodplains (Fig. 1).

Interior Alaska is an area of discontinuous permafrost, with approximately 75%–80% of the ground underlain by permafrost, except on some south-facing slopes and along major river floodplains (Osterkamp and Romanovsky 1999). Permafrost temperatures range from –0.5 to –2 °C, and the ground is covered with snow and ice for 6–9 months of the year (Slaughter and Benson 1986). The region has a continental climate, with extreme temperatures ranging from –70 to 35 °C. Annual precipitation averages 286 mm, of which about 35% falls as snow (Hinzman et al. 2005).

Most of interior Alaska escaped the repeated glaciations of the Quaternary. However, there are large Quaternary glacial deposits along the Yukon River valley. In addition, Illinoian glaciers were present at the northern edge of the study area (the southern slopes of the Brooks Range), and Illinoian and Pre-Illinoian glaciers were present at the southern edge of the study area (along the northern flanks of the Alaska Range). Periglacial processes were active during the Pleistocene and even during the Little Ice Age, so the lowlands are characterized by permafrost, ice wedges, and Aeolian deposits (Pewe et al. 1965).

Although most of interior Alaska was never glaciated, soils show relatively little morphological development. Ninety-seven percent of the mapped areas of interior Alaska are Inceptisols, Entisols, Histosols, or Gelisols (Ahrens et al. 2004). Throughout the region, silt–loam upland soils have developed from loess that was laid down during the last glacial maximum and from underlying schist bedrock, with the

Fig. 1. Location and extent of the study area within Alaska (inset) showing the topography of the region and sites within the Fairbanks region (100 × 100 km grid) and along the climate transect.



loess caps becoming thinner farther away from loess sources. Floodplain soils have developed in sandy or silt-textured alluvium, mostly of glacial origin (Rieger et al. 1963).

Field sampling

We sampled black spruce communities at three scales: (*i*) along a transect that spanned the entire study area, representing a large range of climate variation as related to changes in latitude; (*ii*) within a nearly uniform climate area 100 × 100 km around Fairbanks; and (*iii*) along toposequences within watersheds scattered across the study area. We sampled 54 black spruce sites within a 10 000 km^2 area around Fairbanks during the summer of 2000, then expanded the sampling during the summers of 2001 and 2002 to include an additional 92 sites along the climate transect ranging from the Alaskan–Canadian border to the foothills of the Brooks Range (Fig. 1). Sites were chosen based on their proximity to roads or river systems where they were accessible. Where possible, we selected sites along a toposequence (summit, shoulder, side slope, toe slope, and valley bottom). A modification of the centralized replicate sampling procedure was employed, and we subjectively chose plot locations in areas of homogeneous vegetation that were dominated by a black spruce overstory (Mueller-Dombois and Ellenberg 1974). Approximately 30 sites within the Fairbanks and change in latitude areas were selected because they were previously established by the Forest Growth and Yield Program at the University of Alaska Fairbanks (UAF) Agricultural and Forestry Experiment Station.

At each site, we conducted a relevé, defined as a vegetation sample or stand, that included a list of all plant (vascular and nonvascular) species present and a visual estimate of percent cover of each species using the Braun-Blanquét cover-abundance scale (Braun-Blanquét 1965; Mueller-Dombois and Ellenberg 1974). The same person in every site did this visual estimate so comparisons between sites could be made. Each relevé was established in a homogeneous area of vegetation and topography. Measuring tapes were laid out to determine a 10 000 m^2 area. If this area encompassed major changes in vegetation or topography (i.e., if the site included both the summit and the shoulder of a hill), the area of the site was reduced or moved to encompass a single topographic unit. All relevés were at least 2500 m^2 in size, 90% were greater than 6400 m^2, and 80% were 10 000 m^2. Voucher specimens of all species were deposited in the Bonanza Creek Long Term Ecological Research (LTER) herbarium located at the UAF. Vascular nomenclature follows Hultén (1968) with the exception of sedges (Reznicek 2003) and grasses (Welsh 1974). Nonvascular nomenclature follows Esslinger (1997) for lichens, and Anderson (1990) and Anderson et al. (1990) for bryophytes.

We dug a soil pit at all sites to a depth of 1 m or to frozen ground, whichever came first. We described soil texture by hand texturing the uppermost mineral horizon; measured in situ pH of the uppermost mineral horizon using an Oaklon pH meter; and recorded the depths of the Oi, Oe, and Oa horizons as well as the depth to bedrock or frozen soil. Sites were revisited in September or October of the same year to measure maximum thaw depth. Soil samples were collected from the uppermost mineral horizon (at approximately 10–15 cm), and percent soil moisture and bulk density were determined following the methods of Walker et al. (1994). Mineral soils were dried at 50 °C, sieved, and sent to the UAF Palmer Research Station for the following analyses: pH; concentrations of NH_4, NO_3, P, K, C, N, and total exchangeable cations; cation exchange capacity; texture (sand, silt, and clay); and percent loss on ignition.

We measured, or estimated, the following environmental variables at each site: site moisture index (a visual assessment of topography and vegetation at a site), soil moisture scalar (based on the amount of water that could be squeezed out of the soil in the field and the appearance of gleyed or mottling soils above 15 cm), a disturbance scalar (including fire (presence of charcoal in the soils, fire scars, and standing burnt trees), herbivores, humans, and other), latitude and longitude (using a Trimble Geoexplorer 3 GPS unit), physical characteristics of the site (slope, aspect, elevation, topography, parent material, and geomorphology), microtopography (average of 10 random measurements in centimetres), and gross water flux category (as minerotrophic (noticeable running water through site), ombrotrophic (noticeable standing water at site), or no water visible).

We cored 5–10 of the largest trees in each stand, as close to the base of the tree as possible, to determine the age of the oldest trees as an estimate of time since the last fire. Rings were counted under a microscope and visually cross-dated (Sweetnam and Sutherland 1985). If the pith was missed during coring, the distance to pith was estimated by fitting a circle template to the innermost curved ring, or by subtracting core length from the radius at core height. Tree age was then estimated from age–diameter relationships based on trees in which the pith was obtained. The number of years the tree took to grow to the cored height was estimated by a regression equation developed for black spruce seedlings growing on the Kenai Peninsula, Alaska (Devolder 1999). These ages were analyzed in 10-year age classes to reduce the effects of errors among the age estimates.

We employed the point centre quarter method (PCQ) (Mueller-Dombois and Ellenberg 1974) randomly at five points in each site to quantify density (trees per hectare), basal area, and mean height/DBH (diameter at breast height; 1.37 m) of trees in the stand. To ensure the precision of our estimated density, we performed a power analysis using actual density figures from over 150 black spruce sites in interior Alaska (E.C. Packee, unpublished data). In addition, our estimates were quite comparable (±5%) to true densities measured at five of our sites (C. Rosner, personal communication, 2004). However, the level of accuracy might be limited for these data due to large amounts of variability.

Vegetation classification

Vegetation was classified using the Braun-Blanquét table sorting method, a phtyosociological approach based purely on floristic composition of the sites (Braun-Blanquét 1965) and the specific protocol of Daniëls (1982) for recognizing diagnostic and constant species. Diagnostic species are defined as species with high constancy (occurrence) and abundance within a given community and low constancy and abundance in all other community types. Communities are named first by the most abundant species (black spruce in all cases), followed by one or two of the diagnostic species most indicative of that community. Subtypes are named for the most abundant or important diagnostic species. This classification was derived independently from the ordinations used later in the study to develop species–environmental relationships. Detailed methods and data on percentage cover of each species are available on the *Canadian Journal of Forest Research* archive system and at http://www.lter.uaf.edu/studies_search.cfm.

Use of Braun-Blanquét

Since its acceptance as the internationally accepted method of forest classification by the International Botanical Congress in 1936, Braun-Blanquét has been used worldwide in the delineation of plant communities and assemblages. This forest classification method is the foundation of the future development of a circumpolar boreal forest map supported by the Conservation of Arctic Flora and Fauna. When realized, the circumpolar boreal forest map would be based on phytosociological classes of boreal forest vegetation similar to the circumpolar arctic vegetation map completed in 2003 (CAVM team 2003).

There is some debate about the subjectiveness of table-sorting methods such as Braun-Blanquét, instead of more objective classification techniques such as TWINSPAN (two-way indictor species analysis) (Hill 1979). TWINSPAN produces a tabular matrix arrangement approximating the results of a Braun-Blanquét table (Dufrêne and Legendre 1997); however, it has been criticized (e.g., Oksanen and Minchin 1997; McCune and Grace 2002) because it assumes the existence of only one strong gradient dominating the data structure. Therefore, TWINSPAN may fail to identify secondary gradients, and the cutting points along the dominant axis are arbitrary; instead of separating sites based on large gaps in the data, sites that may be very close in species composition may be separated. McCune and Grace (2002) suggest that ecologists should not use TWINSPAN, except in the very special case where a two-way ordered table is needed for a data set with a simple, one-dimensional underlying structure. Because we did not know a priori if there was more than one strong underlying gradient, we chose not to use TWINSPAN for our classification.

Species diversity

After defining the black spruce communities through the use of Braun-Blanquét classification, we examined plant diversity at three scales: alpha diversity (the species richness within a community), beta diversity (the turnover rate among communities, measured as the ratio between gamma diversity and the average alpha diversity) and gamma diversity (the overall landscape or regional richness). We used multivariate analysis of variance (MANOVA) (SPSS version 11, SPSS Inc., Chicago, Illinois) to analyze the relationship of vascular, moss, lichen species richness, and total species richness (dependent variables) to topographic position and soil acidity (independent variables). The independent variables in the analysis were the categorical variables acidity (i.e., acidic = pH 5.5 or nonacidic > pH 5.5 as defined by Walker and Everett (1991)), and topographic position (summit, shoulder, side slope, toe slope, valley bottom, and lowland), with the dependent variables being total species richness, vascular species richness, moss species richness, and lichen species richness. We assessed significant differences between the categories using univariate ANOVA tests. Assumptions for MANOVA were met for all analyses.

Ordination

We used nonmetric multidimensional scaling (NMDS) with the program PC-ORD, version 4.25 (Kruskal and Wish 1978; McCune and Mefford 1999) to analyze the main relationship between species composition and various environmental variables. NMDS is an ordination technique well suited for data that are nonnormal, or occur along arbitrary or discontinuous scales and is considered the most effective ordination method for ecological community data (McCune and Grace 2002). Unlike direct ordination methods, such as canonical correspondence analysis, NMDS does not assume a unimodal model of species responses to the environment, and allows for the possibility that some of the community variation is related to environmental variables that were not measured. Therefore, important community patterns are retained, regardless of what environmental variables were measured. In this way, NMDS provides a quantitative method of separating sites based on species composition, thus allowing a semiobjective evaluation of the results of the Braun-Blanquét classification of the same data. For example, if the NMDS ordination shows similar separation between sites as the more subjective sorting method, it increases the confidence in the classification method.

Ordinations were performed on the subset of floristic data collected in the Fairbanks region and for all data obtained from interior Alaska, including the Fairbanks region. We used the Sorensen distance measure, with random starting configurations, with 10 runs of real data and 20 runs of randomized data, the latter to provide the basis for a Monte Carlo test of significance of each dimension, or axis. Dimensionality (i.e., number of axes) was assessed by comparing the final stress values among the best solutions, one best solution for each dimensionality. PC-ORD selects the lowest dimensionality that meets this criterion.

Environmental variables were correlated to the NMDS axes using Kendall correlations and related to the ordination with vectors that indicate both the direction and magnitude of the strongest environmental variables in the ordination space.

Results

Regional vegetation classification

The Braun-Blanquét classification revealed three black spruce community types and five subtypes that incorporate the range of vegetation dominated by black spruce in interior Alaska (Table 1, http://www.lter.uaf.edu/studies_search.cfm). Diagnostic species are listed for each community type, as well as diagnostic species for each subtype within the communities. It is important to note that diagnostic species for each subtype are only differential among the subtypes within that community and therefore may overlap with other subtypes in a different community type. Therefore, community and subtypes are defined by a group of species that occur together, not just by the presence or absence of one or two species. In the descriptions below, numbers (1, 2, and 3) indicate communities, and letters (a and b) indicate subtypes.

(1) Acidic black spruce / lichen forest (*Picea mariana* / *Cetraria islandica*): The acidic black spruce / lichen forest is dominated by black spruce, fruticose lichens, and many species of mosses. This community type occurs in both uplands and lowlands of interior Alaska and in areas of low mineral soil pH (less than 5.5). It is usually associated with steep slopes or no slopes and occurs rarely in sites of moderate slopes. Diagnostic species include (in order of decreasing constancy and designated as vasculars (v), lichens (l), and mosses (m)): *Cetraria islandica* (L.) Ach. (l), *Polytrichum commune* Hedw. (m), *Lycopodium annotinum* (La Pyl.) Hult (v), *Spirea beauverdiana* Schneid. (v), *Cladonia sulphurina* (Michaul.) Fr. (l), and *Cladonia deformis* (L.) Hoffm. (l). Within this community type, there is one subtype that is restricted to wet acidic conditions and has clearly delineated diagnostic species. Dry sites within this community type exist but have no recognizable set of diagnostic species and lacked the diagnostic wet species.

(*a*) Wet acidic black spruce muskeg (*Picea mariana* / *Ledum decumbens* / *Sphagnum girgensohnii*): This is an open black spruce subtype that occurs on low-nutrient soils, often in lowland areas of shallow active layer. Black spruce trees are often stunted, and the subtype

Table 1. Black spruce community names and habitat characteristics in interior Alaska, all of which fall within the Braun-Blanquet class *Linnaeo americanae – Piceetea marianae*.

Community (bold), subtype names (italics), and (common name)	Habitat characteristics
Picea mariana* / *Cetraria islandica (acidic)	Acidic (pH < 5.5, average pH 5), tendency towards either steep or flat slope, average elevation 493 m, mostly side slopes
Ledum decumbens / *Sphagnum girginsohhnii* (wet acidic)	Acidic (pH < 5.5, average pH 4.7), mesic
Picea mariana* / *Rosa acicularis* / *Equisetum species (nonacidic)	Nonacidic (pH > 5.5, average pH 6.1), tendency towards well-drained flatlands to slight slope, average elevation 290 m, mostly lowlands
Larix laricina /*Chamadaphne calyculata* (wet nonacidic)	Slightly nonacidic, mesic site conditions
Cladina stellaris – Peltigera malacea (dry nonacidic)	Slightly nonacidic, xeric site conditions
Picea mariana*/*Tofieldia pusilla*/*Cetraria laevigata (tree line)	Tree line, mostly uplands and tendency for steeper slopes, more xeric than above
Loiseluria procumbens / *Cetraria nivalis* (elevational tree line)	Elevational tree line (500 m and above), acidic (pH < 5.5, average 5.2)
Salix reticulata / *Dryas octopetala* (latitudinal tree line)	Latitudinal tree line (between 329 and 350 m), nonacidic pH (average pH 7.6)

Note: Community subtypes and common vegetation type are also named.

tends to be dominated by shrubs (*Ledum decumbens* (Ait.) Hult, *Betula nana* (Sukatsch.) Hult, *Oxycoccus microcarpus* (Turcz.) Fedtsch. & Flerov., and *Rubus chamaemorus* L.), sedges (*Eriophorum vaginatum* L. and *Carex bigelowi* Torr.), and acidic sphagna (*Sphagnum girgensohnii* Russow, *Sphagnum rubellum* Wils., and *Sphagnum magellanicum* Brid.). Other diagnostic species of this subtype are *Aulocomnium palustre* (Hedw.) Schwaegr. (m), *Aulacomnium turgidum* (Wahienb.) (m), and *Polygonum alaskanum* (Small) Wight (v).

(2) Nonacidic black spruce / rose / horsetail forest (*Picea mariana* / *Rosa acicularis* / *Equisetum* spp.): This community is dominated more by vascular species (especially three different *Equisetum* species) than the acidic black spruce forest, with the occasional presence of white spruce (*Picea glauca* (Moench) Voss). This community can occur in both uplands and lowlands, although more often in the lowlands, with a tendency toward well-drained flatlands or slight slopes. Diagnostic species in order of increasing constancy include *Rosa acicularis* Lindl. (v), *Equisetum scirpoides* Michx. (v), *Arctostaphylos rubra* (Rend. & Wilson) Fern. (v), *Mertensia paniculata* (Ait.) G. Don (v), *Pyrola secunda* L. (v), *Tomenthypnum nitens* (Hedw.) Loeske (m), *Picea glauca* (v), *Sausserea angustifolia* (Willd.) DC. (v), *Equisetum arvense* L. (v), and the less acidic *Sphagnum warnstorfii* Russow (m). Within this community type, there are two subtypes defined by the moisture status of the site.

(*a*) Wet nonacidic black spruce / larch fen (*Picea mariana* / *Larix laricina* / *Chamaedaphne calyculata*): This subtype is restricted to the lowlands and is usually codominated by Alaska larch (*Larix laricina* (Du Roi) K. Koch). Because of recent larch sawfly outbreaks in interior Alaska, many of these larches are now dead. This subtype occurs in minerotrophic areas, which indicate a fen rather than a bog. The active layer can be shallow in this subtype, but permafrost conditions are more variable than in the wet acidic subtype. Trees in this subtype can have the same stunted appearance as in the wet acidic black spruce subtype, and some of the same diagnostic species, such as *Betula nana* (v), *Rubus chamaemorus* (v), and *Eriophorum vaginatum* (v). Therefore, these particular species should not be used as sole indicators of community type. They are more an indication of site moisture status than of acidity. It is the combination of nonacidic diagnostic species with the wet diagnostic species that are the indicators of this subtype.

(*b*) Dry nonacidic black spruce forest (*Picea mariana* / *Cladina stellaris – Peltigera malacea*): This subtype occurs in xeric conditions, mostly in the uplands. Like the acidic black spruce forest, this subtype is dominated by lichens, yet the lichen species are different. In addition to the nonacidic diagnostic species, this subtype can be recognized by the presence of *Equisetum pratense* L. (v), *Cladina stellaris* (Opiz) Brodo (l), *Peltigera malacea* (Ach.) Funck (l), and *Cornus canadensis* L. (v).

(3) Tree-line black spruce woodland (*Picea mariana* / *Tolfielda pusilla* / *Cetraria laevigata*): Although white spruce is usually associated with tree line in interior Alaska, black spruce does occur at altitudinal and occasionally latitudinal tree line, sometimes codominating with white spruce or as the only dominant tree. Therefore, we describe a third community type with two subtypes. The tree-line black spruce woodland subtype tends to occur at higher elevations, on steeper slopes, and in much more xeric conditions than the two previous black spruce communities. Diagnostic species that are typical of tree-line areas include *Ledum decumbens* (v), *Tolfieldia pusilla* (Michx.) Pers. (v), *Cetraria islandica* subsp. *crispiformis* (Räsänen) Kämfellt (l), *Pedicularis labradorica* Wirsing (v), *Cladonia uncialis* (L.) F.H. Wigg (l), *Dicranum flexicaule* Brid. (m), *Stereocaulon tomentosum* Fr. (l), and *Polygonum bistorta* L. (v). Within this community type, there are two subtypes that are indicative of latitudinal versus elevational tree line.

(*a*) Elevational acidic tree-line woodland (*Picea mariana* / *Loiseleuria procumbens* / *Cetraria nivalis*): This subtype occurs at high elevation (500 m and above) and tends to be quite acidic. Therefore, it has many of the diagnostic species of the acidic black spruce forest such as *Polytrichum commune* (m), *Lycopodium annotium* (v), and *Spiraea beauverdiana* (v), and there are many diagnostic species fairly distinct to this subtype, including *Cetraria nivalis* (L.) Ach. (l), *Anemone narcissiflora* L. (v), *Salix brachycarpa* Nutt. (v), and many *Cladonia and Cladina* species including *Cladonia deformis* (L.) Hoffm. (l), *Cladina rangiferina* (L.) Nyl (l), and *Cladonia gracilis* (L.) Willd. (l).

(*b*) Latitudinal nonacidic tree line (*Picea mariana* / *Salix reticulata* / *Dryas octopetala*): This subtype occurs at lower elevations (329–350 m) than the elevational tree-line subtype and is typical of all northern tree-line sites. It has a more distinct species group than any other black spruce type, with many species in common with moist nonacidic tundra (Walker and Everett 1991). Diagnostic species include *Tomenthypnum nitens* (m), *Potentilla fruticosa* L. (v), *Saussurea angustifolia* (v), *Andromeda polifolia* L. (v), *Equisetum arvense* (v), and *Equisetum scirpoides* (v), which occur in other nonacidic black spruce community types, as well as *Dryas octopetala* L. (v), *Salix reticulata* L. (v), *Carex coccina* R.Br. (v), *Parnassia palustris* (Fern) Hult. (v), *Plantanthera obtusata* (Pursh) Lindl. (v), *Ranunculus lapponicus* L. (v), and *Spiranthes romanzoffiana* L.C. Rich (v), which are mostly restricted to northern tree-line sites.

Regional patterns of species richness and diversity

We encountered a total of 275 species in the course of this study. Of those, 146 are vascular, 67 are bryophytes, and 62 are lichens (Table 2). Among the vascular species, we encountered 6 trees (the entire tree flora of the region), 38 shrubs, and 102 forbs. Of the three black spruce community types, the tree-line type has the highest alpha diversity and the lowest beta and gamma diversity, indicating that diversity occurs at a finer scale in the tree-line community type. The acidic black spruce community type has the lowest alpha diversity, and the nonacidic black spruce community has the highest gamma diversity (Table 2).

Results from the MANOVA showed a significant effect of pH class ($F = 6.908$, $P < 0.0001$) and of topographic position ($F = 3.530$, $P < 0.001$) but no significant interaction between pH and topographic position (Table 3). Univariate tests showed that uplands (defined as summit, shoulder, and side slopes) have significantly greater lichen richness, and lowlands (defined as toe slopes, valley bottoms, and lowlands) have significantly greater moss richness ($F = 4.998$, $p = 0.0003$ and $F = 4.8998$, $p = 0.0004$ respectively) (Figs. 2*c* and 2*d*). Univariate results also showed that acidic sites have significantly more moss species, and nonacidic sites significantly more vascular species ($F = 10.309$, $p = 0.0017$ and $F = 7.594$, $p = 0.0067$) (Figs. 3*b* and 3*c*).

Regional stand ages and structural characteristics

We encountered a wide range of age classes with 20 stands established prior to 1801, 25 stands established between 1911 and 1920, and 10 stands established after 1930 (Table 4). We captured a fairly large amount of variation in black spruce stand ages; however, because o the late-successional aspect of black spruce, we found more older (>100 years) stands (78 stands) than younger (< 100 years) stands (68 stands) (Table 4).

Table 2. (A) Number of sites, diversity (alpha, beta, gamma) within each community and subtype, and (B) total vascular, moss, and lichen richness across the entire study region.

(A) Community diversity.

		Diversity measure		
Community and subtype	*n*	Alpha	Beta	Gamma
Tree line	9	47	3	161
Acidic	6	46	3	115
Nonacidic	3	49	2	93
Nonacidic	61	41	5	220
Wet	23	42	4	177
Dry	38	38	5	184
Acidic	72	38	5	191
Wet	44	40	4	162

(B) Numbers of species.

Taxon	No. of species
Total vascular	146
Trees	6
Shrubs	38
Forbs	102
Total moss	67
Total lichens	62
Total	275

The three black spruce community types that we defined based on floristics differ substantially in stand structure and environmental characteristics (Table 5). Mean tree density of the tree-line black spruce sites is only about 25% of the other two black spruce types, and this was associated with shorter, younger trees and a thinner organic mat. The nonacidic black spruce community differs most strikingly from the acidic black spruce community in having high basal area (resulting from both greater density and DBH), taller trees, and deeper active layer (Table 5). One of the most interesting results is that some of the structural and physical characteristics (e.g., density, basal area, maximum active layer, and maximum microtopography) are quite variable across the full range of sites and exhibited a large range of variability within each vegetation type. This finding is important because the variability is as large as previous descriptions of structural characteristics across four major forest types in interior Alaska (white spruce, black spruce, balsam poplar, and alder (Viereck 1983*a*)). Prediction of community type based on these variables alone, as in previous structural-based community classifications in Alaska is, thus, problematic.

Ordinations

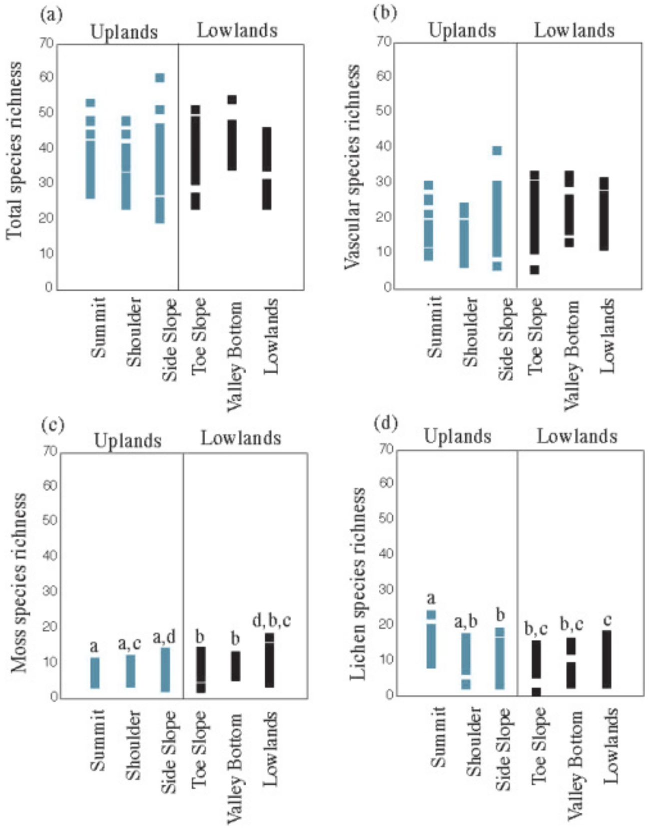
Local patterns

Two major gradients captured 61% of the variance in species composition in the Fairbanks region. The strongest environmental gradient corresponds to a paludification gradient while the second major gradient corresponds to a topographic gradient (Fig. 4). Higher dimensions added little explanatory power.

Table 3. Results of multivariate analysis of variance for species richness (total, vascular, moss, and lichen) under the influence of topographic position (summit, shoulder, side slope, toe slope, valley bottom, and lowlands) and soil pH (nonacidic and acidic).

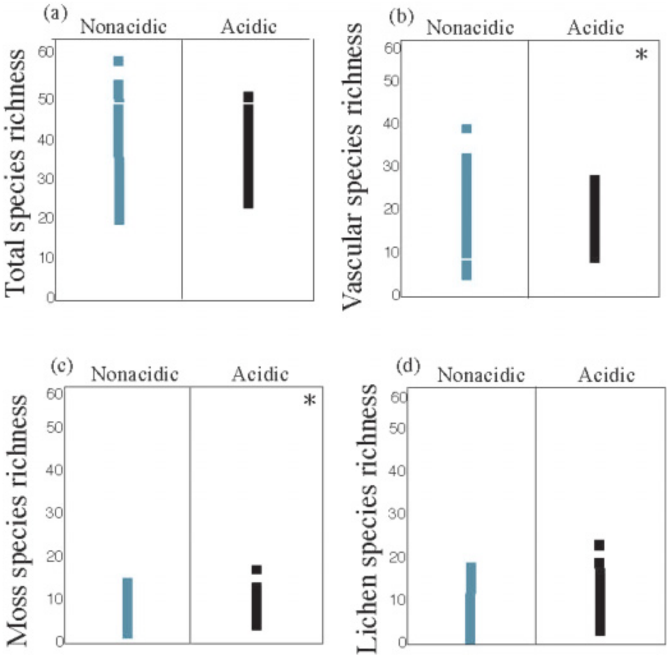
	Value	*F*	df	*P*	Power
Topographic position					
Wilks' λ	0.68	3.530	15	<0.0001	0.999
Pillai's trace	0.34	3.275	15	<0.0001	0.999
pH					
Wilks' λ	0.86	6.908	3	<0.0001	0.976
Pillai's trace	0.14	6.908	3	<0.0001	0.976
Topographic position × pH					
Wilks' λ	0.92	0.721	15	0.764	0.44
Pillai's trace	0.1	0.728	15	0.756	0.487

Fig. 2. Species richness for the total flora and for vascular, moss, and lichen species across the entire study region, separated by topographic position. Values with different letters (a, b, c, or d) are significantly different ($p < 0.05$) among topographic positions.



Axis 1, which we relate to a paludification gradient, is positively correlated with attributes of poorly drained organic lowlands (i.e., percent carbon, percent nitrogen, cation exchange capacity, loss on ignition, percent moisture, and depth of the Oi horizon) (Table 6). The first axis also correlates negatively with attributes of more well-drained sites, including pH, percent tree cover, percent dead tree, average tree height of the stand, and tree density (Fig. 4, Table 6). The second axis of the ordination separates uplands (summits, shoulders and side slopes) from lowlands (toe slopes, valley bottoms, and lowlands) (Fig. 4). This axis correlates positively with attributes of uplands, including slope and elevation, and negatively with attributes typical of lowland bogs, including pH, Ca, Mg, Na, and percent graminoids (Table 6).

Fig. 3. Species richness for the total flora and for vascular, moss, and lichen species across the entire study region, separated by acidity. Values with asterisks are significantly different ($p < 0.05$).



Regional patterns

The axes that captured variance in species composition at the scale of interior Alaskadiffered from those in the Fairbanks region. Three axes captured 81% of the variance in species composition for all sites across interior Alaska. The strongest environmental gradient corresponds to an acidity gradient along axis 1, axis 2 corresponds to a topography/soil drainage gradient, and axis 3 represents a productivity gradient. We present only axis 1 versus axis 2 (Fig. 5).

Axis 1, a complex soil acidity gradient, correlates negatively with laboratory pH, in situ pH, Ca, Mg, Na, deciduous shrub cover, evergreen shrub cover, and seedling cover, and slope (Table 7). The second axis corresponds to a site topo-

Table 4. Number of stands in each age class (approximate year of stand establishment).

Year of establishment	No. of stands
<1800	20
1801–1810	8
1811–1820	8
1821–1830	11
1831–1840	7
1841–1850	5
1851–1860	6
1861–1870	3
1871–1880	7
1881–1890	3
1891–1900	9
1901–1910	13
1911–1920	25
1921–1930	7
1931–1940	5
1941 or later	5

Note: Stand ages are based on tree cores taken from 10–15 of the largest trees in each stand.

graphic and drainage gradient, which is most likely a combination of the two important axes in the Fairbanks ordination. This axis correlates negatively with variables associated with poorly drained sites such as Ca, Mg, laboratory pH, Na, moss cover, water content, and stand density, and positively with elevation and percent lichens. Axis 3 likely represents a productivity gradient, possibly associated with time since last disturbance, and is correlated with Oa thickness and stand structural characteristics such as mean DBH of the stand, mean height of stand, and stand density. The third axis is negatively correlated with attributes related to soil organic matter accumulation, such as percent K, C, and N, Na, percent clay, and seedlings (Table 7).

Discussion

Classification implications

This work provides the first extensive phytosociological analysis of Alaskan black spruce forests and therefore constitutes the first step toward including Alaska into a circumboreal forest classification. Peinado et al. (1998) proposed a broad class, *Linnaeo americanae – Piceetea marianae* (North American coniferous forests), with four associations (within two alliances) for North American black spruce vegetation. Based on fewer than 20 black spruce relevés, they suggested that Alaskan black spruce sites would fall into two of the Canadian black spruce associations. Based on our study of 146 stands, we propose that our stands fall into the class *Linnaeo americanae – Piceetea marianae*, but the three interior Alaska black spruce community types should be described as three new associations because of differences in local flora including many species unique to Alaska.

The black spruce communities that we describe for Alaska differ floristically from those described previously in eastern and central Canada (e.g., Orloci and Stanek 1979; Foster 1984; Peinado et al. 1998). For example, although La Roi and Stringer (1975) described similar bryophyte flora for black spruce stands across the North American boreal forest, earlier results (La Roi 1967) reported the vascular flora of black spruce communities with high presence of *Vaccinium myrtilloides* Michx., *Vaccinium angustifolium* Ait., *Petasites palmatus* (Ait.) Gray, and *Gaultheria hispiduta* (L.) Muhl. ex Bigelow, none of which occur in the black spruce communities we described. Our wet acidic and wet nonacidic black spruce subtypes are similar to community types described for the southern boreal forest in Alberta (La Roi 1967) as *Picea mariana* / *Rubus chamaemorus* and *Picea mariana* / *Carex aquatilis*. Overall, our black spruce community types are most similar to types described for the Yukon Territory and other western parts of Canada (e.g., Orloci and Stanek 1979) with a few species differences, most notably the presence of white spruce instead of black spruce in many of the otherwise similar community descriptions.

These differences in species composition reflect substantial differences in environment, fire regime, and biogeographic history, all of which contribute to the local flora of a region. The continental climate of interior Alaska contrasts with the more maritime climate of eastern Canada. Much of interior Alaska has never been glaciated, unlike most of Canada (Larsen 1980). In addition, Alaskan black spruce ecosystems are thought to be relatively young, with black spruce entering the floral record approximately 5000 years ago (Keenan and Cwynar 1992). Finally, differences in disturbance regimes and substrate might contribute to the differences in species composition and, consequently, community classifications.

Viereck et al. (1992) provided the most widely used classification of black spruce in interior Alaska. The Alaskan vegetation classification describes seven black spruce community types with four broad classes (closed needleleaf forest, open needleleaf forest, needleleaf woodland canopy, and dwarf tree scrub woodland) based on stand structural characteristics, such as tree size and density. In our study, we found no significant correlations between stand density and species composition at the spatial scale of interior Alaska (Table 6, Fig. 5), indicating that floristic and physiognomic approaches can lead to quite different community classifications. The physiognomic approach may be a better predictor of processes such as productivity and energy exchange that are dominated by the tree canopy (Chapin et al. 1996). The floristic approach is particularly useful in predicting those ecosystem processes that are strongly affected by the understory species composition. These processes include thermal insulation of permafrost, nutrient cycling, fire regime, herbivory, and pollination (Walker et al. 1994; Chapin and Danell 2001). Our study extent was limited by accessibility, and it is highly probable that including an even larger area of Alaska would result in additional communities and subtypes.

Scale-dependent patterns

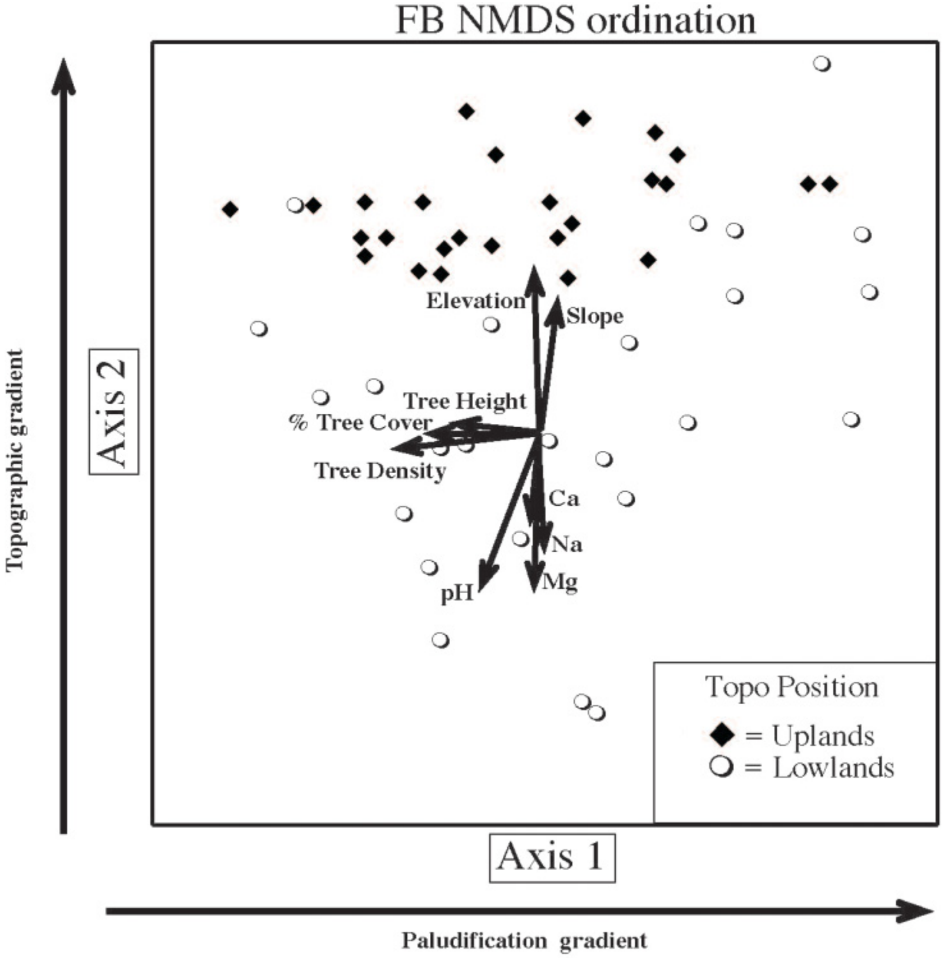
This study revealed the importance of spatial scale in determining the patterns and controls over community composition in interior Alaska. Black spruce communities vary not only with the spatial scale represented (i.e., local vs. regional patterns) but also with time. For example, weathering of parent material, which happens on the time scale of landscape development (≥1000 years), and time since distur-

Table 5. Stand structural characteristics for each black spruce community type.

	Vegetation type			
	Nonacidic	Acidic	Tree line	Range
Tree characteristics				
Density of stand (trees/ha)	5133.74±516.07	4153.24±472.15	1158.71±266.40	88.66 – 23 668.6
Stand age (years)	142±9	150±6	88±15	~10–408
Height of trees (m)	4.8±0.03	4.12±0.15	3.03±0.26	1.81–16.00
Basal area of stand (m^2/ha)	13.38±1.19	10.11±1.08	3.77±1.16	0.14–42.5
DBH of trees (cm)	5.51±0.03	5.03±0.19	5.13±0.66	1.53–18.27
Ground characteristics				
Live moss thickness (cm)	4.4±0.3	4.75±0.29	4.2±1.0	0.5–13
Oi depth (cm)	5.2±0.4	5.73±0.44	3.5±0.8	0–18
Oe depth (cm)	7.4±0.5	6.6±0.4	3.7±0.6	1–21
Oa depth (cm)	7.5±0.6	6.3±0.5	4.7±0.8	0.5–23
Physical characteristics				
Mean active layer depth (cm)	55.1±0.3	50.3±0.2	51.3±0.7	23 to >130
Max. microtopography (cm)	27.0±2.0	27.6±1.7		27.2±3.8

Note: Values are means ± SE. Ranges over all three community types are also given.

Fig. 4. The Fairbanks (FB) region ordination grouped by topographic position, where summits, shoulders, and side slopes are grouped as uplands and toe slopes, valley bottoms, and lowlands are grouped as lowlands. Vectors indicate the environmental variables that are most strongly correlated with the ordination axes, where length and direction represent magnitude and direction of correlation, respectively.



bance, which happens on a shorter successional timescale (~100 years), both contribute to the patterns observed in mature black spruce forests in interior Alaska. We, therefore, discuss two spatial scales (local versus regional) and within those spatial scales we examine temporal patterns (landscape age versus succession).

Table 6. Kendall correlations of environmental variables and site characteristics and nonmetric multidimensional scaling axis 1 and axis 2 for the Fairbanks Region ordination.

Environmental variable	Axis 1: paludification gradient	Axis 2: topographic gradient
% slope	0.125	0.478*
Elevation	–0.062	0.373*
pH of mineral layer	–0.300*	–0.529*
% C	0.323*	0.044
% N	0.414*	0.083
Cation exchange capacity	0.287*	–0.060
Ca	–0.048	–0.336*
Mg	–0.104	–0.420*
Na	–0.076	–0.279*
% loss on ignition	0.286*	–0.058
% moisture	0.272*	–0.001
In situ pH	0.038	–0.301*
Oi (cm)	0.283*	0.129
% trees	–0.470*	–0.054
% deciduous shrubs	0.287*	–0.205
% gramminoids	0.005	–0.298*
% dead trees	–0.342*	–0.149
% water	0.108	–0.413*
Mean stand height	–0.315*	0.011
Density of stand	–0.299*	–0.029

Note: Values with asterisks are significantly correlated with the axis ($P < 0.05$). Variables that show no significant ($P > 0.05$) correlations with either axis are not shown.

Local patterns

Within the 10 000 km^2 Fairbanks Region, topography created the environmental gradient that explained the most variation in composition and structure of black spruce stands (Fig. 4, Table 6). All of our acidic black spruce sites occurred in the uplands regardless of parent material (loess versus schist). This suggests that within the Fairbanks uplands topography of a site is more important than the nature of parent material as an independent control over floristic composition. However, all of our alluvial sites around Fairbanks were nonacidic black spruce communities, suggesting that soil pH as related to soil drainage, soil moisture, or some other consequence of this topographic position could be controlling species composition in the floodplains of the Fairbanks region.

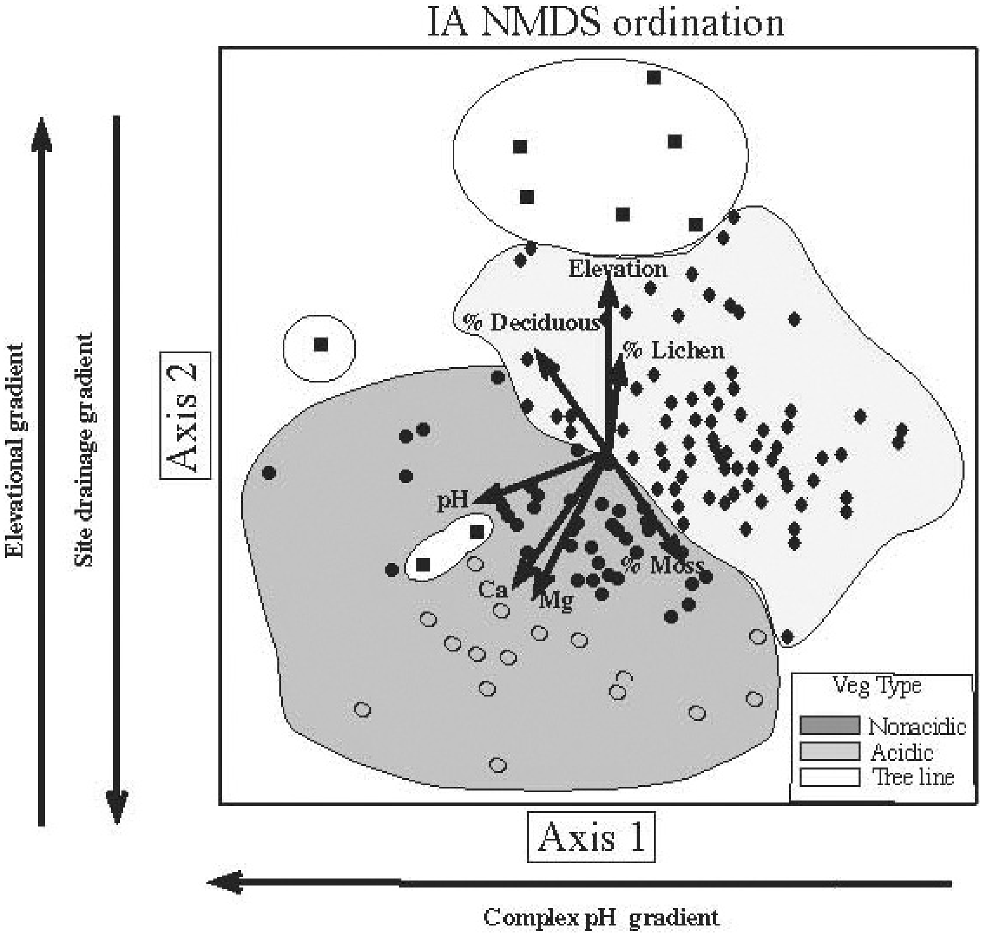
(1) Landscape development patterns: Within the uplands surrounding Fairbanks, topography affects soil–vegetation interactions through several mechanisms. Slope affects redistribution of moisture, which in turn affects soil properties, causing valley-bottom sites to become wetter over time as a result of paludification, i.e., the formation of peatlands (Birkeland 1999). Paludification leads to restricted drainage, acidification, and the introduction of *Sphagnum* mosses, which in turn acidify the soil and contribute to cooler soil temperatures and permafrost development (Jorgenson 1984). In paludified landscapes, variations in hydrology and permafrost can also influence site chemistry, leading either to ombrotrophic communities, where most of the water derives from precipitation and is highly acidic, or to minerotrophic communities in areas of groundwater upwelling, where soils are more influenced by groundwater. This hydrologic contrast is one of the driving factors that gives rise to the acidic and nonacidic black spruce community types that we described in the uplands of the Fairbanks region and is especially important in the formation of the "wet acidic black spruce muskeg" (*Ledum decumbens* / *Sphagnum girginsohhnii*) (Table 1). Topographic control over permafrost is, therefore, the most important driver in the structure and floristic composition of black spruce systems in the Fairbanks region.

(2) Successional patterns: Previous work in both uplands and lowlands around Fairbanks has suggested that succession after disturbance (fire or flooding) is a major driver of species compositional change over time (e.g., Viereck 1983*b*; Van Cleve et al. 1991; Mann et al. 1995). However, we found that our sites (most of which would be considered "mature black spruce") had a large variety of species composition and stand structure (Fig. 4, Table 5). There are at least two potential explanations: either successional trajectories after fire are highly variable, leading to differing vegetation communities of the same age, or the floristic composition of communities is determined within the first decades after fire. Johnstone et al. (2004) showed that successional trajectories of dominant trees in central Alaska and the Yukon are determined within 10–20 years after a fire. Our work suggests that the trajectories of not only the dominant tree species, but also entire species assemblages, could be determined relatively rapidly after fire.

Broad-scale patterns

When the spatial scale of our study is expanded to include a much larger extent of interior Alaska, the role of topogra-

Fig. 5. The interior Alaska (IA) ordination grouped by vegetation type as recognized by our Braun-Blanquét classification. (◆) *Picea mariana* / *Cetraira islandica*; (●) *Picea mariana* / *Rosa acicularis* / *Equisetum* spp., subtype *Cladina stellaris* / *Peltigera malacea*; (○) *Picea mariana* / *Rosa acicularis* / *Equisetum* spp., subtype *Larix laricina* / *Chamaedaphne calyculata*; (■) *Picea mariana* / *Tofieldia pusilla* / *Cetraria islandica* subsp. *crispoformis*. Vectors show correlated variables as in Fig. 4.



phy, soil moisture, and soil temperature become secondary to the influence of mineral soil pH (Fig. 5, Table 7). These results are interesting for several reasons. Firstly, it is now clear that earlier descriptions of Alaskan black spruce forest types (e.g., Van Cleve 1983), which were concentrated in the Fairbanks region, did not incorporate the full range of variability in species composition and potential ecosystem processes. Overall, the black spruce sites we sampled in the Fairbanks region were more acidic than areas to both the north and the south. The bedrock in much of the Fairbanks uplands is metamorphic rock of the Yukon–Tanana crystalline complex, formerly termed the Birch Creek schist. The Yukon–Tanana schist extends about 50 km north and west of Fairbanks, 100 km south of Fairbanks, and almost 300 km to the east. The Yukon–Tanana schist is the ultimate source of the gold in the Fairbanks mining district (Connor and O'Haire 1988) that in turn brought extensive fires and logging to this area. Therefore, mining and human-caused fires, coupled with the Precambrian schist bedrock, could contribute to the paucity of nonacidic sites and the subsequent decrease in community and species diversity of these uplands. As mentioned earlier, most of the nonacidic black spruce sites in the Fairbanks region occur on the Tanana River alluvium, which was scoured by glaciers from high-pH bedrock in the Alaska Range. This distinct difference in community distribution between the uplands and floodplains is not representative of the patterns of black spruce community types found across the broader scale of interior Alaska (Fig. 5).

Nonvascular species composition and diversity are often lumped into one or two functional groups, yet it is clear from our results that the diversity and composition of both lichens and mosses are integral in determining black spruce community patterns and, consequently, ecosystem processes (Figs. 2 and 3). For example, some *Sphagnum* mosses have a strong acidifying effect and are less decomposable than other mosses, leading to more rapid accumulation of soil organic matter and a lower pH (Kuhry and Nicholson 1993). Foliose and some fruticose lichens such as *Stereocaulon* fix nitrogen and are important contributors to the nitrogen economy of black spruce forests (Billington and Alexander 1983), whereas non-nitrogen-fixing lichens provide important winter forage for caribou (Klein 1982).

(1) Landscape development patterns: The relationship between pH and vegetation communities has been explored in the Alaskan Arctic to the north (e.g., Walker and Everett 1991) Minnesota bogs to the south (e.g., Glaser et al. 1990), and Western Canadian boreal forest to the east (e.g., Timoney et al. 1993); however, to our

Table 7. Kendall correlations of environmental variables and site characteristics and nonmetric multidimensional scaling axes 1, 2, and 3 for the interior Alaska ordination.

Environmental variable	Axis 1: pH gradient	Axis 2: drainage gradient	Axis 3: productivity gradient
% slope	0.273*	0.233	–0.045
Elevation	0.017	0.491*	–0.096
pH of mineral layer	–0.477*	–0.323*	–0.202
% P	0.031	–0.098	0.22
% K	–0.057	–0.107	–0.367*
% C	0.168	–0.084	–0.424*
% N	0.116	–0.039	–0.25*
Ca	–0.371*	–0.446*	0.036
Mg	–0.333*	–0.427*	–0.058
Na	–0.258*	–0.285*	–0.305*
% clay	–0.079	0.151	–0.298*
In situ pH	–0.413*	–0.088	–0.069
Oa (cm)	–0.053	–0.166	0.488*
% deciduous shrubs	–0.302*	0.213	–0.096
% evergreen shrubs	–0.347*	–0.067	–0.246
% seedlings	–0.219	–0.153	–0.259*
% moss	0.13	–0.328*	–0.129
% lichens	–0.056	0.343*	0.32*
% water	–0.001	–0.252*	–0.233
Mean DBH of stand	–0.047	0.078	0.268*
Mean stand height	0.029	–0.05	0.406*
Stand density	–0.011	–0.254*	0.277*

Note: Values with asterisks are significantly correlated with the axis ($P < 0.05$). Variables that show no significant ($P > 0.05$) correlations with any of the axes are not shown.

knowledge, this is the first description of a prominent pH effect in the boreal forests of Alaska. Soil pH in interior Alaska has been described as a product of vegetation that results from patterns associated with topography, paludification, and stand age (e.g., Van Cleve 1983). At a broad spatial scale, however, pH appeared to exert a strong primary effect on floristic composition that was independent of topographic controls and unrelated to stand age (Fig. 5, Table 7). Thus, our study sheds new light on the environmental gradients controlling floristic variability at the regional scale in interior Alaska and links interior Alaska to the rest of the North American boreal forest.

(2) Successional patterns: Our stand age results (Table 4) showed a fairly wide range, which, surprisingly, did not correlate with species composition (Tables 6 and 7). In other words, stands of similar age did not necessarily have similar species composition, and stands of different ages did not necessarily have larges differences in species composition.

Biologically, the influence of mineral soil pH in permafrost-dominated terrain seems counterintuitive, because roots are concentrated in the organic horizon rather than in mineral soil. However, the importance of fire to this ecosystem is well documented (Rowe and Scotter 1973; Viereck 1983*a*; Bergeron et al. 1998), and some species are rooted in mineral soil (Kummerow et al. 1983). Immediately after a severe fire, species colonize directly on mineral soil, utilizing nutrients mineralized by the fire and those provided by the mineral soil. If successional trajectories of floristic composition are determined in the first 10–30 years after fire (Johnstone et al. 2004), then variations in mineral soil pH could influence community composition long after mineral soils are directly accessed by most plant species. In addition, pH differences among sites may be amplified over multiple fire cycles, because of the strong acidifying effects of the *Sphagnum* species characteristic of acidic sites. It is still unclear why mineral soil pH is so variable throughout interior Alaska. However, it seems likely that site drainage, deposition of loess, organics derived from dead roots or the surface organic mat, fire history of the site, and geologic and glacial history of the site could all contribute to the variability in soil pH and, consequently, plant community patterns.

Conclusions

This comprehensive analysis of the community composition and structure of Alaskan boreal black spruce forests demonstrates not only a surprising amount of floristic diversity, particularly of nonvascular species, but also large variations in stand structure and complexity. The patterns of floristic composition that we observed suggest a spatially complex mosaic (Bergeron et al. 1998) that develops in response to a hierarchy of environmental controls, including broad-scale variation in pH, local variation in paludification, and fine-scale topographic variation in drainage. In addition, community composition in the stands that we studied (mostly >50 years postfire) was more sensitive to stage of landscape development (i.e., degree of paludification) than to the time since last disturbance. The effect of glacial history, parent material, and fire has been studied in other parts of the North American boreal forest (e.g., Foster 1984;

Timoney et al. 1993), but this is the first large scale study of this kind in boreal Alaska. Therefore, regardless of minor differences in the local flora of interior Alaska, the broad-scale landscape development processes appear to be similar across the North American boreal forest.

Acknowledgements

We thank Andrea Lloyd for assistance collecting and analyzing tree cores; Jamie Hollingsworth for assistance with maps and statistical analysis; Edward Packee, Tom Malone, and Carolyn Rosner of the Forest Growth and Yield program and Eric Kasischke for input into site selection; Lorien Nettleton, Matt Cave, Tina Buxbaum, and numerous others for field and laboratory assistance; Mikhail Zhurbenko, Olga Afonina, Leslie Viereck, Carolyn Parker, and Allan Batten for help in verification of specimens; the UAF Palmer Research Station for soil analysis; Andrea Lloyd, Sydonia Bret-Harte, Roger Ruess, Rod Seppelt, David Valentine, David Verbyla, Leslie Viereck, and two anonymous reviewers for comments on previous drafts. Finally, we thank Roger Ruess for invaluable discussions on the nature of black spruce in interior Alaska. This work was funded through a LTER grant to the Bonanza Creek research facility (NSF grant numbers 9810217 and 0080609), the USDA Forest Service Pacific Northwest Research Station directly and through agreement no. PNW01-JV11261952-231 to the University of Alaska Fairbanks, a student research grant from the Center for the Study of Global Change and Arctic System Research at the University of Alaska Fairbanks, and a UAF Austin Cooley Talent grant.

References

Ahrens, R.J., Bockheim, J.G., and Ping, C. 2004. The Gelisol order in soil taxonomy. *In* Cryosols: permafrost-affected soils. *Edited by* J. Kimble. Springer-Verlag, New York. pp. 2–10.

Allen, T.F.H., and Hoekstra, T.W. 1990. The confusion between scale-defined levels and conventional levels of organization in ecology. J. Veg. Sci. **1**: 5–12.

Anderson, L.E. 1990. A checklist of *Sphagnum* in North America north of Mexico. Bryologist, **93**: 500–501.

Anderson, L.E., Crum, H.A., and Buck, W.R. 1990. List of mosses of North America north of Mexico. Bryologist, **93**: 448–499.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: introduction. J. Veg. Sci. **9**: 464–467.

Billington, M.M., and Alexander, V. 1983. Site-to-site variations in nitrogenase activity in a subarctic black spruce forest. Can. J. For. Res. **13**: 782–788.

Birkeland, P.W. 1999. Soils and geomorphology. Oxford University Press, New York.

Bisbee, K.E., Gower, S.T., and Norman, J.M. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia, **129**: 261–270.

Braun-Blanquét, J. 1965. Plant sociology: the study of plant communities. Hafner, London.

Brown, J.K., and Smith, J.K. 2000. Wildland fire in ecosystems: effects of fire on flora. Vol. 2. USDA For. Serv. Gen. Tech. Rep. GTR-RMRS-42.

CAVM Team. 2003. Circumpolar arctic vegetation map (scale 1:7,500,000) [online]. Available from http://www.geobotany.uaf.edu/cavm/finalcavm/index.html [accessed 3 January 2004].

Chapin, F.S., III, and Danell, K. 2001. Boreal forest. *In* Biodiversity in a changing climate. *Edited by* F.S. Chapin III, O.E. Sala, and E. Huber-Sannwald. Springer, New York. Ecol. Stud. 152. pp. xx–xx.

Chapin, F.S., III, Bret-Harte, M.S., Hobbie, S.E., and Zhong, H. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. J. Veg. Sci. **7**: 347–358.

Connor, C., and O'Haire, D. 1988. Roadside geology of Alaska. Mountain Press Publishing Company, Missoula, Mont.

Currie, D.J., and Paquin, V. 1987. Large-scale biogeographical patterns of species richness in trees. Nature (Lond.), **329**: 326.

Daniëls, F.J.A. 1982. Vegetation of the Angmagssalik District, southeast Greenland IV—shrubs, dwarf shrubs, and terricolous lichens. Medd. Gronl. Biosci. **10**: 1–78.

Devolder, A. 1999. Fire and climate history of black spruce forests, Kenai National Wildlife Refuge, Alaska. M. Sc. thesis, Northern Arizona University, Flagstaff, Ariz.

Dierbenik, K. 1996. Vegetation Nordeuropas. Eugen Ulmer Verlag, Stuttgart, Germany.

Driscoll, K.G., Arocena, J.M., and Massicotte, H.B. 1999. Post-fire soil nitrogen content and vegetation composition in sub-boreal spruce forest in B.C. central interior. For. Ecol. Manage. **121**: 227–237.

Dufrêne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345–366.

Ellenberg, H. 1988. Vegetation ecology of central Europe. 4th ed. Cambridge University Press, Cambridge, UK.

Esslinger, T.L. 1997. A cumulative checklist for the lichen-forming lichenicolous and allied fungi of the continental United States and Canada [online]. Available from http://www.ndsu.nodak.edu/instruct/esslinge/chcklst/chcklist7.htm [accessed September 2002].

Flanagan, P.W., and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res. **13**: 795–817.

Foster, D.R. 1984. Phytosociological description of the forest vegetation of southeastern Labrador. Can. J. Bot. **62**: 899–906.

Fridley, J.D., Peet, R.K., Wentworth, T.R., and White, P.S. 2005. Connecting fine-and broad-scale patterns of species diversity: species–area relationships of southeastern U.S. flora. Ecology, **86**: 1172–1177.

Glaser, P.H., Janssens, J.A., and Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. J. Ecol. **78**: 1021–1048.

Hill, M.O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University Press, Ithaca, N.Y.

Hinzman, L., Viereck, L.A., Adams, P., Romanovsky, V.E., and Yoshikawa, K. 2005. Climatic and permafrost dynamics in the Alaskan boreal forest. *In* Alaska's changing boreal forest. *Edited by* M. Oswood and F.S. Chapin III. Oxford University Press, New York. pp. 39–61.

Hultén, E. 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford, Calif.

Johnstone, J.F., and Kasischke, E. 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. Can. J. For. Res. **35**: 2151–2163.

Johnstone, J.F., Chapin, F.S., III, Foote, J., Kemmett, K., Price, K., and Viereck, L.A. 2004. Decadal observations of tree regeneration following fire in boreal forests. Can. J. For. Res. **34**: 267–273.

Jorgenson, T. 1984. The response of vegetation to landscape evolution on glacial till near Toolik Lake, Alaska. *In* Proceedings of an International Symposium, Society of American Foresters Regional Technical Conference, Fairbanks, Alaska, 23–26 July 1984. *Edited by* V.J. Labau and C.L. Kerr. Society of American Foresters, Bethesda Md. pp. 134–141.

Keenan, T.J., and Cwynar, L.C. 1992. Late quaternary history of black spruce and grasslands in southwest Yukon Territory. Can. J. Bot. **70**: 1336–1345.

Klein, D.R. 1982. Fire, lichens, and caribou. J. Range Manage. **35**: 390–395.

Korotkov, K.O., Morozova, O.V., and Belonovskaja, E.A. 1991. The USSR vegetation syntaxa prodromus. G.E. Vilchek, Moscow, Russia.

Kruskal, J B., and Wish, M. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, Calif.

Kuhry, P., and Nicholson, B.J. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. Can. J. Bot. **71**: 10–22.

Kummerow, J., Ellis, B.A., Kummerow, S., and Chapin, F.S., III. 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. Am. J. Bot. **70**: 1509–1515.

La Roi, G.H. 1967. Ecological studies in the boreal spruce–fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monogr. **37**: 229–253.

La Roi, G.H. 1991. Classification and ordination of southern boreal forests from the Hondo-Slave Lake area of central Alberta. Can. J. Bot. **70**: 614–628.

La Roi, G.H., and Stringer, M.H.L. 1975. Ecological studies in the boreal spruce–fir forests of the North American taiga. II. Analysis of the bryophyte flora. Can. J. Bot. **54**: 619–643.

Larsen, J.A. 1980. The boreal ecosystem. Academic Publishing, New York.

Latham, E., and Ricklefs, R.E. 1993. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. Oikos, **67**: 325–333.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, **73**: 1943–1967.

Mann, D.H., Fastie, C.L., Rowland, E.L., and Bigelow, N.H. 1995. Spruce succession, disturbance, and geomorphology on the Tanana River floodplain, Alaska. Ecoscience, **2**: 184–199.

McCune, B., and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Ore.

McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data [computer program], version 4.25. MjM Software Design, Gleneden Beach, Ore.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Oksanen, J., and Minchin, P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. J. Veg. Sci. **8**: 447–454.

Orloci, L., and Stanek, W. 1979. Vegetation survey of the Alaska Highway, Yukon Territory: types and gradients. Vegetatio, **41**: 1–56.

Osterkamp, T.E., and Romanovsky, V.E. 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost Periglac. Process. **10**: 17–37.

Peinado, M., Aguirre, J.L., and de la Cruz, M. 1998. A phytosociological survey of the boreal forest (*Vaccinio–Piceetea*) in North America. Plant Ecol. **137**: 151–202.

Pewe, T.L., Hopkins, D.M., and Giddings, J.L. 1965. The Quaternary geology and archaeology of Alaska. *In* The Quaternary of the United States. A review volume for the VII Congress of the International Association for Quaternary Research. *Edited by* H.E. Wright, Jr., and D.G Frey. Princeton University Press, Princeton, N.J. pp. 355–374.

Raisa, M. 1999. Response patterns of *Vaccinium myrtillus* and *V. vitis-idaea* along nutrient gradients in boreal forest. J. Veg. Sci. **10**: 17–26.

Reed, R.A, Peet, R.K., Palmer, M.W., and White, P.S. 1993. Scale dependence of vegetation–environment correlations: a case study of a North Carolina piedmont woodland. J. Veg. Sci. **4**: 329–340.

Reznicek, T. 2003. Flora of North America. Magnoliophyta: Commelinidae (in part): *Cyperaceae*. Vol. 23. Oxford University Press, New York.

Rieger, S., Dement, J.A., and Sanders, D. 1963. Soil survey, Fairbanks area, Alaska. US Soil Conservation Society, Fairbanks, Alaska.

Rowe, J.S., and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. **3**: 444–464.

Scott, A.J. 1995. Canada's vegetation: a world perspective. McGill–Queen's University Press, Montreal, Que.

Slaughter, C.W., and Benson, C.S. 1986. Seasonal snow and aufeis in Alaska's taiga. *In* Proceedings of the Cold Regions Hydrology Symposium, Fairbanks, Alaska, 22–25 July 1986. *Edited by* D.L. Kane. American Water Resources Association, Bethesda, Md. pp. 101–109.

Sweetnam, T., and Sutherland, E.K. 1985. Using dendrochronology to measure the growth of defoliated trees. USDA Agric. Handb. 639.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology, **74**: 2179–2191.

Timoney, K.P., La Roi, G.H., Zoltai, S.C., and Robinson, A.L. 1993. Vegetation communities and plant distributions and their relationships with parent materials in the forest–tundra of northwestern Canada. Ecography, **16**: 174–188.

Van Cleve, K. 1983. Introduction and overview of a multidisciplinary research project: the structure and function of a black spruce (*Picea mariana*) forest in relation to other fire-affected taiga ecosystems. Can. J. For. Res. **13**: 695–702.

Van Cleve, K., Oechel, W.C., and Hom, J.L. 1990. Response of black spruce ecosystems to soil temperature modification in interior Alaska. Can. J. For. Res. **20**: 1530–1535.

Van Cleve, K., Chapin, F.S., III, Dyrness, C.T., and Viereck, L.A. 1991. Element cycling in taiga forest: state-factor control. Bioscience, **41**: 78–88.

Viereck, L.A. 1983*a*. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. **13**: 703–720.

Viereck, L.A. 1983*b*. The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley & Sons, Ltd., New York. pp. 201–219.

Viereck, L.A., Dyrness, C.T., Batten, A.R., and Wenzlick, K.J. 1992. Alaska vegetation classification. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-286.

Vogel, J., Valentine, D., and Ruess, R.W. 2005. Soil and root respiration in mature Alaskan black spruce that vary in soil organic matter decomposition rates. Can. J. For. Res. **35**: 161–171.

Walker, D.A., and Everett, K.R. 1991. Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. Ecol. Monogr. **61**: 437–464.

Walker, M.D., Walker, D.A., and Auerbach, N.A. 1994. Plant clandscape in the Brooks Range foothills, Alaska. J. Veg. Sci. **5**: 843–866.

Welsh, S.L. 1974. Anderson's flora of Alaska. Brigham Young University Press, Provo, Utah.

Whittaker, R.J. 1975. Communities and ecosystems. Macmillan, New York.

Yarie, J. 1983. Environmental and successional relationships of the forest communities of the Porcupine River drainage, interior Alaska. Can. J. For. Res. **13**: 721–728.