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## Carbon isotope composition of boreal plants: functional grouping of life forms

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**Abstract** We tested the hypothesis that life forms (trees, shrubs, forbs, and mosses; deciduous or evergreen) can be used to group plants with similar physiological characteristics. Carbon isotope ratios ( $\delta^{13}\text{C}$ ) and carbon isotope discrimination ( $\Delta$ ) were used as functional characteristics because  $\delta^{13}\text{C}$  and  $\Delta$  integrate information about  $\text{CO}_2$  and water fluxes, and so are useful in global change and scaling studies. We examined  $\delta^{13}\text{C}$  values of the dominant species in three boreal forest ecosystems: wet *Picea mariana* stands, mesic *Populus tremuloides* stands, and dry *Pinus banksiana* stands. Life form groups explained a significant fraction of the variation in leaf carbon isotope composition; seven life-form categories explained 50% of the variation in  $\delta^{13}\text{C}$  and 42% of the variation in  $\Delta$  and 52% of the variance not due to intraspecific genetic differences ( $n=335$ ). The life forms were ranked in the following order based on their values: evergreen trees < deciduous trees = evergreen and deciduous shrubs = evergreen forbs < deciduous forbs = mosses. This ranking of the life forms differed between deciduous (*Populus*) and evergreen (*Pinus* and *Picea*) ecosystems. Furthermore, life forms in the *Populus* ecosystem had higher discrimination values than life forms in the dry *Pinus* ecosystem; the *Picea* ecosystem had intermediate  $\Delta$  values. These correlations between  $\Delta$  and life form were related to differences in plant stature and leaf longevity. Shorter plants had lower  $\Delta$  values than taller plants, resulting from reduced light intensity at lower

levels in the forest. After height differences were accounted for, deciduous leaves had higher discrimination values than evergreen leaves, indicating that deciduous leaves maintained higher ratios of intracellular to ambient  $\text{CO}_2$  ( $c_i/c_a$ ) than did evergreen leaves in a similar environment within these boreal ecosystems. We found the same pattern of carbon isotope discrimination in a year with above-average precipitation as in a year with below-average precipitation, indicating that environmental fluctuations did not affect the ranking of life forms. Furthermore, plants from sites near the northern and southern boundaries of the boreal forest had similar patterns of discrimination. We concluded that life forms are robust indicators of functional groups that are related to carbon and water fluxes within boreal ecosystems.

**Key words** Functional groups · Life forms · Deciduous/evergreen · Carbon isotope discrimination · Boreal forests

### Introduction

The scaling up of responses from individual plants to the globe is critical for our ability to predict global climates and their effects on vegetation distribution (Sellers et al. 1996). Integrating plant responses to the environment on a regional or a global scale can only be successfully modeled when species are consolidated into functional groups (Box 1995). However at present, global circulation models (GCMs) only incorporate very general information about plants, such as biome distributions, and the vegetation is generally treated as a giant leaf within a  $1^\circ \times 1^\circ$  or larger cell. Often, global vegetation is separated into biomes or “vegetation types”, and the vegetation is characterized by features of the dominant species and their current distribution. Furthermore, this simplification of plant systems does not allow for temporal changes within plant communities, although this is an almost certain response to climate change (Bazzaz 1993; Spear et al. 1994). Plants will not respond to climate change as

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communities or biomes; rather, each species will respond independently (Schulze and Mooney 1994) according to its sensitivity to disturbance regimes or variations in temperature and/or moisture (Spear et al. 1994). However, including the detail of individual species within GCMs is not presently feasible. Another category of model that describes response to global changes is that of individual-based models of plant competition (Botkin et al. 1972; Shugart 1990). These models can successfully predict community composition based on species' physiological characteristics and current resource availability, but their complexity also limits the spatial scale at which they can be used (Smith et al. 1993).

Functional grouping of plants is one concept that has been suggested for scaling plant physiological responses to environmental conditions, thus removing one level of complexity from global models (Bazzaz 1993; Smith et al. 1993; Körner 1994a; Box 1995). The question then becomes; how does one categorize plants into functional groups? Drought and light tolerances have been used to categorize plants, but this requires detailed knowledge of the physiological characteristics of many species (Smith and Huston 1989). Smith et al. (1993) pointed out that most functional classification systems are based on features such as morphology, life spans, and seed dispersal, whereas most models used to predict plant responses to global change require information about stomatal conductance, photosynthesis rates, and carbon allocation patterns.

The most common and simplest method for classifying plants is by life form. Usually, classification into trees, shrubs, and forbs is based on morphological features of a species that are insensitive to environmental change, but easy to determine (Schulze 1982). Furthermore, Chapin (1993) pointed out that many dominant life forms can be recognized by remote sensing, and therefore could be used to provide an index of ecosystem function at regional and global scales. Life forms can be useful for functional grouping because they imply estimates of physiological variables required by global change models (Chapin 1993; Smith et al. 1993). For example, Buchmann et al. (1996) found that when  $^{15}\text{N}$  was added to the ecosystem, understory grasses in a *Picea abies* forest were the most competitive at taking up this nitrogen and also had higher nitrogen concentrations, followed by shrubs and then by trees. Schulze et al. (1994) found that at Alaskan sites where nitrogen is limiting, different life forms exploited different nitrogen pools within the ecosystem. Nadelhoffer et al. (1996) found similar patterns of nitrogen partitioning by tundra plant species. Because higher nitrogen concentrations are often related to higher photosynthetic capacities (Field and Mooney 1986), this grouping can give information about physiological function. Moreover, Ehleringer and Cooper (1988) found that water-use efficiency varied with life span: short-lived shrubs were less water-use-efficient than long-lived shrubs. Ehleringer (1994) speculated that in desert environments, perennials that persist through multiple droughts should have lower hydraulic

conductivities than short-lived annuals. Furthermore, he noted that life-form diversity was positively correlated with the climatic diversity of a site, indicating some form of functionality associated with life forms in desert environments.

Using the concept of functional grouping by life form, how do we evaluate whether life forms are appropriate as functional groups for physiological properties such as regulation of gas exchange? Leaf carbon isotope ratio ( $\delta^{13}\text{C}$ ) and carbon isotope discrimination ( $\Delta$ ) integrate information about how a plant regulates carbon dioxide and water fluxes as they relate to the ratio of intracellular to ambient  $\text{CO}_2$  ( $c_i/c_a$ ; Farquhar et al. 1989). In addition,  $\Delta$  is more stable over time than are absolute fluxes, thereby providing a better indicator of whole-plant constraints rather than environmental constraints. For example, Stewart et al. (1995) examined how  $\delta^{13}\text{C}$  changed in plants along a rainfall gradient, and found that the  $\delta^{13}\text{C}$  of a community reflected the longer-term average of precipitation for that site. Lloyd and Farquhar (1994) predicted that vegetation type would significantly affect carbon isotope discrimination on a global basis. Körner et al. (1988, 1991) used carbon isotope ratios to examine altitudinal and longitudinal effects on plant physiological processes for a broad spectrum of plants across the globe, and found that  $\delta^{13}\text{C}$  values change with altitude and latitude. Although the data of Körner et al. (1988, 1991) were not collected to test for the effects of life form, Kelly and Woodward (1995) used this data set to test for life-form influences on  $\delta^{13}\text{C}$  and found no significant effect. However, after accounting for the influence of altitude and taxonomic relatedness, their sample size was limited, thus reducing the power of the test.

In this study, we focus on the question of whether life forms are appropriate groups to predict the physiological characteristics of boreal plants, such as the balance between carbon dioxide and water fluxes. We test this hypothesis using  $\delta^{13}\text{C}$  and  $\Delta$  values of trees, shrubs, forbs, mosses, and lichens in three ecosystems at the northern and southern boundaries of the boreal forest biome in central Canada.

## Methods

This study was conducted in association with the Boreal Ecosystem-Atmosphere Study (BOREAS). The southern study area (SSA) was located 40 km north of Prince Albert, Saskatchewan, and covered an area of 130 km $\times$ 90 km (approximately 600 m above sea level). Mean annual precipitation (1967–1994) for Prince Albert is 420 mm. In 1993, total precipitation was 414 mm and in 1994 was 495 mm (data provided by Environment Canada). The northern study area (NSA) was 100 km $\times$ 80 km (approximately 200 m above sea level), and included the town of Thompson, Manitoba. Mean annual precipitation (1967–1994) for Thompson is 513 mm. In 1993, total precipitation was 443 mm, and in 1994, 371 mm. In both SSA and NSA, three different ecosystems were chosen for study; the dominant tree species were, *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides*. These ecosystems vary in stand density and canopy openness: the *Pinus* ecosystem has the lowest leaf area index (LAI, 1–2 m $^2$ /m $^2$ ), *Populus* was intermediate in LAI (2–3 m $^2$ /m $^2$ ) and the *Picea* ecosystems had the highest

(3–6 m<sup>2</sup>/m<sup>2</sup>). These six sites are described in detail in Brooks et al. (1997).

Leaf samples were collected for carbon isotope analysis in August 1993 and in early September 1994. In 1993 samples were collected only at the four conifer sites, whereas in 1994 samples were collected at all six sites. At each site, the most abundant 10–15 plant species were identified, and leaf samples were collected from ten individuals of the dominant tree species and from five individuals of the other species. From each individual sampled, four to five mature leaves were collected from the top of the plant and bulked into a single sample. Our total sample size was  $n=175$  in 1993 and  $n=335$  in 1994.

In addition to the six main sampling sites, we collected leaf samples from the dominant tree species along a transect between SSA and NSA in 1993. *Pinus banksiana* samples were collected from two stands along Saskatchewan Highway 106, north of Nipawin Provincial Park, and from one stand along Manitoba Highway 39. *Picea mariana* samples were collected from two stands along Saskatchewan Highway 106, and two stands along Manitoba Highway 39 and 6. At each stand, sun foliage in the upper canopy was collected from five trees. We collected current (foliage formed in 1993), 1-year-old, 2-year-old, and 3-year-old foliage from each tree, and age classes were kept as separate samples (total  $n=140$  for the transect).

Leaf samples were dried at 70°C for 48 h and ground to a fine powder using a mortar and pestle. Sub-samples of 2 mg were combusted and the resulting CO<sub>2</sub> was analyzed on an isotope mass spectrometer (delta S, Finnigan MAT, Bremen, Germany) for  $\delta^{13}\text{C}$  (‰, Ehleringer 1991) at the SIRFER facility at the University of Utah (mass spectrometer precision  $\pm 0.1\text{‰}$ ).

Carbon isotope discrimination ( $\Delta$ ) was calculated from leaf  $\delta^{13}\text{C}$  using Eq. 1 (Farquhar et al. 1989):

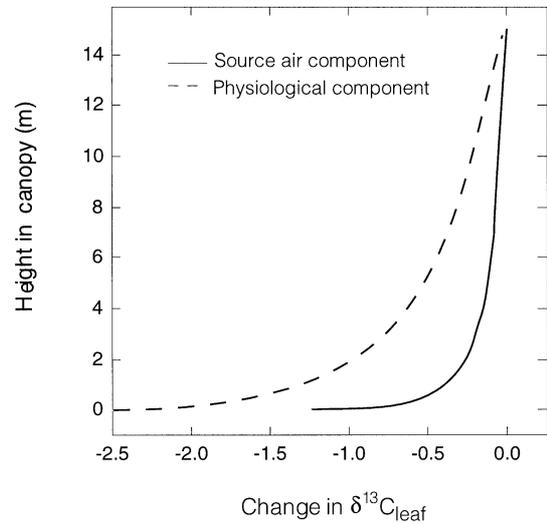
$$\Delta = \frac{\delta_{\text{air}} - \delta_{\text{leaf}}}{1 + \delta_{\text{leaf}}} \quad (1)$$

where  $\delta_{\text{leaf}}$  is the carbon isotope ratio of the foliage sample, and  $\delta_{\text{air}}$  is the carbon isotope ratio of the source CO<sub>2</sub> for photosynthesis.  $\delta_{\text{air}}$  can vary temporally and spatially within a canopy depending on the mixture of CO<sub>2</sub> from the convective boundary layer above the vegetation and CO<sub>2</sub> from plant and soil respiration, which have very different isotopic ratios (–8‰ and –27‰, respectively). As the proportion of respired CO<sub>2</sub> increases nearer to the soil surface,  $\delta_{\text{air}}$  becomes more depleted in <sup>13</sup>C (Fig. 1; Keeling 1961; Schleser and Jayasekera 1985; Sternberg 1989). We calculated  $\delta_{\text{air}}$  using photosynthetically weighted CO<sub>2</sub> concentration profiles (Brooks et al., 1997) and the relationships between [CO<sub>2</sub>] and  $\delta^{13}\text{C}$  (Flanagan et al., 1997) measured at these six sites. We measured [CO<sub>2</sub>] and  $\delta^{13}\text{C}$  within the canopies at each site three times over the growing season.  $\delta_{\text{air}}$  was related to height in the canopy (m) as described by Eq. 2 for the six BOREAS sites used in this study:

$$\delta_{\text{air}} = 0.128 \ln(ht) - 7.95 \quad (r^2=0.40, df=67, F=14.4, P<0.0001) \quad (2)$$

We evaluated the pattern of  $\delta_{\text{air}}$  within the canopy for different sites and for different seasons. In the end, one overall equation for all sites and seasons was used because there was no distinct pattern with seasons or sites; the simplest model was therefore selected. Using the mean plant height for a species at each site, we estimated the source air  $\delta^{13}\text{C}$  from Eq. 2, and used that value and plant  $\delta^{13}\text{C}$  to calculate carbon isotope discrimination from Eq. 1. Our estimates for discrimination for the mosses were similar to on-line gas-exchange measurements made by Williams and Flanagan (in press), which support our source air equation.

Plant species were categorized into the following life forms: deciduous or evergreen; trees, shrubs, forbs, mosses, or lichens. In addition the data were categorized by ecosystem type (*Pinus*, *Picea*, or *Populus* ecosystems), location (north or south) and site (a combination of ecosystem and location). Table 1 is a complete listing of species sampled at each study site. Each life-form category included between two and seven species, except lichens. Some plant species, such as *Cornus canadensis* and *Vaccinium vi-*



**Fig. 1** Change in leaf  $\delta^{13}\text{C}$  with canopy height attributed to the effects of source CO<sub>2</sub> for photosynthesis and leaf physiology affecting  $c_i/c_a$ . The line for the effect of source air was from Eq. 2 ( $\delta_{\text{air}}=0.128 \ln(ht) - 7.95$ ) and the line for the effect of leaf physiology was calculated from the relationship between canopy height ( $\Delta=21.4 - 0.46 \ln(ht)$ )

*tis-idaea*, were common in all ecosystems. However, other species were more site-specific: *Corylus cornuta* was only abundant in the *Populus* ecosystem in the south, and *Pyrola secunda* was only abundant in the *Populus* ecosystem in the north. In most cases, each ecosystem had at least one species in each life-form category.

Data were analyzed using both ANOVA and regression analysis on JMP 3.0 (1993, SAS Institute Inc.). If ANOVAs were significant, category means were tested using the Tukey-Kramer honestly significant difference (HSD) test. In addition, tree-based modeling (Clark and Pregibon 1992) was used to separate species categories into groups based on their  $\Delta$  values; these species groups were then compared to see how closely they resembled life-form categories. Tree-based models were also run using life-form categories. Tree-based models were run using S-PLUS (Version 3.1, 1992, Statistical Sciences Inc.). For most analyses we eliminated lichens since the carbon isotope ratio for lichens depends primarily on the algal species involved (Lange et al. 1988).

## Results

The leaf carbon isotope ratios of boreal plant species spanned a range of over 9‰ in 1993 and over 11‰ in 1994. In 1993, the mean  $\delta^{13}\text{C}$  was  $-29.5\text{‰}$  ( $\pm 1.7$  SD) for the 16 species sampled, ranging between  $-24.4\text{‰}$  for the evergreen tree, *Picea mariana*, and  $-33.7\text{‰}$  for the deciduous forb, *Petasites palmatus*. Similarly in 1994, the mean  $\delta^{13}\text{C}$  of the 29 species sampled was  $-29.4\text{‰}$  ( $\pm 2.2$  SD), ranging between  $-23.5\text{‰}$  for the evergreen tree, *Pinus banksiana*, and  $-35.2\text{‰}$  for the evergreen forb, *Linnaea borealis*. Within the ecosystems at NSA and SSA,  $\delta^{13}\text{C}$  varied with plant height ( $\delta^{13}\text{C}=0.59 \times \ln(\text{height in m}) - 28.7$ ,  $r^2_{\text{adj}}=0.41$ ,  $n=335$ ,  $F=248$ ), where  $\delta^{13}\text{C}$  became more depleted near the forest floor (Fig. 1). This variation in leaf  $\delta^{13}\text{C}$  with height was attributed to changes in leaf  $c_i/c_a$ , and changes in

**Table 1** Mean leaf  $\delta^{13}\text{C}$  (‰,  $\pm$ SD,  $n=5$ ,  $n=10$  for tree species) of the dominant species at each site. Species are separated into life-form categories. *Height* refers to the mean height of the species

Species	Height (m)	<i>Populus</i> ecosystem		<i>Pinus</i> ecosystem		<i>Picea</i> ecosystem	
		North	South	North	South	North	South
Deciduous trees							
<i>Populus tremuloides</i> Michx	15	-28.0 $\pm$ 0.79	-27.2 $\pm$ 1.14			-29.3 $\pm$ 0.92	
<i>Salix</i> spp.	2					-29.8 $\pm$ 0.71	
Evergreen trees							
<i>Picea mariana</i> (Mill.) B.S.P.	10					-26.5 $\pm$ 0.72	-26.5 $\pm$ 0.66
<i>Pinus banksiana</i> Lamb.	10			-24.8 $\pm$ 0.75	-26.6 $\pm$ 0.44		
Deciduous shrubs							
<i>Alnus crispa</i> (Ait.) Pursh	1.5	-27.8 $\pm$ 0.79		-27.3 $\pm$ 0.14	-28.4 $\pm$ 1.09	-29.8 $\pm$ 0.31	
<i>Corylus cornuta</i> Marsh.	1.5		-28.8 $\pm$ 1.21				
<i>Rosa acicularis</i> Lindl.	1	-29.6 $\pm$ 0.39	-27.9 $\pm$ 1.55			-30.5 $\pm$ 0.70	-28.8 $\pm$ 1.63
<i>Vaccinium myrtilloides</i> Hook	0.25	-31.1 $\pm$ 0.77		-29.1 $\pm$ 0.28	-29.4 $\pm$ 0.30		-31.6 $\pm$ 0.30
<i>Viburnum edule</i> (Michx.) Raf.	1.5	-27.6 $\pm$ 0.80					
Evergreen shrubs							
<i>Arctostaphylos uva-ursi</i> (L.) Spr.	0.0	-32.2 $\pm$ 0.58		-28.6 $\pm$ 1.23	-29.0 $\pm$ 0.73		
<i>Gaultheria procumbens</i> L.	0.15			-29.4 $\pm$ 0.21			
<i>Ledum groenlandicum</i> Oeder.	0.5						-28.5 $\pm$ 0.54
<i>Vaccinium vitis-idaea</i> L. var. <i>minus</i> Lodd	0.05	-30.5 $\pm$ 0.38		-27.6 $\pm$ 0.71	-28.5 $\pm$ 0.88		-30.8 $\pm$ 0.60
Deciduous forbs							
<i>Apocynum androsaemifolium</i> L.	0.5				-29.5 $\pm$ 0.19		
<i>Aralia nudicaulis</i> L.	0.2		-31.7 $\pm$ 0.55				
<i>Fragaria virginiana</i> Hall	0.05	-31.0 $\pm$ 0.90	-31.7 $\pm$ 0.39				
<i>Maianthemum canadense</i> Desf. var. <i>interius</i> Fern	0.1				-27.9 $\pm$ 0.27		
<i>Petasites palmatus</i> Ait.	0.1	-32.4 $\pm$ 0.49	-33.7 $\pm$ 0.43			-33.2 $\pm$ 0.50	-32.7 $\pm$ 1.73
<i>Potentilla palustris</i> (L.) Scop.	0.15						-29.6 $\pm$ 0.84
<i>Solidago canadensis</i> L.	0.25				-30.4 $\pm$ 1.50		
Evergreen forbs							
<i>Cornus canadensis</i> L.	0.1	-28.8 $\pm$ 0.48	-31.0 $\pm$ 0.52	-26.8 $\pm$ 0.31		-28.8 $\pm$ 0.50	-27.9 $\pm$ 0.50
<i>Linnaea borealis</i> Torr.	0.05		-33.2 $\pm$ 1.29				
<i>Pyrola secunda</i> L.	0.2	-31.3 $\pm$ 0.80					
Mosses							
<i>Dicranum polysetum</i>	0			-30.3 $\pm$ 0.38			
<i>Hylocomium splendens</i>	0	-31.0 $\pm$ 0.50				-30.3 $\pm$ 0.40	
<i>Pleurozium shreberi</i>	0	-32.3 $\pm$ 0.94		-30.6 $\pm$ 0.86	-31.3 $\pm$ 0.61	-31.7 $\pm$ 0.68	-32.5 $\pm$ 0.87
<i>Ptilium crista-cretensis</i>	0					-32.5 $\pm$ 0.70	
<i>Sphagnum</i> spp.	0						-31.4 $\pm$ 2.14
Lichen							
<i>Cladina mitis</i>	0			-26.0 $\pm$ 0.62	-25.7 $\pm$ 0.72		

the  $\delta^{13}\text{C}$  of source  $\text{CO}_2$  available for photosynthesis. Separating these two effects, we found that leaf physiology accounted for 78% of the change in  $\delta^{13}\text{C}$ , while source  $\text{CO}_2$  accounted for the remaining 22%. In this study, we are interested in physiological effects on carbon isotope composition; therefore, we calculated carbon isotope discrimination ( $\Delta$ ) which eliminates the effect of variation in source  $\text{CO}_2$  (Eq. 1). Discrimination values were similar between the two years; ranging from 16.3‰ to 27.8‰ in 1994, with a mean of 21.9‰ ( $\pm$ 2.1 SD), and ranging from 17.1‰ to 26.3‰ in 1993, with a mean of 21.8‰ ( $\pm$ 1.7 SD).

Our goal was to determine whether life forms could adequately describe the variation in  $\Delta$  observed among species. Prior to testing life forms, we determined how much of the variation in the data set originated from species and site differences (explainable using our categories), and how much was phenotypic variation within the

populations (unexplainable using our categories). Species alone only explained 64% of the variation. Using species as the main factor, in combination with sites nested within species (Species, S[species]; Table 2), the model explained 81% and 80% of the variation within the data set for  $\delta^{13}\text{C}$  and  $\Delta$  values, respectively. The remaining 20% was attributed to phenotypic variation within the populations. Since the Species, S[species] model explained the most variation within the data set, we used this model for comparison with other models, and refer to it as the *maximum* model. The maximum model used 59 categories to explain the variation within the data. Our goal was to simplify the model by reducing the number of categories, while maximizing the variation it explains. The *F*-statistic balances these two properties (number of categories and variation explained), so we

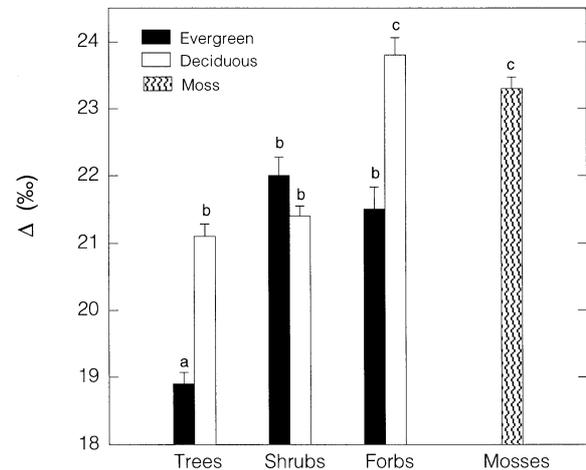
**Table 2** Modeling statistics for carbon isotope discrimination ( $\Delta$ , ‰) for 1993 and 1994.  $df_{\text{model}}$  are the degrees of freedom used by the model,  $r^2_{\text{adj}}$  is the adjusted coefficient of determination and  $F$  is the overall  $F$ -statistic of the model. For the 1994 data, % represents the percent of variation explained compared to the model that explains the maximum amount of variation. [Brackets] indicate a nested design with the main factor in the bracket. The 1994

data set includes all six sites, while the 1993 data set only contains the conifer sites. Lichens were removed from both data sets. All factors were highly significant in the model ( $P < 0.0001$ ) except location (north or south) which was not significant (ns,  $\alpha = 0.05$ ) in 1993 and barely significant in 1994. Sample sizes were  $n = 165$  for 1993 and  $n = 325$  for 1994

Model description	1993 $\Delta$			1994 $\Delta$			
	$df_{\text{model}}$	$r^2_{\text{adj}}$	$F$	$df_{\text{model}}$	$r^2_{\text{adj}}$	$F$	%
Life forms (LF)	6	0.44	22.5	6	0.42	43.1	53
Location (L)		ns		1	0.01	5.0	1
Site (S)	3	0.25	18.8	5	0.11	9.6	14
Ecosystem (Eco)	1	0.24	<b>53.0</b>	2	0.09	18.7	11
LF and S	9	0.60	27.9	11	0.51	35.0	64
LF and Eco	7	0.59	35.0	8	0.51	<b>47.6</b>	64
LF, Eco [LF]	12	0.72	36.0	18	0.62	34.2	78
LF, S [LF]	21	0.75	24.6	32	0.66	22.6	83
Species	15	0.64	20.5	28	0.64	23.7	80
Species and Eco	16	0.73	28.7	30	0.71	30.3	89
Species and S	18	0.75	28.7	33	0.72	29.3	90
Species, Eco [species]	19	0.75	26.9	42	0.76	27.7	95
Species, S [species]	32	<b>0.81</b>	23.1	58	<b>0.80</b>	26.0	100

also used this parameter to compare models. Comparing the two years (1993 and 1994), all models were quite similar in explaining the variation. Since the 1994 data set was more extensive and covered all six sites, we focused on those results.

Life forms (LF), using just seven categories to separate the data (lichens were excluded), explained 42% of the total variation in the data set, and 53% of the variation of the maximum model. Its  $F$ -statistic (43.1) was the second highest of all the models, indicating that for the number of categories used, life forms were an appropriate unit for classifying carbon isotope discrimination values. However, the model with the highest  $F$ -statistic (47.6) contained both life form and ecosystem categories (LF and Eco). The LF and Eco model explained 51% of the total variation, and 64% of the maximum model. Interestingly, location (whether plants were located at sites near the southern or northern boundary of the boreal forest) explained only 1% of the variation in  $\Delta$  in 1994, and was not significant in 1993. Thus, plants had similar  $\Delta$  values at both boundaries of the boreal forest; therefore, knowing a species' life form and ecosystem type was much more important than knowing its location within the boreal biome. This observation was also supported by the similarity between the variation explained by the Site model and the Ecosystem model. Since the LF and Eco model was one of the simplest models, using only nine categories and with the highest  $F$ -statistic, we selected this model as the best model for explaining variation in  $\Delta$  within these boreal ecosystems. Since we recognize that calculating  $\Delta$  is not always possible, we should note that the LF and Eco model was also the best for classifying variation in  $\delta^{13}\text{C}$ , explaining 58% ( $F = 63.2$ ) of the total variation and 72% of the variation in the maximum model.



**Fig. 2** Mean carbon isotope discrimination  $\Delta$  ( $\pm$ SE) for the different life forms. Different letters represent significant differences among the means ( $\alpha = 0.05$ , Tukey-Kramer HSD test)

Life forms showed distinct differences in carbon isotope discrimination (Fig. 2, Table 3). Evergreen trees, which dominated two ecosystems, had the lowest  $\Delta$  values of all the life forms, with a mean  $\Delta$  of 18.9‰. When all ecosystems were combined, deciduous trees, shrubs and evergreen forbs were indistinguishable with a mean of 21.6‰. However within an ecosystem, these groups differed significantly (Table 3), but their ranking depended on whether the ecosystem was dominated by evergreen or deciduous trees (Fig. 3). Within a life form, deciduous forms maintained similar discrimination values between ecosystems. However, evergreen forms had higher  $\Delta$  values in the deciduous forest than in the evergreen forests. In the evergreen ecosystems, evergreen trees and evergreen forbs had the lowest  $\Delta$ , whereas in

the deciduous ecosystems, deciduous trees and deciduous shrubs had the lowest  $\Delta$ . Mosses and deciduous forbs had the highest  $\Delta$  values, regardless of ecosystem, with a mean of 23.5‰ (Figs. 2 and 3).

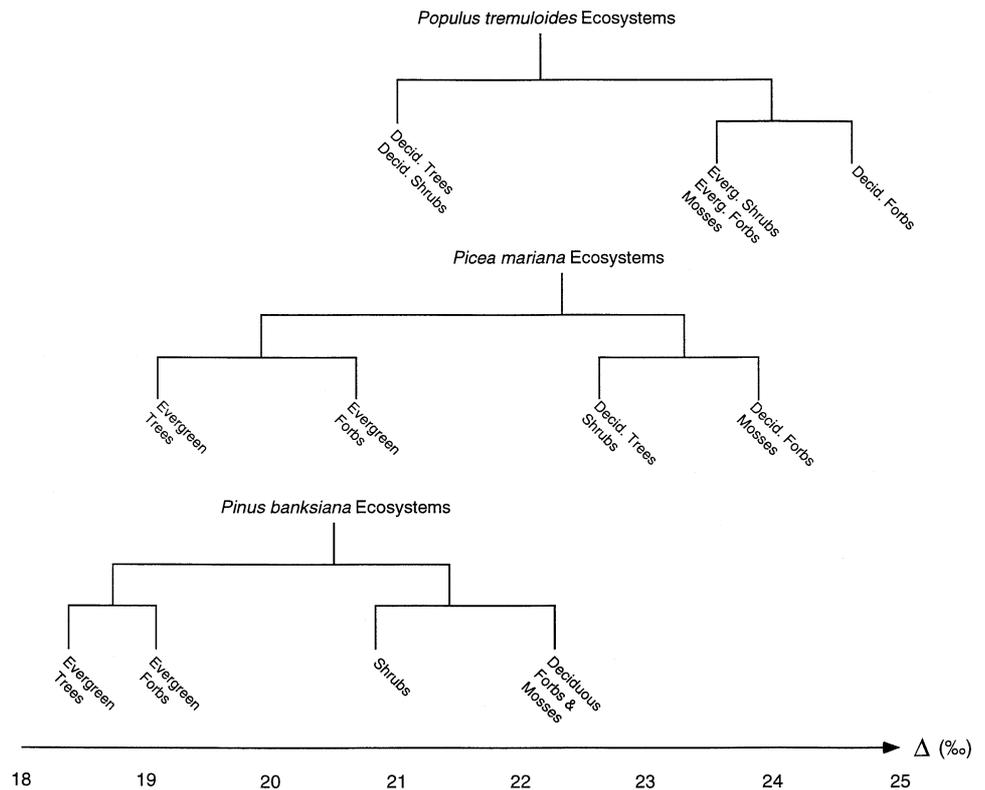
To see whether the species naturally separated into groups that were similar to the life form categories and ranking order, we used tree-based modeling for species within an ecosystem. These tree-based models produced classifications very similar to those in Fig. 3 that were based on life-form categories rather than species. However, certain species did not fit into their proper life form categories. For example, *Vaccinium myrtilloides*, a deciduous shrub, had a  $\Delta$  of approximately 24‰, which was higher than other deciduous shrubs (mean  $\Delta$ =21.4‰), but similar to deciduous forbs (mean  $\Delta$ =23.8‰). Generally, species tended to branch into groups that reflected their life form, indicating that some physiological and morphological features associated with the life-form categories influenced carbon isotope discrimination within these ecosystems.

We explored whether one of these physiological/morphological features affecting  $\Delta$  could be plant stature as it relates to vertical variation in leaf physiological characteristics within the forest (Fig. 1). Since we removed the effects of source CO<sub>2</sub> in calculating  $\Delta$ , we are only exploring the effect of plant height on leaf physiology. We regressed  $\Delta$  against the natural logarithm of height and found that plant stature significantly influenced  $\Delta$  ( $r^2_{adj}$ =0.27,  $F$ =132,  $P$ <0.0001). The slope of this relationship was the same for all ecosystems, but the intercept increased from the *Pinus banksiana* ecosystem (20‰), to the *Picea mariana* ecosystem (21.6‰), to the *Populus tremuloides* ecosystem (22.1‰). This height effect is probably related to changes in  $c_i/c_a$  with light attenuation. Using the residuals from this regression, thus subtracting the influence of plant stature on discrimination, we found that life forms still explained a significant amount of the remaining variation in  $\Delta$  ( $r^2_{adj}$ =0.24,  $F$ =19.2,  $P$ <0.0001), but the ranking pattern of life forms changed:

**Table 3** Leaf  $\Delta$  in 1994 (‰,  $\pm$ SE) of life forms in the different ecosystems and combined for all sites. Different letters denote significantly different  $\Delta$ s ( $\alpha$ =0.05) in a Tukey-Kramer all pairs comparison across all ecosystems and life-form categories (1994, SAS Institute Inc.). The combined ecosystem data were tested among life-form categories only

Life forms	<i>Populus</i> ecosystems	<i>Pinus</i> ecosystem	<i>Picea</i> ecosystem	All ecosystems
Evergreen trees		18.4 $\pm$ 0.26 <sup>a</sup>	19.2 $\pm$ 0.19 <sup>a</sup>	18.9 $\pm$ 0.17 <sup>a</sup>
Deciduous trees	21.0 $\pm$ 0.19 <sup>b</sup>		22.6 $\pm$ 0.41 <sup>bcde</sup>	21.1 $\pm$ 0.19 <sup>b</sup>
Evergreen shrubs	24.3 $\pm$ 0.39 <sup>de</sup>	20.7 $\pm$ 0.21 <sup>b</sup>	22.1 $\pm$ 0.38 <sup>bc</sup>	22.0 $\pm$ 0.28 <sup>b</sup>
Deciduous shrubs	21.0 $\pm$ 0.20 <sup>b</sup>	21.1 $\pm$ 0.22 <sup>b</sup>	22.9 $\pm$ 0.30 <sup>cd</sup>	21.4 $\pm$ 0.15 <sup>b</sup>
Evergreen forbs	22.9 $\pm$ 0.35 <sup>cd</sup>	19.1 $\pm$ 0.14 <sup>ab</sup>	20.7 $\pm$ 0.21 <sup>ab</sup>	21.5 $\pm$ 0.33 <sup>b</sup>
Deciduous forbs	24.6 $\pm$ 0.23 <sup>e</sup>	21.8 $\pm$ 0.39 <sup>bc</sup>	24.4 $\pm$ 0.53 <sup>de</sup>	23.8 $\pm$ 0.26 <sup>c</sup>
Mosses	23.6 $\pm$ 0.33 <sup>cde</sup>	22.8 $\pm$ 0.18 <sup>cd</sup>	23.5 $\pm$ 0.29 <sup>cde</sup>	23.3 $\pm$ 0.17 <sup>c</sup>
Lichen		18.0 $\pm$ 0.22 <sup>a</sup>		18.0 $\pm$ 0.22 <sup>a</sup>

**Fig. 3** The ranking of life forms based on carbon isotope discrimination within each ecosystem. The tree models were generated using tree-based models with life-form categories to split the data. Vertical lines represent the mean carbon isotope discrimination for a branch of the tree model



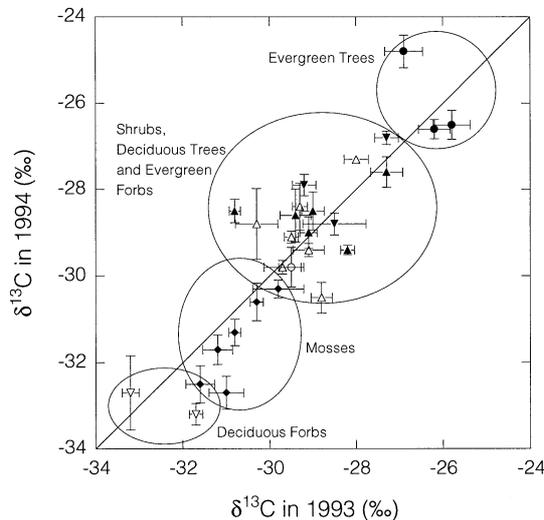
evergreen forbs=evergreen trees<evergreen shrubs< mosses=deciduous shrubs=deciduous trees<deciduous forbs. All evergreen life forms had lower discrimination values than the deciduous life forms and mosses ( $t=7.22$ ,  $P<0.0001$ ). Thus, foliage longevity was an additional morphological feature that influenced plant discrimination, with higher  $\Delta$  in short-lived leaves than in long-lived leaves.

In addition to plant stature and leaf longevity of a life form, ecosystem type also influenced discrimination. The *Pinus banksiana* ecosystem had the lowest mean of all ecosystems ( $20.8\% \pm 0.18$  SE), whereas both the *Picea mariana* and the *Populus tremuloides* ecosystems had higher mean  $\Delta$  values ( $22.4\% \pm 0.22$  and  $22.2\% \pm 0.15$  respectively,  $F=19$ ,  $P<0.0001$ , Fig. 3). This ecosystem effect was also seen in the relationship between discrimination and plant height, where the intercept shifted with ecosystem as reported above. Plants in the *Picea mariana* ecosystem showed the largest variation in  $\Delta$  values,

a range of over 5‰, with evergreen trees at 19.2‰ and deciduous forbs at 24.4‰. Plants in the other two ecosystems varied less (approximately 4‰), but the ranges were quite different. The  $\Delta$  values of plants in the *Populus tremuloides* ecosystem ranged between 21‰ and 24.6‰, while  $\Delta$  values in the *Pinus banksiana* ecosystem ranged between 18.4‰ and 22.8‰ (Table 3, Fig. 3).

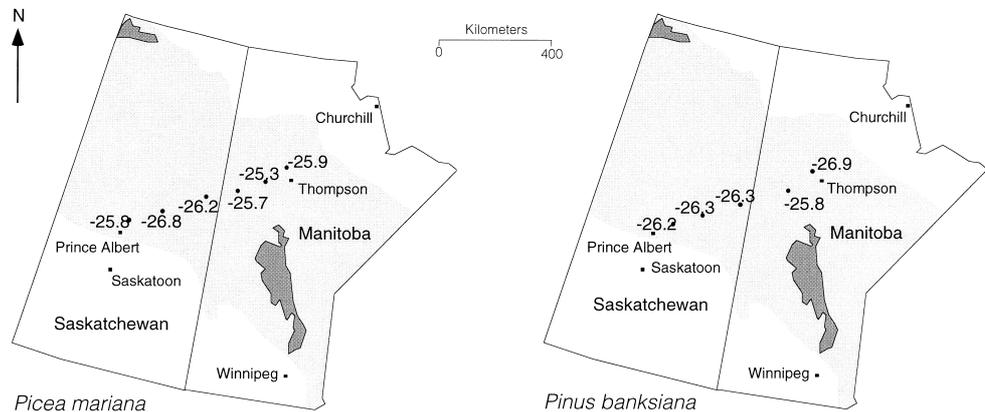
The ranking of life forms was also consistent between years. Although, 1993 and 1994 had different environmental conditions (415 and 495 mm rainfall, respectively, for Prince Albert, and 440 and 370 mm for Thompson),  $\Delta$  values and the pattern of variation among life forms remained the same in the two years. The overall mean was the same between the study years (21.9‰ vs. 21.8‰,  $t=0.64$ ,  $df=498$ ,  $P>0.5$ ) as well as for individual species (Fig. 4). In both 1993 and 1994, evergreen trees had  $\Delta$  values most enriched in  $^{13}\text{C}$  and deciduous forbs and mosses were the most depleted in  $^{13}\text{C}$ . In addition, the models that described carbon isotope discrimination (Table 2) explained similar amounts of variation for both years, indicating that discrimination and the life-form and ecosystem factors that influence it were stable through time. Even large weather fluctuations did not disturb these patterns of carbon isotope discrimination.

Besides being temporally stable,  $\delta^{13}\text{C}$  and  $\Delta$  remain spatially constant as well. Carbon isotope discrimination patterns were similar at sites near both the northern and southern boundaries of the boreal forest for both 1993 and 1994 data. This similarity persisted despite precipitation differences between the northern and southern sites, where 1993 was drier at the southern site and 1994 was drier at the northern site. In addition,  $\delta^{13}\text{C}$  did not vary significantly along a transect between the northern and southern boundaries of the boreal forest, which spanned over 600 km (Fig. 5). This constant  $\delta^{13}\text{C}$  across the transect was found in four different age classes of foliage, indicating that this spatial consistency was robust over time (Table 4). Therefore, neither environmental fluctuations across the boreal forest nor fluctuations between years altered the patterns of carbon isotope discrimination that we found.



**Fig. 4** A comparison of leaf  $\delta^{13}\text{C}$  values between 1993 and 1994. Each symbol represents a species mean for a given site (the four conifer sites only). Open symbols represent deciduous forms, and filled symbols represent evergreen forms or mosses (circles trees, triangles shrubs, inverted triangles forbs, diamonds mosses)

**Fig. 5** Maps of central Canada showing needle  $\delta^{13}\text{C}$  (‰) along a transect for both coniferous tree species. The shaded area represents the range of the boreal forest. The southern study area (SSA) was located just north of Prince Albert, and the northern study area (NSA) was located northwest of Thompson



**Table 4** Mean  $\delta^{13}\text{C}$  (‰,  $\pm\text{SD}$ ,  $n=5$ ) of sun foliage from the dominant conifers along a transect from the southern study area (SSA) to the northern study area (NSA) (see fig. 5). All samples were collected in 1993: the different years represent the years in which the

needles were formed (different foliage age classes). ANOVAs across the transect were not significant ( $\alpha=0.05$ ) for both species in all age classes except for *Pinus banksiana* foliage formed in 1991 when NSA had significantly lower  $\delta^{13}\text{C}$  than stand 3

<i>Picea mariana</i>	SSA	Stand 1	Stand 2	Stand 3	Stand 4	NSA
1993	-25.8 $\pm$ 0.8	-26.8 $\pm$ 0.4	-26.3 $\pm$ 0.7	-25.7 $\pm$ 0.6	-25.4 $\pm$ 1.2	-26.6 $\pm$ 0.7
1992	-24.9 $\pm$ 1.0	-26.5 $\pm$ 0.8	-25.9 $\pm$ 0.9	-25.9 $\pm$ 0.8	-25.2 $\pm$ 1.1	
1991	-26.2 $\pm$ 1.0	-26.8 $\pm$ 0.8	-26.1 $\pm$ 1.0	-26.1 $\pm$ 1.1	-25.6 $\pm$ 1.0	
1990	-25.4 $\pm$ 0.7	-26.4 $\pm$ 0.9	-25.7 $\pm$ 0.6	-25.9 $\pm$ 1.2	-25.6 $\pm$ 1.0	
<i>Pinus banksiana</i>						
1993	-26.9 $\pm$ 0.7	-26.3 $\pm$ 0.6	-26.3 $\pm$ 0.9	-25.8 $\pm$ 0.4		-26.9 $\pm$ 0.9
1992	-27.4 $\pm$ 1.0	-26.9 $\pm$ 0.4	-26.8 $\pm$ 0.8	-26.3 $\pm$ 0.4		-27.2 $\pm$ 1.1
1991	-27.8 $\pm$ 0.8	-26.7 $\pm$ 0.7	-26.8 $\pm$ 0.8	-26.3 $\pm$ 0.7		-28.3 $\pm$ 1.1
1990	-27.8 $\pm$ 0.9	-27.1 $\pm$ 0.9	-27.2 $\pm$ 1.1	-26.1 $\pm$ 0.5		-27.6 $\pm$ 0.8

## Discussion

Although life-form groups are based on morphological and structural features, we found that life forms were a robust indicator of physiological processes, such as carbon isotope discrimination. Thus, life forms have characteristics which would allow them to be used as functional groups to scale physiological processes within boreal ecosystems. Life form alone explained 42% of the variation in  $\Delta$  values, and 52% of the variance not due to intraspecific genetic differences. Differences in carbon isotope discrimination among life forms were strongly related to plant stature and leaf longevity: plants in the upper canopy had lower  $\Delta$  values than plants in the lower canopy, while evergreen leaves had lower  $\Delta$  values than deciduous leaves. In addition, ecosystem type also influenced carbon isotope discrimination. Plants in the deciduous *Populus tremuloides* ecosystem had higher  $\Delta$  values than plants in the evergreen ecosystems, while plants in the dry *Pinus banksiana* ecosystem had the lowest  $\Delta$  values. These relationships among carbon isotope discrimination, life form, and ecosystem type were spatially stable: similar patterns were found in ecosystems located at the northern and southern boundaries of the boreal forest. Furthermore, these patterns were consistent through time, even in years with vastly different environmental conditions.

Leaf  $\delta^{13}\text{C}$  values increased by approximately 3‰ from the bottom to the top of the canopy in these boreal forests. Vertical gradients in  $\delta^{13}\text{C}$  have been found in other forest types ranging from tropical to temperate including both evergreen and deciduous forms (Schleser and Jayasekera 1985; Ehleringer et al. 1986; Garten and Taylor 1992; Gutierrez and Meinzer 1994; Buchmann et al. 1997; Berry et al. 1997), and these  $\delta^{13}\text{C}$  gradients ranged between 1 and 6‰. Of the gradient in our boreal canopies, 22% was attributed to changes in the  $\delta^{13}\text{C}$  of the source  $\text{CO}_2$ , and the remaining 78% resulted from changes in  $\Delta$  (Fig. 1), which is related to  $c_i/c_a$  of the leaf (Farquhar et al. 1989). The relationship between height in the canopy and was probably mediated through canopy sheltering effects, which include light attenuation, increased relative humidity (Hinckley et al. 1994; Hollin-

ger et al. 1994; Parker 1995), and potentially changes in hydraulic conductance (Panek and Waring 1995; Walcroft et al. 1996). However, Brooks et al. (1997) found that within these canopies, photosynthesis decreased with light attenuation faster than stomatal conductance, resulting in an increase in  $c_i/c_a$  at lower canopy positions. Although these patterns were found for the dominant tree species, a similar relationship between gas exchange and canopy position probably exists for all species, resulting in the vertical pattern for  $\Delta$  we observed. The decrease in carbon isotope discrimination with increasing height above the forest floor occurred at the same rate regardless of the ecosystem. This result was unexpected since these ecosystems vary in leaf area index (LAI) and stand structure, two factors that affect light attenuation. For example, Buchmann et al. (in review) found that the gradient in leaf  $\delta^{13}\text{C}$  increased in *Acer* and *Populus* canopies with increasing LAI. However, in this study changes in LAI were also associated with differences between evergreen and deciduous vegetation types for which canopy architecture and light attenuation patterns can vary substantially for a given LAI (Sprugel 1989). In addition, there were environmental differences between these ecosystems, such as water and nutrient availability, that cause changes in vegetation composition and structure. The relationship between canopy structure and gradients in carbon isotope discrimination warrants further investigation.

Once changes in plant stature were accounted for (using residual analysis), life forms were still significant in explaining the variation in carbon isotope discrimination. We found that deciduous species had higher  $^{13}\text{C}$  discrimination values than evergreen species, regardless of life form. Evergreen leaves have been noted for having higher intrinsic water-use-efficiency, lower stomatal conductance, and lower photosynthetic rates compared to deciduous species (Chabot and Hicks 1982; Schulze 1982; Körner 1994b; Reich et al. 1995). Marshall and Zhang (1994) noted that discrimination against  $^{13}\text{C}$  was greater in deciduous trees than in evergreen trees for species growing at similar elevations in the Rocky Mountains. Some differences between evergreen and deciduous species have been found because the evergreen species tend

to inhabit more xeric sites compared to the deciduous species (Garten and Taylor 1992). However in this study, deciduous and evergreen species coexisted on all three sites, and in each case deciduous species maintained greater discrimination rates. This indicates that deciduous species maintain higher  $c_i/c_a$  than evergreen species within the same boreal forest site.

Interestingly, life form (i.e., tree, shrub, forb) showed no consistent pattern of variation in  $\delta^{13}\text{C}$  or  $\Delta$  values after accounting for differences in plant stature and leaf longevity. In fact, the difference between evergreen and deciduous species within a life-form group was the greatest for forbs, intermediate for trees, and the least for shrubs. Forb species have been noted to be highly variable. Körner et al. (1986) found that plants within the forb life form varied more along an altitudinal gradient than did plants in either tree or shrub life-form groups. The reason that evergreen and deciduous shrubs are more similar than evergreen and deciduous trees are may be related to canopy coupling and the sheltered environment within the canopy. Evergreen trees are generally better coupled to ambient atmospheric conditions than are deciduous trees, which could create differences in discrimination values (McNaughton and Jarvis 1991). However, because shrubs occur lower in the canopy, differences between their environments would probably be less than for trees.

Carbon isotope discrimination also depended on ecosystem type. Plants in the deciduous *Populus tremuloides* ecosystem had the highest  $\Delta$  values, whereas plants in the dry *Pinus banksiana* ecosystem had the lowest  $\Delta$  values. Even for a single species growing in all three ecosystems,  $\Delta$  was always greater in plants in the *Populus tremuloides* ecosystem than in the *Pinus banksiana* ecosystem (Table 1). These differences between ecosystems are probably driven by nutrient and water availability. Nitrogen concentration in *Populus tremuloides* leaves was greater than in *Pinus banksiana* leaves (2% vs. 1% respectively, H. Margolis and M. Ryan, unpublished work). In addition, the *Pinus banksiana* ecosystems were located on sandy substrates which had limited water holding capacities compared to the other ecosystems (Stangel et al. 1995). Both water and nutrient availability have been noted to affect intrinsic water-use efficiency (Field et al. 1983) and thus  $\Delta$ . Within a species, Garten and Taylor (1992) found that trees growing in riparian zones had lower  $\delta^{13}\text{C}$  values than trees growing along ridges; presumably this was caused by differences in water availability. Environmental differences among sites probably influenced the average discrimination values observed for the different boreal forest ecosystems.

The patterns in  $\Delta$  in relation to plant height, leaf longevity, and ecosystem type were both spatially and temporally stable. These patterns were similar, independent of whether the ecosystems were located near the northern or southern boundaries of the boreal forest. Brooks et al. (1997) found that tree gas exchange rates were greater in the SSA than the NSA, but trees at both sites had similar carbon gain to water loss ratios, as measured by car-

bon isotope ratios. This study demonstrated that this spatial stability is more general, covering most members of the plant community and not just the dominant trees. In addition, carbon isotope data collected along a transect from the southern to the northern site demonstrated that this similarity is not just between the northern and southern study areas, but also includes the forests between the boundaries (Fig. 5).

The patterns were also consistent over time. We measured  $\delta^{13}\text{C}$  and  $\Delta$  values for different life forms within the evergreen ecosystems over two years with different environmental conditions and found the patterns to be robust. Garten and Taylor (1992) found that  $\delta^{13}\text{C}$  values for trees growing in mesic sites were similar in years that ranged between 500 mm and 1000 mm in precipitation, but were consistently lower than those of trees growing in the xeric sites. Stewart et al. (1995) also found that  $\delta^{13}\text{C}$  was strongly correlated with the long-term average rainfall of a site. Thus, year-to-year fluctuations in water availability may be less important for carbon isotope discrimination than long-term averages. Although Garten and Taylor (1992) did find differences in  $\delta^{13}\text{C}$  between wet and dry years at the xeric site, carbon isotope discrimination did not differ between our northern and southern sites despite a difference in precipitation of 125 mm in 1994. It is possible that for years with greater environmental fluctuations carbon isotope discrimination patterns could change, particularly at the drier sites. However, normal fluctuations in environmental conditions did not alter the way in which these boreal species balance water loss and carbon gain.

Within the last few years, the effects of vegetation on global processes have been incorporated into GCM models (Sellers et al. 1996). To scale plant responses up to higher levels of organization, the concept of functional groups of plants has been proposed (Bazzaz 1993; Chapin 1993; Smith et al. 1993; Körner 1994a; Box 1995). Box (1995) pointed out three contrasting approaches for grouping plants into functional types: an ecological approach based on structural characteristics, a physiological approach based on plant internal functions, and a geophysical approach based on plant interactions with the atmosphere. The ecological approach of using life forms as potential functional groups has gained wide appeal since life forms are easily recognized, and have been characterized for most of the world's biomes (Chapin 1993; Dawson and Chapin 1993; Box 1995). Chapin (1993) argues that life forms are a logical link between physiology and ecosystem or global processes because species within a life form share similar physiological traits, and these traits can have important ecosystem consequences. We provide evidence that species within a life form do indeed have similar physiological traits, and can be used as functional groups for scaling and integrating the ways in which plants balance water and carbon fluxes within boreal communities. Carbon isotope discrimination integrates over both the physiological and geophysical levels (Farquhar et al. 1989) In addition, our results indicate that  $\Delta$  also includes information at the eco-

logical level:  $\Delta$  differences among life forms were based on structural differences (plant height and leaf longevity) and were stable both temporally and spatially within the boreal forest biome. Therefore, life forms integrate aspects of all three approaches to functional grouping of plants. Furthermore, we hypothesize that life forms can potentially be used in other biomes as well. The model of Lloyd and Farquhar (1994) predicted that deciduous and evergreen biomes would differ in terms of carbon isotope discrimination. Smedley et al. (1991) found that life forms within more arid grassland communities also varied in carbon isotope discrimination. Thus, the use of life forms for classifying physiological characteristics may be more general, and not restricted to desert and boreal forest communities. These data strengthen the argument that life-form groupings can be used to integrate plant responses at the physiological, ecological, and geophysical levels, and that this integration can be used over large areas.

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