

Implications of floristic and environmental variation for carbon cycle dynamics in boreal forest ecosystems of central Canada

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Abstract. Species composition, detritus, and soil data from 97 boreal forest stands along a transect in central Canada were analysed using Correspondence Analysis to determine the dominant environmental/site variables that differentiate these forest stands. *Picea mariana* stands were densely clustered together on the understorey DCA plot, suggesting a consistent understorey species composition (feather mosses and Ericaceae), whereas *Populus tremuloides* stands had the most diverse understorey species composition (ca. 30 species, mostly shrubs and herbs). *Pinus banksiana* stands had several characteristic species of reindeer lichens (*Cladina* spp.), but saplings and *Pinus* seedlings were rare. Although climatic variables showed large variation along the transect, the CCA results indicated that site conditions are more important in determining species composition and differentiating the stand types. Forest floor characteristics (litter and humus layer, woody debris, and drainage) appear to be among the most important site variables. Stands of *Picea* had significantly higher average carbon (C) densities in the combined litter and humus layer (43530 kg-C.ha⁻¹) than either *Populus* (25500 kg-C.ha⁻¹) or *Pinus* (19400 kg-C.ha⁻¹). The thick surface organic layer in lowland *Picea* stands plays an important role in regulating soil temperature and moisture, and organic-matter decomposition, which in turn affect the ecosystem C-dynamics. During forest succession after a stand-replacing disturbance (e.g. fires), tree biomass and surface organic layer thickness increase in all stand types as forests recover; however, woody biomass detritus first decreases and then increases after ca. 80 yr. Soil C densities show slight decrease with ages in *Populus* stands, but increase in other stand types. These results indicate the complex C-transfer processes among different components (tree biomass, detritus, forest floor, and soil) of boreal ecosystems at various stages of succession.

Keywords: CANOCO; Carbon dynamics; Correspondence analysis; Disturbance; Forest succession; Ordination.

Abbreviations: BFTCS = Boreal Forest Transect Case Study; BOREAS = BOREal Ecosystem-Atmosphere Study; DCCA = Detrended Canonical Correspondence Analysis; NSA = Northern study area; SSA = Southern study area.

Introduction

The circumpolar boreal forests play a critical role in the global carbon (C) cycle (Apps et al. 1995). Although boreal forests are floristically simple (Rowe 1972; Payette 1992), the ecological processes that determine forest productivity and vegetation patterns at the landscape scale involve complex interactions and environmental factors (Bonan 1992). Some phytosociological studies have been conducted on eastern Canadian upland boreal forests (e.g. Maycock & Curtis 1960; Carleton & Maycock 1980; Louis et al. 1993) and on western boreal peatlands (e.g. Belland & Vitt 1995), but few such studies have been conducted in upland boreal forests of western Canada (Swan & Dix 1966; Corns et al. 1983; La Roi 1992). Such studies, however, can provide understanding about how floristic and environmental variations affect C-cycle dynamics.

Boreal lowland and upland forest ecosystems have been an important C-sink historically (Gorham 1991; Apps et al. 1993). Vegetation and upland soils in Canada's boreal forest have been estimated to contain 36.4 Pg C, representing ca. 40% of the total biospheric C in Canadian upland forests (Kurz & Apps 1999). Peat contributes another 135 Pg C (Gorham 1991) to the Canadian total biospheric C-pool. Most (> 80%) of this peat is found in the boreal zone, and an estimated 20–25% (27–34 Pg C) is associated with lowland forests (Zoltai & Marikainen 1996). Vegetation growth and decomposition rates in the boreal zone are limited by short growing seasons, low temperatures, available nitrogen, and high moisture content (Kimmins 1996). However, though critical to prediction of changes in the C-cycle, the relative importance of the different C-pools and the processes that govern their changes over time are still poorly understood (Gower et al. 1997; Nalder & Wein 1999).

A large data set of boreal vegetation, soils and environmental data was collected during the BOREal Ecosystem-Atmosphere Study (BOREAS) and the related Boreal Forest Transect Case Study (BFTCS) (Halliwell

et al. 1995; Halliwell & Apps 1997a-c). These databases can be used to improve understanding of forest stand/species relations and C-dynamics of different forest components. The data may also be used for designing model experiments to link forest-response models (e.g. FORSKA, CENTURY and LINKAGES) with C assessment models, such as the Carbon Budget Model – Canadian Forest Sector (CBM-CFS) (Kurz & Apps 1999). Despite some progress (e.g. Peng et al. 1998; Price et al. 1999), the information has been underutilized because of the high variability of some variables and the presence of confounding factors affecting observed patterns (Nalder & Wein 1999; Bhatti & Apps 2000). Ordination techniques, notably DCA (Detrended Correspondence Analysis) and CCA (Canonical Correspondence Analysis), can provide a holistic view of the data (ter Braak 1987), deal with noisy data and skewed sampling schemes in a robust way, and hence can help to classify and order ecosystems (Palmer 1993). Although such analyses do not infer cause-effect relationships among the variables involved, they do identify the

links between the different components of ecosystems to guide the development of process-based simulation models and the design of further sampling programs.

The objectives of the present study were (1) to describe and organize the vegetation (overstorey and understorey), soils and environmental data from the 97 BFTCS forest sites through ordination (DCA and CCA); (2) to interpret the emerging floristic gradients in terms of dominant environmental and site factors; and (3) to explore the implications of stand type, stand age and understorey species composition on the C-dynamics of different C-pools during forest succession. In this paper, we address several key questions related to boreal ecosystem and C-cycle dynamics: What is the relative importance of regional climate vs. site characteristics in determining species composition of different forest stands? How do these factors determine the carbon distribution/allocation of different carbon pools in different stands? How do ecosystem carbon contents change over time during the fire-initiated succession in different stands and for different carbon pools?



Fig. 1. Location of the study area in continental western Canada. The rectangle shows the approximate coverage of the Canadian Boreal Transect (Price & Apps 1995). Open circles are forest stands, and filled circles are climate stations. SSA = southern study area; NSA = northern study area.

Material and Methods

Study area

The Boreal Forest Transect Case Study (BFTCS) (Price & Apps 1995) is located from central Saskatchewan to north-central Manitoba in continental western Canada (Fig. 1). The transect is one of the transects identified in the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the International Geosphere-Biosphere Programme (IGBP; Koch et al. 1995). The BFTCS is aligned with an ecoclimatic gradient (Anon. 1989) and spans several major vegetation biomes – proceeding in a NE direction from the agricultural prairies into a *Populus* parkland transition to the boreal forest biome and into the sparsely treed subarctic tundra. Along the transect, climatic conditions change from warm and dry in the SW to cold and wet in the NE. The general thermal and moisture patterns from four climate stations (Thompson, Flin Flon, Prince Albert and Saskatoon) are similar, but show large moisture deficiency at the southern stations, especially during the spring and fall seasons, with generally increasing precipitation and decreasing temperatures NE-ward (Fig. 2). The climatic moisture index (precipitation minus potential evapotranspiration) increases from less than -15 cm in the SW to 25 cm in the NE (Hogg 1994). Vegetation growth rates are limited by low mean annual temperatures in the north and by seasonal moisture conditions in the south (Hogg 1994; Sellers et al. 1997).

Much of the study area is in the boreal region (Rowe 1972). For the region as a whole, the three dominant tree species are *Picea mariana* (Black spruce), *Pinus banksiana* (Jack pine) and *Populus tremuloides* (Trembling aspen). *Picea* tends to be restricted to low-lying organic soils in the southern boreal regions but in the central and northern forests often forms pure stands on uplands as well as on organic soils (Ritchie 1987). *Pinus* germinates and establishes only in full light on mineral soils, and thus tends to be found early in succession on fire-disturbed sites (Burns & Honkala 1990a). *Populus tremuloides*, the most widely distributed tree in North America, is a fast-growing, short-lived, shade-intolerant species (Burns & Honkala 1990b). It occurs on well- to moderately-drained upland sites, and like *Pinus*, is found early in succession after fire; unlike *Pinus*, however, *Populus* can also quickly occupy sites after other forms of stand replacing disturbances through coppice regeneration.

Study sites and data sets

The present study analyses the data sets from field sampling programs in 1993 and 1994 as summarized in Halliwell & Apps (1997a-c). The majority of sites are

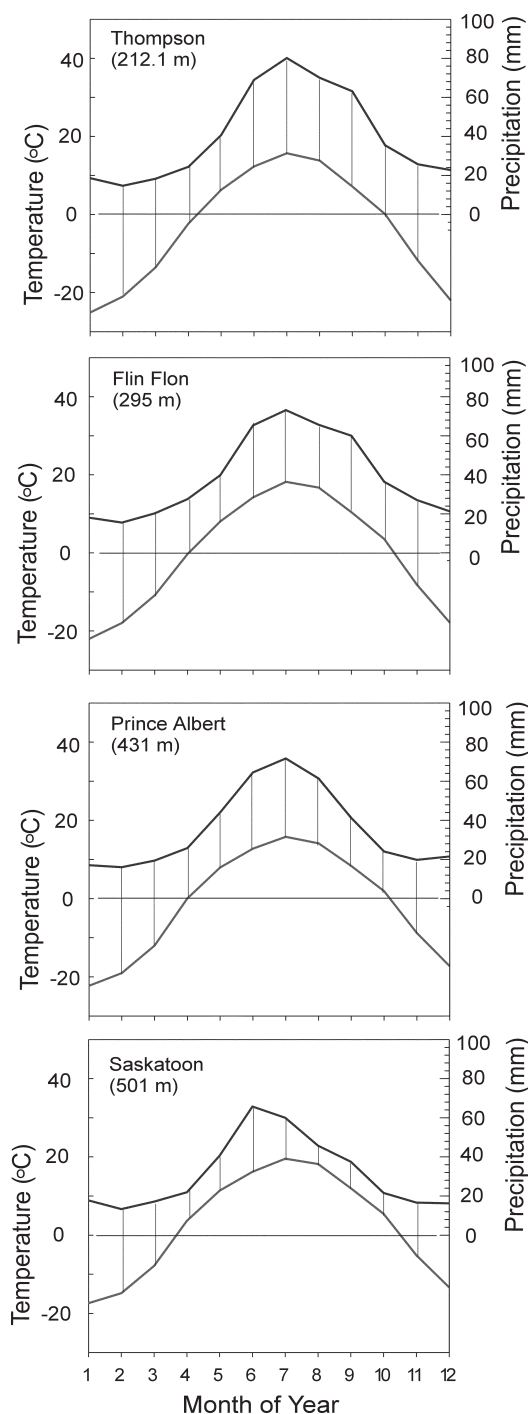


Fig. 2. Climate diagrams from four climate stations along the transect: Thompson, Flin Flon, Prince Albert and Saskatoon. The top curves represent the long-term mean monthly precipitation, whereas the lower curves represent the long-term mean monthly temperature. The area in between represents the relative moisture availability during different months. See Walter (1973) for details about the presentation of climatic information in climate diagrams.

clustered around the BOREAS NSA and SSA (Sellers et al. 1997), with additional sampling sites near Flin Flon, midway between the NSA and SSA (Fig. 1). Despite the large geographical range of the BFTCS (Fig. 1), the variation in climatic conditions across the sampled BFTCS sites is not large (Fig. 2).

The database consists of 97 sites with data on overstorey and understorey vegetation, as well as detritus and soil measurements on all or parts of these sites. The 97 stands have been classified into four stand types based on the dominant tree species: *Picea mariana* ($n = 37$), *Pinus banksiana* ($n = 29$), *Populus tremuloides* ($n = 19$) and mixed wood stands ($n = 12$). The stands described by Gower et al. (1997) are from the same general area but at different specific sites located adjacent to BOREAS flux towers. Site selection criteria and detailed measurement methods were presented in Halliwell & Apps (1997a-c) and Halliwell et al. (1995). The sites and stands were selected to ensure characteristics such as relative homogeneity, even age and sufficient stand size to meet the remote sensing requirements of BOREAS (no less than 100 m \times 100 m). Overstorey and understorey measurements were mostly taken for three plots at each site. The overstorey consists of trees and shrubs taller than breast height (1.3 m). A point-sampling method was used for sampling the overstorey vegetation in most cases, though a fixed-area plot method was used for a

few sites. Understorey vegetation was sampled using fixed-area plots. A detailed description of these methods and calculation procedures can be found in Halliwell & Apps (1997b). Debris measurements were taken along micro-transects at two locations, and soil samples taken from pits at one point for each site. The soil and detritus measurement and calculation procedures are described in Halliwell & Apps (1997c). All numerical data used in the analyses are available in the three reports by Halliwell & Apps (1997a-c).

Multivariate analysis

We analysed species composition data through an indirect gradient analysis and the relationship between species and environmental data through a direct gradient analysis (Prentice 1980). DCA, CCA and DCCA were used on different subsets of the data using CANOCO (ter Braak 1988). To check the linearity of the data, a DCA was carried out initially for all data sets (Table 1). DCA results show that the gradient lengths of the ordination axes are always greater than 3 SD (standard deviations), suggesting that most of the response curves (or surfaces) are non-linear and thus the use of unimodal methods is more appropriate (ter Braak 1987). DCA extracts the dominant compositional gradients from species data, whereas CCA and

Table 1. Eigenvalues, gradient lengths (SD) and percentages of variance for the first and second axes of DCA and CCA ordinations for the overstorey and understorey data sets with different number of species.

		DCA			CCA			
		Eigen-	SD	%Variance	Eigen-	Spec-env	% Spec	% spec-env
		value			value	correlation	variance	variance
Overstorey (13 species)	Axis 1	0.85	3.06	28.4	0.54	0.83	18.0	47.8
	Axis 2	0.42	2.26	13.8	0.42	0.73	13.9	37.0
	Total 1	3.01			3.01			
	Total 2				1.13			
213 species understorey	Axis 1	0.68	6.15	7.5	0.43	0.84	4.8	21.9
	Axis 2	0.52	3.80	5.7	0.37	0.84	4.1	18.7
	Total 1				9.06			
	Total 2				2.00			
152 species understorey	Axis 1	0.67	5.32	8.3	0.42	0.83	5.3	23.2
	Axis 2	0.48	3.77	5.9	0.35	0.84	4.4	19.2
	Total 1	8.03			8.03			
	Total 2				1.83			
100 species understorey	Axis 1	0.65	4.61	9.7	0.40	0.82	6.0	24.3
	Axis 2	0.48	4.11	7.1	0.34	0.83	5.2	20.7
	Total 1	6.66			6.67			
	Total 2				1.66			
60 species understorey	Axis 1	0.62	4.00	12.3	0.37	0.80	7.4	26.6
	Axis 2	0.40	3.74	8	0.32	0.81	6.3	22.8
	Total 1	5.01			5.01			
	Total 2				1.39			
33 species understorey	Axis 1	0.65	4.71	13.4	0.37	0.79	7.7	27.1
	Axis 2	0.39	3.71	8	0.32	0.79	6.5	23.2
	Total 1	4.88			4.88			
	Total 2				1.38			

SD = standard deviations; Total 1 = sum of all uncontrolled eigenvalues; Total 2 = sum of all canonical eigenvalues.

DCCA constrain ordination axes to be linear combinations of supplied environmental/site variables (ter Braak 1986, 1987).

Importance values of tree species that combine relative frequency, relative density and relative dominance are commonly used indices in plant community studies (e.g. Maycock & Curtis 1960). For the present analyses of overstorey data, only the relative density for each of 13 tree species was used in the analyses. The use of relative density alone in this study is not expected to significantly affect the results because unimodal methods (such as DCA and CCA) emphasize qualitative variation (presence/absence) in species composition.

The estimates of cover percentage by Halliwell & Apps (1997b) were used for the analyses of understorey data. The 213 species/taxa in understorey vegetation were further grouped into the four subsets based on their frequency of observation for individual analyses. The first understorey data set consists of the 152 species that occur in at least two of the 97 sites (2% frequency). The second data set includes 100 species with > 5% occurrence, the third data set includes 60 species with > 10% occurrence. The final data set includes 33 species that occur in > 10% of the sites and also have an average cover > 2%. Table 2 lists the species in this last data set. The actual number of stands used in the analyses depended on the availability of measurements for certain variables in the database.

Environmental and stand variables ($n = 11$) are included in the CCA and DCCA analyses:

January and July temperatures (°C);
Annual precipitation (mm);
Drainage (7 classes from very rapid (1) to very poor (7));
Soil C-content (t-C.ha⁻¹);
Top soil clay content (%);
Woody biomass detritus (t-C.ha⁻¹);
Duff layer thickness (cm);
Tree biomass (t.ha⁻¹);
Stand age (yr);
Number of understorey species.

Stand age was determined from the maximum number of tree rings from selected tree cores (3-16 cores each site, with a mean of 9 cores per site), which represents minimum stand age and reflects the time since the last major disturbance, likely fires. The duff layer thickness was the measured depth of surficial organic matter (litter and humus but excluding coarse woody debris) above the mineral soil (see Halliwell & Apps 1997c). Woody biomass detritus data in Halliwell & Apps (1997c) represent accumulated dead woody matter on the forest floor surface in 7 diameter classes (from < 0.5 cm to > 7 cm) and does not include below-ground (roots) mortality.

Table 2. List of 33 understorey species and symbols used to label sites in the understorey ordination analyses.

Aln cri	<i>Alnus crispa</i>	Pic gla	<i>Picea glauca</i>
Aln sp.	<i>Alnus spec.</i>	Pic mar	<i>Picea mariana</i>
Ara nud	<i>Aralia nudicaulis</i>	Pin ban	<i>Pinus banksiana</i>
Arc uva	<i>Arctostaphylos uva-ursi</i>	Ple sch	<i>Pleurozium schreberi</i>
Car sp.	<i>Carex spec.</i>	Pol com	<i>Polytrichum commune</i>
Cla mit	<i>Cladina mitis</i>	Pol sp.	<i>Polytrichum spec.</i>
Cla sp.	<i>Cladina spp.</i>	Pop tre	<i>Populus tremuloides</i>
Cla ste	<i>Cladina stellaris</i>	Pti cri	<i>Ptilium crista-castrensis</i>
Cla cor	<i>Cladonia cornuta</i>	Ros aci	<i>Rosa acicularis</i>
Cor can	<i>Cornus canadensis</i>	Rub ida	<i>Rubus idaeus</i>
Dic pol	<i>Dicranum polysetum</i>	Rub pub	<i>Rubus pubescens</i>
Dic sp.	<i>Dicranum spec.</i>	Sal sp.	<i>Salix spec.</i>
Hyl spl	<i>Hylocomium splendens</i>	Sph sp.	<i>Sphagnum spp.</i>
Lat och	<i>Lathyrus ochroleucus</i>	Vac myr	<i>Vaccinium myrtilloides</i>
Led gro	<i>Ledum groenlandicum</i>	Vac vit	<i>Vaccinium vitis-idaea</i>
Lin bor	<i>Linnaea borealis</i>	Vib edu	<i>Viburnum edule</i>
Mos sp.	Moss spp.		

Results

Forest stand data

Marked variations in some of the ecological and site variables were observed among different types of forest stands (Fig. 3). *Picea* stands have the thickest duff layers, but lowest woody biomass detritus (Fig. 3a, b). Along the transect, the C-content of the forest floor (duff layer) has a mean value of 25 500 kg-C.ha⁻¹ (with a range of 5800 to 38 500 kg-C.ha⁻¹) in the 19 *Populus* stands. For the 29 *Pinus* stands, the mean forest floor C was lower (19400 kg-C.ha⁻¹) but the range (5200-49 000 kg-C.ha⁻¹) is somewhat greater. *Picea* stands (37 sites) had the highest forest floor C with a mean value of 43 530 kg-C.ha⁻¹ and a range of 13400 -147000 kg-C.ha⁻¹. Biomass detritus, primarily from coarse woody debris, ranges from < 1 to 81 t.ha⁻¹, with the lowest average values of 5 t.ha⁻¹ in *Picea* stands and the highest average of 17 t.ha⁻¹ in *Populus* stands (Fig. 3b). These variables also show different patterns with increasing stand ages (Figs. 4 and 5).

Gradient analysis

We compared DCCA with CCA and found that their results are very similar, suggesting that detrending in CCA is not necessary (Palmer 1993). Overstorey data have higher eigenvalues, shorter gradient lengths and higher percentages of variance than any subsets of the understorey data (Table 1). CCA eigenvalues are lower than the DCA eigenvalues, indicating that environmental/site variables markedly rearrange the configuration of species and samples.

For the different data sets in understorey vegetation, eigenvalues in DCA and CCA become slightly smaller as more rare species are removed from the analyses. It

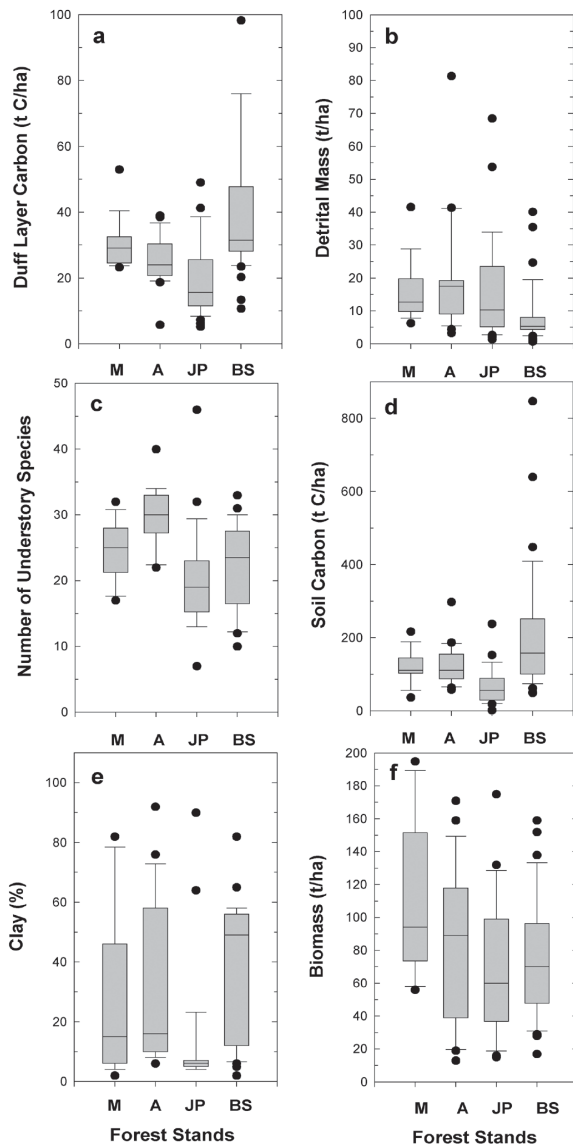


Fig. 3. Summary graphs of selected site variables for four forest types in 97 forest stands. **a.** Duff layer carbon (t C/ha); **b.** Woody debris mass (t/ha); **c.** Number of understorey species; **d.** Total soil carbon (t C/ha); **e.** Clay content of top (0-20 cm) mineral soils (%); **f.** Living tree biomass (t/ha). The box plots portray the median, interquartile range, adjacent values (lines), and outside values (dots) of the distribution. Stand types: M = mixed wood; A = *Populus tremuloides*; JP = *Pinus banksiana*; BS = *Picea mariana*.

appears that the first axis is more sensitive to rare species removal in DCA, whereas the second axis is more sensitive to the removal in CCA. In general, the first two axes are broadly similar on basis of eigenvalues, gradient lengths and percentages of variance, with regard to different understorey data sets.

Compositional gradients

The overstorey DCA joint plot reflects the classification of stand types based on dominant tree species (Fig. 6; Halliwell & Apps 1997b), as expected. *Picea* and *Populus* stands show relatively distinctive and confined clusters, whereas *Pinus* stands in the middle are loosely clustered. The diagram also shows dominant species within each of stand types/clusters. The first two DCA axes account for 42.2% of the variance in species composition (Table 1).

The understorey DCA joint plot of 95 stands with understorey measurements also exhibits clustering of stands (as classified from the overstorey dominant species), but with more overlap and scatter (Fig. 7). The first axis separates the *Populus* stands on the left from *Picea* and *Pinus* stands on the right. The second axis marginally separates *Picea* stands from *Pinus* stands but with some overlap. In addition to *Picea* seedlings and saplings, some moss species tend to occur only in *Picea* stands, including *Pleurozium schreberi*, *Ptilidium crista-castrensis*, *Hylocomium splendens* as well as un-differentiated *Sphagnum* and other moss species. *Pinus* stands tend to have shrubs *Vaccinium vitis-idaea*, *V. myrtilloides* and *Arctostaphylos uva-ursi*, the mosses *Dicranum polysetum* and *Polytrichum* spec., and the reindeer lichens *Cladonia cornuta*, *Cladonia mitis*, and *C. stellaris*. *Populus* stands have understorey species such as the shrubs *Alnus crispa*, *Rosa acicularis*, *Viburnum edule*, *Linnaea borealis*, *Rubus idaeus* and *R. pubescens*, and the herbs *Cornus canadensis*, *Lathyrus ochroleucus* and *Aralia nudicaulis*. The first two axes account for 13.2-21.4% of the variance in species composition data, depending on the number of understorey species used in the analysis (Table 1). DCA analyses from different understorey subsets show similar results (Table 1).

Environmental gradients

Species scores, stand scores and environmental vectors for CCA ordinations of overstorey data from 96 stands and understorey data from 95 stands are shown in Figs. 8 and 9, respectively. In the overstorey CCA ordination (Fig. 8), the first CCA axis was most strongly and negatively correlated with the forest floor depth, stand age and drainage (a nominal variable, shown as a filled square) and positively correlated with detritus mass. The second CCA axis was negatively correlated with the number of understorey species. The third CCA axis (not shown) was strongly correlated with stand biomass and correlated negatively with clay content of top (0-20 cm) soils. The arrows for environmental variables in Fig. 8 account for 84.8% of the variance in the

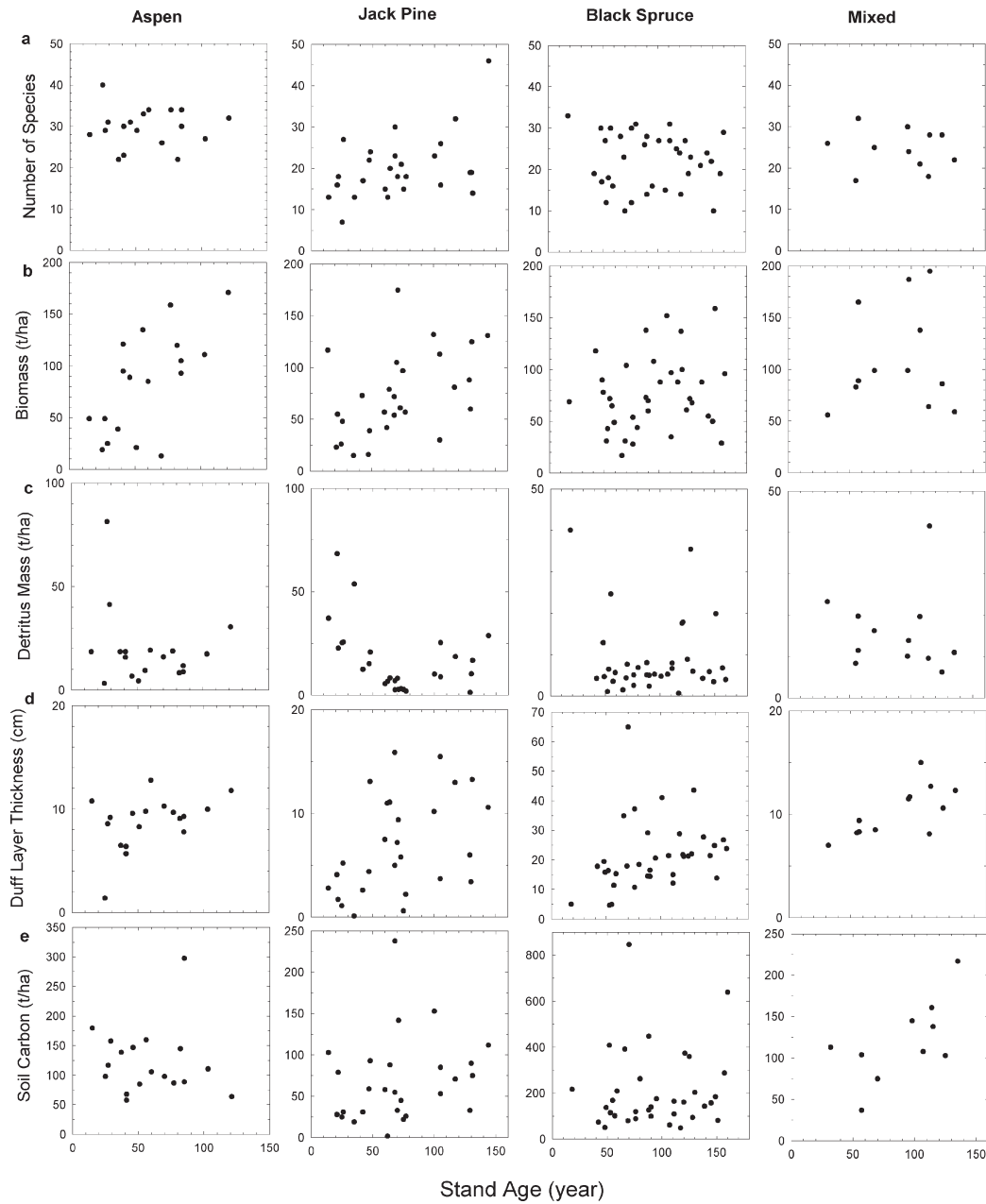


Fig. 4. Change of selected site variables at four different types of forest stands during succession after stand-replacing disturbance. **a.** Number of understorey species; **b.** Tree biomass (t/ha); **c.** Woody debris mass (t/ha); **d.** Duff layer thickness (cm); **e.** Soil C content (t/ha). Ages are based on the tree-ring counts from selected trees in each stand. Aspen = *Populus tremuloides*; Jack Pine = *Pinus banksiana*; Black Spruce = *Picea mariana*.

weighted average of the 13 species with respect to the 11 environmental variables (Table 1).

In the 33-species understorey CCA ordination (Fig. 9), the first CCA axis was strongly correlated with understorey species number, stand biomass and woody biomass detritus. The second CCA axis was negatively correlated with duff layer thickness, drainage, stand age and soil C-contents. The arrows for environmental variables in Fig. 9 account for 50.3% of the variance in the

weighted average of the 33 species with respect to the 11 environmental variables (Table 1). The 60-species CCA ordination shows similar configuration of species, stands and site variables, whereas the 33-species DCCA ordination provides essentially the same information as in CCA but showing 180° rotation of axes.

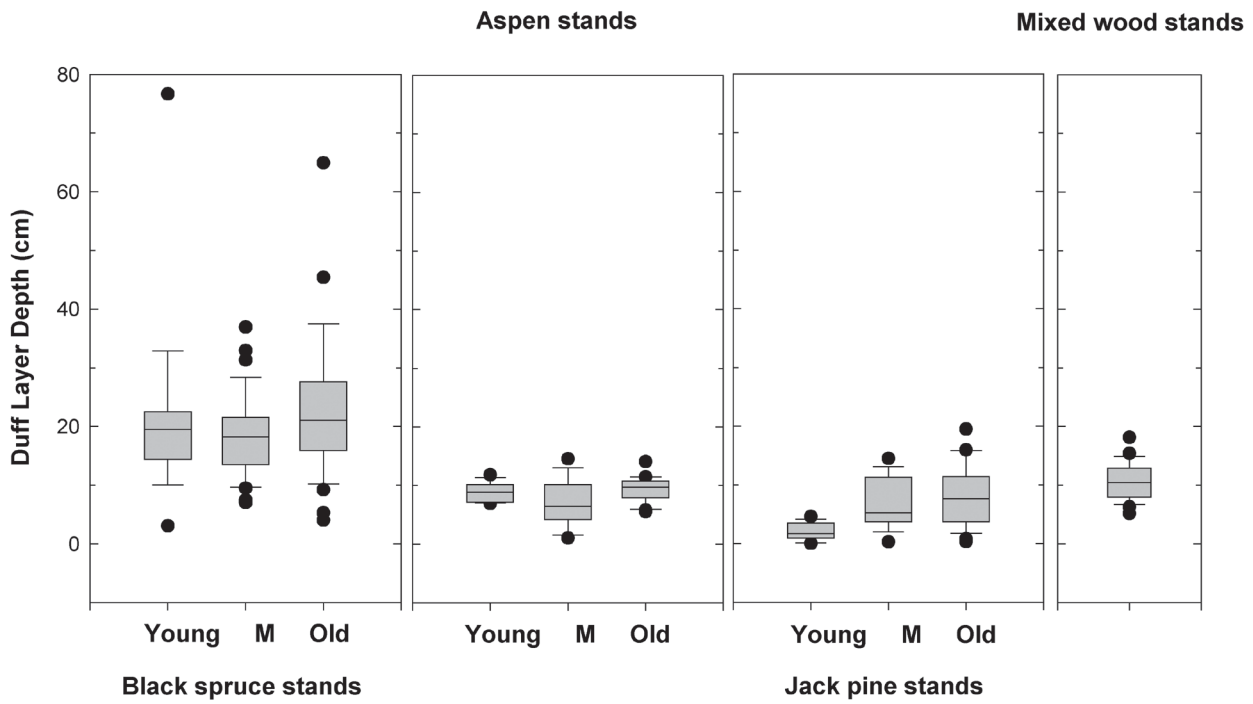


Fig. 5. Differences in duff layer thickness in forest stands of different stand age. Ages are based on the classification (young, intermediate and old) by Halliwell & Apps (1997b). For species names, see Fig. 4.

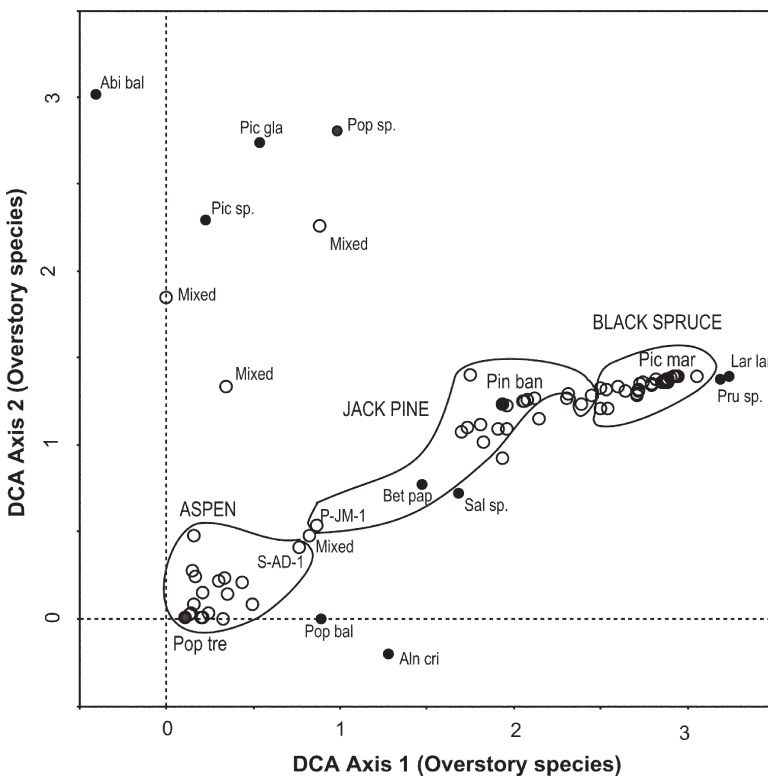


Fig. 6. Detrended Correspondence Analysis (DCA) of overstorey species composition data. DCA Axis 1 accounts for 28.4% of the variance of species data, DCA Axis 2 for 13.8%. Open circles are stands, and filled circles are species. The three encircled clusters represent *Populus tremuloides* (Aspen), *Pinus banksiana* (Jack pine) and *Picea mariana* (Black spruce) stands, as identified from the dominant tree species (Halliwell & Apps 1997b). Tree species are:

- Pic mar = *Picea mariana*;
- Lar lar = *Larix laricina* (tamarack);
- Pru sp. = *Prunus spec.*;
- Pin ban = *Pinus banksiana*;
- Bet pap = *Betula papyrifera*;
- Sal sp. = *Salix spec.*;
- Pop bal = *Populus balsamea*;
- Aln cri = *Alnus crispa*;
- Pop tre = *Populus tremuloides*;
- Pic sp. = *Picea spec.*;
- Pic gla = *Picea glauca*;
- Pop sp. = *Populus spec.*;
- Abi bal = *Abies balsamea*.

Fig. 7. Detrended Correspondence Analysis (DCA) of understorey species data. Results are shown for 33 major understorey species (see Table 2 for species list) that occur in more than 10% of stands and have an average cover of > 2%. DCA axis 1 accounts for 13.4% of the variance of species data, axis 2 for 8% of the variance. Clusters as in Fig. 6.

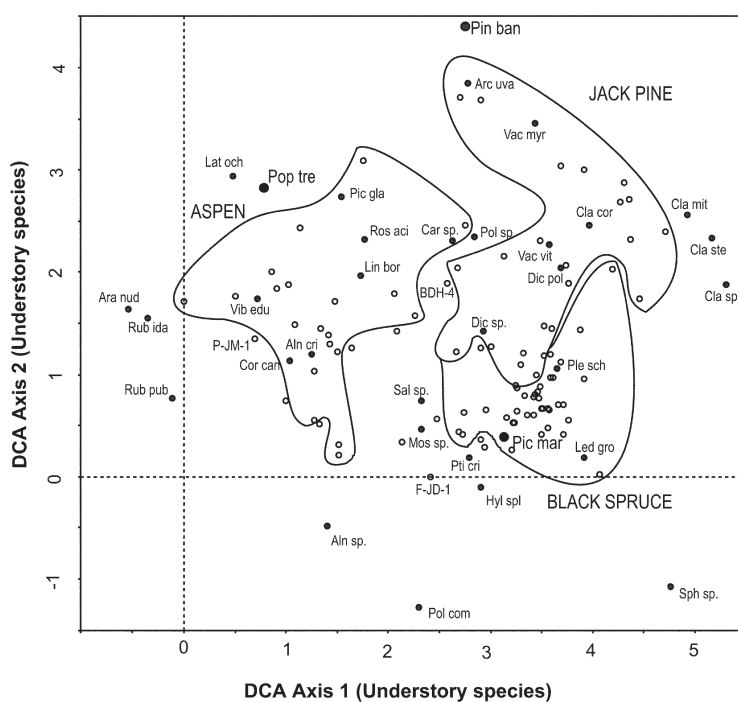
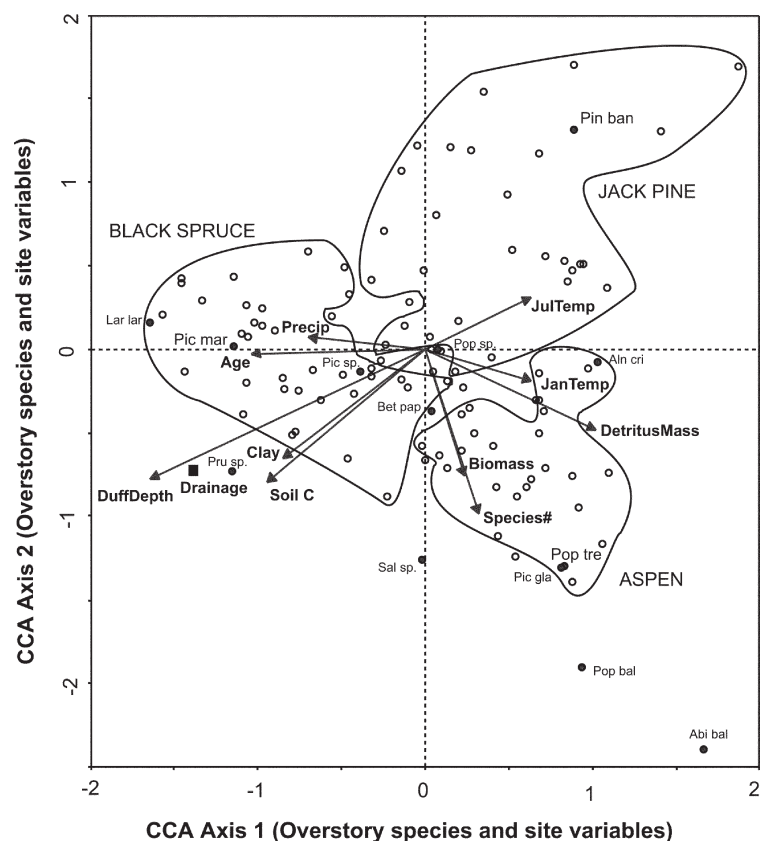


Fig. 8. Canonical Correspondence Analysis (CCA) of overstorey species and environmental/site data. The three encircled clusters represent *Populus tremuloides*, *Pinus banksiana* and *Picea mariana* stands, as identified from the dominant tree species (Halliwell & Apps 1997b). Tree species are the same as in Fig. 6. The site/environmental variables are:

- JulTemp = July temperature;
- JanTemp = January temperature;
- Precip = precipitation;
- DetritusMass = woody debris biomass;
- Species# = understorey species number;
- Biomass = living tree biomass;
- SoilC = whole profile soil C-content;
- Clay = clay content of top (0-20 cm) mineral soil;
- Duff depth = Duff layer thickness;
- Age = stand age.

Drainage is a nominal variable, shown as a filled square here.



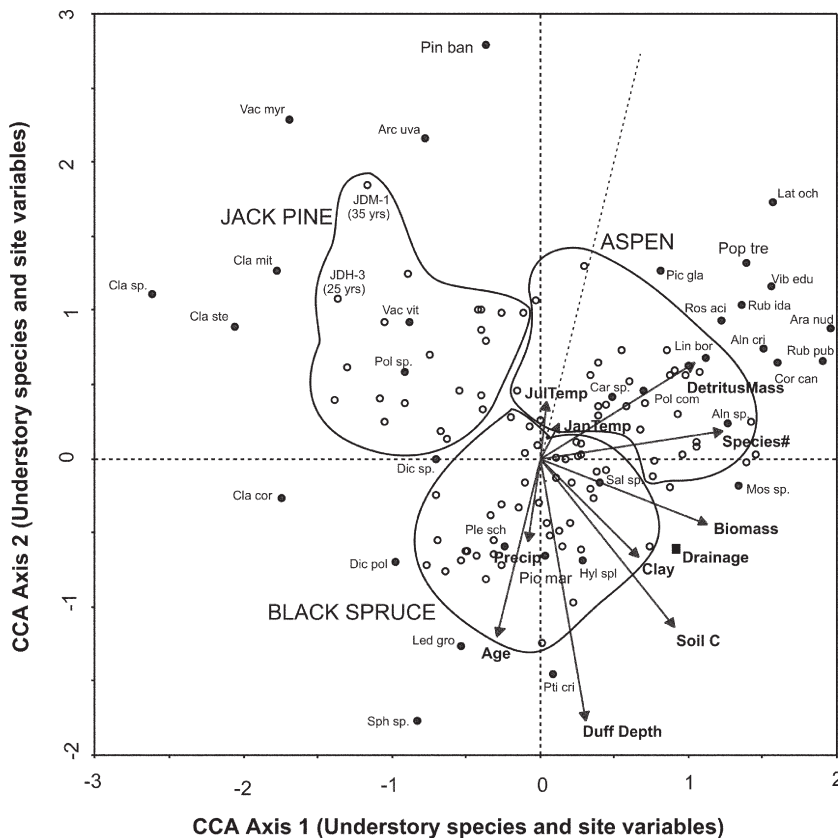


Fig. 9. Canonical Correspondence Analysis (CCA) of understory species and environmental/site data. Here shown are results from 33 major understory species that occur in more than 10% of stands and have an average cover of > 2%. Clusters as in Fig. 6. Understorey species are listed in Table 2. The site/environmental variables are:

JulTemp = July temperature;
 JanTemp = January temperature;
 DetritusMass = woody debris biomass;
 Species# = understory species number;
 Biomass = living tree biomass;
 SoilC = whole profile soil C-content;
 Duff depth = Duff layer thickness;
 Age = stand age.

Discussion

Overstorey and understory species composition

The four stand types, i.e. *Picea*, *Pinus*, *Populus* and mixed wood, were initially defined based on dominant tree species prior to beginning of field measurements in the BOREAS and BFTCS projects (Halliwell et al. 1995). This sampling strategy was reflected in the overstorey ordination results, with the majority of samples in each stand type densely clustered together (Fig. 6) indicating the dominant tree species in each stand.

At the top of the understory DCA ordination diagram (Fig. 7), *Pinus* as a species is separated from the *Pinus* stand cluster, indicating that *Pinus* saplings and seedlings are rare in their own stands. A few stands close to understory *Pinus* also contain shrubs of *Vaccinium myrtilloides* and *Arctostaphylos uva-ursi*. These are dwarf shrubs that thrive in gravelly or sandy soils and relatively open overstorey canopies, such as are found in dry *Pinus* stands (Rowe 1956). *Pinus* occurs as an understory species only in 15 stands (29 *Pinus* stands in the data set), with an average cover of 5%. This indicates that *Pinus* does not even regenerate well in its own stands. In contrast, *Picea* occurs in 59 stands (37

Picea stands in the data set) and *Populus* in 36 stands (19 *Populus* stands in the data set) as saplings and seedlings. This indicates that regeneration in the understory (uneven age cohorts) may play a more important role in successional dynamics for these stand types than for *Pinus*. On the other end of the *Pinus* cluster (right side), several species of reindeer lichens (*Cladina* spp.) are characteristic of *Pinus* stands. These reindeer lichens more commonly occur in continental and more northern boreal woodlands (lichen woodlands), especially in *Pinus banksiana* stands associated with sandy deposits (Ahti 1977).

The present results are consistent with early findings using different techniques on a limited number of sites. Swan & Dix (1966) analysed 32 upland forest stands on mineral soils using the Polar Ordination technique of Bray & Curtis (1957). These stands were from the Candle Lake region in Saskatchewan, which is very close to the SSA sites (Fig. 1). Almost half of the stands examined by Swan & Dix were dominated by a single species with *Populus*, *Pinus* and *Picea* stands forming the three major stand types. Their results also showed that moss cover dominates in *Picea* stands, whereas *Populus* stands have the highest number of understory species, including *Aralia nudicaulis* and *Lathyrus ochroleucus*.

Regional climate versus site characteristics

The 97 stands in the data set of Halliwell & Apps span about four degrees of latitude (from 52.7 to 56.4° N) and 12 degrees of longitude (from 94.3 to 106.2° W). Although there were large differences in climate among individual sites, the vector lengths in Figs. 8 and 9 indicate that regional climate variables were not the most important in explaining the variation in species composition of these 97 stands: site conditions and microclimate appear to play a greater role in determining the species composition.

Forest floor characteristics (duff layer, woody debris, and drainage) were among the most important site variables in explaining the species variation and in separating forest stand types in an ordination plot. Climatic differences do, however, play a strong role in the spatial distribution of stand types across the transect. For example, *Picea* stands tend to occur in the north where precipitation is higher and temperatures lower, while *Pinus* stands are found further south where high summer temperatures prevail. Similarly, *Populus* stands tend towards locations where winter temperatures are higher, and precipitation is lower. Halliwell & Apps (1997c) examined the woody detritus and soil data from these stands and found that, as compared to the northern sites, stands in the southern regions have higher woody debris C (due to higher productivity) and lower C-content in mineral soils, especially in *Populus* stands (due to higher decomposition rates). These findings are also evident in the CCA diagrams (Figs. 8 and 9), which show that soil C and duff layer depth have a negative dependence on temperatures, whereas woody debris and stand biomass tend to vary directly with temperature.

Gower et al. (1997) discussed the C-distribution among vegetation, forest floor and soils from the eight BOREAS tower stands in the Halliwell & Apps (1997b) data set and concluded that C-allocation, as well as above-ground net primary production, differ more among forest types in a similar climate than for a similar forest type in the two contrasting climates (NSA and SSA). Their findings are consistent with the present results, which are based on a much larger data set. Nalder & Wein (1999) found that forest floor C showed no significant dependence on climatic variables for *Pinus* stands, but a positive dependence on temperatures and negative dependence on precipitation for *Populus* stands. Given the higher tree productivity and forest floor C-content in the southern sites, this suggests that litter production may be more important factor than litter decomposition in determining the forest floor C-pools and their changes over time.

Role of forest floor (duff layer and woody debris)

Forest floor C represents a significant component (16-33%) of the total non-soil C-pool in western boreal forests (Gower et al. 1997; Nalder & Wein 1999). For the 19 *Populus* sites sampled along the BFTCS, the forest floor (duff layer) C-contents have a mean value of 25 500 kg-C.ha⁻¹. This is somewhat higher than the estimates by Gower et al. (1997) of 15 880-19 430 kg-C.ha⁻¹ in the two *Populus* stands from the BOREAS tower sites, but similar to the mean estimate of 27 800 kg-C.ha⁻¹ reported by Nalder & Wein (1999) for 45 *Populus* stands across western continental Canada. Mean forest floor C-content of *Pinus* stands was 19 400 kg-C.ha⁻¹. In comparison, Gower et al. (1997) reported estimates of 11 480-14 560 kg-C.ha⁻¹ from the tower old *Pinus* stands, while Nalder & Wein (1999) gave a mean of 13 100 kg-C.ha⁻¹ for 36 *Pinus* stands across the larger region. At even a larger spatial scale, the Canadian soil carbon database (Siltanen et al. 1997) reports forest floor C densities in the western boreal forest of 17 800 and 13 500 kg-C.ha⁻¹ for *Pinus* and *Populus* stands, respectively.

From our ordination analyses, it appears that the single most important environmental/site variable measured that distinguishes different stand types was the duff layer thickness (and thus its C-content). Thick duff layers are especially associated with *Picea* stands (Fig. 3a) with very poor drainage, and the association applies to both overstorey and understorey species (Figs. 8 and 9). In contrast, *Pinus* stands on well-drained sandy soils have the thinnest duff layer (Fig. 3a). Nalder & Wein (1999) also found that forest floor C is strongly dependent on species and forest type.

The ground cover of many coniferous forests in the boreal biome is comprised of a thick moss-organic layer (Van Cleve et al. 1986; Bonan & Shugart 1989). The analyses presented here support this conclusion for low-lying *Picea* forest types, but also indicate important exceptions in upland forests of other species associations. In all forest types in the boreal biome, however, the forest floor layer plays an important role in the C-dynamics. This is especially true in lowland *Picea* forests (Bonan 1992) where low soil temperatures, poor nutrient supply and moisture conditions result in low rates of organic matter decomposition that promote accumulation of a thick forest floor layer.

Biomass detritus, primarily from coarse woody debris, has the lowest average values of 5 t.ha⁻¹ in *Picea* stands and the highest average of 17 t.ha⁻¹ in *Populus* stands (Fig. 3b), as demonstrated in the ordination diagrams (Figs. 8 and 9). Coarse woody debris (CWD) performs an important ecosystem function of many forest ecosystems (Harmon et al. 1986). Many proc-

esses determine the dynamics of tree mortality and hence input rates to the CWD pools, but species identity, size and decay stage of CWD are particular factors that influence vegetation species composition (Harmon et al. 1986).

Disturbance, succession and ecosystem carbon density

The 97 stands have stand ages ranging from 14 to 194 yr, with an average of 81 yr. The young ages of these forest stands indicate the early successional nature of most of these forests after fire disturbance (e.g. Dix & Swan 1971). In continental western Canada, fire intervals are usually less than 100 yr (Weir et al. 2000), so on average a forest stand would be burned at least once every 100 yr. Fires are also an important determinant of the mosaic pattern of distinct boreal forest types (Larson 1980).

Because stand age was included as a stand variable in the analysis, the CCA diagram reflects successional changes of species as well as other stand variables. By extending the age arrow along the opposite direction (dashed line close to positive direction of CCA Axis 2 in Fig. 9), the projected position of each stand on the age vector would approximately represent the relative age of that stand. *Pinus* stands from the top to the centre, for example, reflect an increase in stand ages. It is interesting to note that young *Pinus* stands (e.g. 35-yr old JDM-1 and 25-yr JDH-3) were dominated by *Arctostaphylos uva-ursi*, *Vaccinium myrtilloides* and *Cladina mitis* and also contained *Pinus* as understorey components. In contrast, old stands tend to be dominated by *C. cornuta*, *C. stellaris*. This is consistent with the observation of Gower et al. (1997) at the four BOREAS tower sites that both *Arctostaphylos* and *Cladina* were dominant in the ground cover in young stands while *Cladina* forms a nearly complete ground cover in the mature stands. It also appears that species richness changes over time differently for different forest types (Fig. 4a). In *Pinus* stands, the number of understorey species, although smaller than the other stand types (Fig. 3c), increases with increasing stand age. In other forest types, the species number shows a slight decline with stand age.

Living tree biomass shows an increase with increasing stand age for all forest types (Fig. 4b), which is as expected when trees grow old and large, but the size of the present data set does not allow assignment of growth curves (biomass over age) of definite shape as described in the literature based on inventory data (e.g. Kurz & Apps 1999). A more complex pattern appears to occur with woody debris mass, which suggest a decreasing trend initially with a subsequent increase again after ca. 80 yr, at least for *Populus* and *Pinus* stands (Fig. 4c). The increase in CWD pools after ca. age 80 suggested

by the data, for example, may be due to a combination of self-thinning (*Pinus*), stand-breakup (*Populus*) and changes in decomposition rates associated with forest floor microclimate changes. Carbon content and thickness of the forest floor (duff layer) increase with increasing ages in all stand types (Fig. 4d). Interestingly, soil C-content shows a slight decline with ages in *Populus* stands (Fig. 4e).

Gower et al. (1997) found that young *Pinus* stands have higher forest floor C (18 000 to 40 260 kg-C.ha⁻¹) than do old stands (11 480-14 560 kg-C.ha⁻¹) in the four stands reported for the NSA and SSA BOREAS sites. This finding appeared to be opposite to the results presented here for 29 *Pinus* stands across the BFTCS (Figs. 4d and 5). Nalder & Wein (1999), finding that forest floor is a large component of C-storage in *Populus* and *Pinus* stands, also concluded that forest floor C increases significantly with stand age in *Populus* stands, but not in *Pinus* stands. The lack of support for long-term forest floor C-accumulation for *Pinus* stands in their study is opposite to our results. These various patterns in these studies may reflect differences in disturbance histories of these sites.

Conclusions and implications

1. Multivariate analysis of upland boreal ecosystems in continental western Canada indicates that the ecosystem carbon distribution and species composition vary across landscape scales and are strongly influenced by the site-environmental variables, such as soil moisture regime and the site's disturbance history (including time since last disturbance or stand age). The thickness of duff layer appears to be the single most important measured environmental/site variable that distinguishes different stand types in the region. A thick duff layer was found to be associated with *Picea* stands under very poor drainage conditions relative to *Pinus* stands on well-drained sandy soils, which have thin duff layers.

2. Multivariate analysis also indicates that complex interactions exist between different components (living biomass, dead organic matter, forest floor, and soil) and are important in the dynamics of the carbon cycle in these ecosystems. Understanding the processes influencing carbon transfer among these carbon pools at various stages of succession following a major stand-replacing disturbance is particularly critical for determining when an individual boreal ecosystem becomes either a source or a sink for atmospheric carbon. Knowing the spatial coherency of the factors causing these transitions is necessary for predictions of changes in the net carbon balance over landscapes.

3. The findings of this analysis have several implica-

tions for models that seek to examine climate-driven changes in the contribution of these ecosystems to the global carbon budget or to explain the present carbon balance of these systems. Many of the larger scale carbon budget models are generally inadequate for capturing the site variations and the different responses that might be expected in a changing climatic environment or disturbance regime. Many such models treat the site as if they were in steady state and fail to reflect changes in carbon indicators that are related to stand age (e.g., thickness of duff layer, understorey species composition), or their variation with changing stand growth. The results from the present study provides the relationships between the environmental/site variables and carbon distribution in different forest ecosystems that improved models need to emulate or use to reduce the uncertainty and capture the variability in C-estimates.

4. The results also suggest that it may not be necessary to represent individual species in such models: for boreal regions it may be adequate to represent species groups or functional types, together with other ecological/site characteristics. However, the results do suggest a specific need for the models to represent differences between the ecological niches occupied by wet conifer ecosystems, dry conifer ecosystems and mixed wood ecosystems in order to understand or predict the response to changes in the hydrological regime.

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