

Photosynthesis and carbon isotope discrimination in boreal forest ecosystems: A comparison of functional characteristics in plants from three mature forest types

Lawrence B. Flanagan

Department of Biology, Carleton University, Ottawa, Ontario, Canada

J. Renee Brooks¹ and James R. Ehleringer

Department of Biology, Stable Isotope Ratio Facility for Environmental Research, University of Utah
Salt Lake City

Abstract. In this paper we compare measurements of photosynthesis and carbon isotope discrimination characteristics among plants from three mature boreal forest types (Black spruce, Jack pine, and aspen) in order to help explain variation in ecosystem-level gas exchange processes. Measurements were made at the southern study area (SSA) and northern study area (NSA) of the boreal forest in central Canada as part of the Boreal Ecosystem-Atmosphere Study (BOREAS). In both the NSA and the SSA there were significant differences in photosynthesis among the major tree species, with aspen having the highest CO₂ assimilation rates and spruce the lowest. Within a species, photosynthetic rates in the SSA were approximately twice those measured in the NSA, and this was correlated with similar variations in stomatal conductance. Calculations of the ratio of leaf intercellular to ambient CO₂ concentration (c_i/c_a) from leaf carbon isotope discrimination (Δ) values indicated a relatively low degree of stomatal limitation of photosynthesis, despite the low absolute values of stomatal conductance in these boreal tree species. Within each ecosystem, leaf Δ values were strongly correlated with life-form groups (trees, shrubs, forbs, and mosses), and these differences are maintained between years. Although we observed significant variation in the ¹³C content of tree rings at the old Jack pine site in the NSA during the past decade (indicating interannual variation in the degree of stomatal limitation), changes in summer precipitation and temperature accounted for only 44% of the isotopic variance. We scaled leaf-level processes to the ecosystem level through analyses of well-mixed canopy air. On average, all three forest types had similar ecosystem-level Δ values (average value \pm standard deviation, 19.1‰ \pm 0.5‰), calculated from measurements of change in the concentration and carbon isotope ratio of atmospheric CO₂ during a diurnal cycle within a forest canopy. However, there were seasonal changes in ecosystem discrimination for aspen forests, while the evergreen conifer forests exhibited relatively constant discrimination values throughout the active growing season.

1. Introduction

The terrestrial biosphere plays a major role in affecting global aspects of climate. Anthropogenic changes in the composition of our atmosphere have the potential to alter physiological responses of terrestrial vegetation with subsequent feedback effects on our global climate system [Sellers *et al.*, 1996]. In order to analyze ecosystem function and vegetation-atmosphere interactions in the context of predicting response to global change, it is necessary to have models of ecosystem function based on a mechanistic understanding of the underlying processes of exchange with the atmosphere [Jarvis, 1995]. However, in making approaches to upscaling, it is usually not

possible to integrate all the component processes and species into ecosystem models because of the consequent complexity. Rather, it is necessary to focus on important synthetic properties that are understood in a precise manner at one scale, but which can also be extended to larger spatial and temporal scales without loss of information [Field and Ehleringer, 1993].

One approach to dealing with the diversity apparent in nature is to classify vegetation into categories based on their functional properties [Chapin, 1993; Dawson and Chapin, 1993; Smith *et al.*, 1993; Körner, 1994; Jarvis, 1995]. For example, characteristics that describe energy balance properties, water-use efficiency, and aerodynamic coupling between leaves and the atmosphere can be used to classify world vegetation into categories that behave in similar ways during interactions with the atmosphere [Jarvis, 1995]. Similar interactions with the atmosphere may occur in two examples of a particular functional type of vegetation, despite wide differences in taxonomic affinities of their component species.

There are a number of possible functional characteristics that can be used to describe and predict vegetation-atmosphere

¹Now at Department of Biology, University of South Florida, Tampa.

interactions. Obviously, the photosynthetic gas exchange characteristics, net CO₂ assimilation, and stomatal conductance rates of the vegetation are important. However, gas exchange measurements are often taken only during short periods of time and therefore are of limited utility in obtaining information about the longer-term functioning of plants and ecosystems. We suggest that the measurement and analysis of carbon isotope ratios of leaf, tree ring, and atmospheric CO₂ samples can provide synthetic information that integrates important plant functional characteristics spatially and temporally. For example, measurement of the carbon isotope ratio of leaf tissue provides an assimilation-weighted average of the ratio of intercellular (c_i) to ambient CO₂ concentration (c_a) [Farquhar *et al.*, 1982, 1989]. This ratio (c_i/c_a) is important because it is primarily a function of photosynthetic capacity and stomatal conductance. Photosynthetic capacity refers to the physiological and biochemical characteristics of a leaf that determine its ability to fix carbon dioxide. For example, leaves with different photosynthetic capacity have different maximum CO₂ assimilation rates observed under saturating light intensity and moderate temperature and humidity conditions. Since the leaf carbon isotope ratio provides information about photosynthetic gas exchange processes integrated over the whole life of the leaf, it is particularly useful for examining interactions among a variety of physiological and environmental factors affecting CO₂ assimilation. There are a number of important leaf physiological characteristics such as water-use efficiency (ratio of net CO₂ assimilation and transpiration) [Farquhar *et al.*, 1989], stomatal limitation of photosynthesis [Farquhar and Sharkey, 1982; Jones, 1992], optimal stomatal behavior [Cowan and Farquhar, 1977], and leaf nitrogen-use efficiency (ratio of net CO₂ assimilation and leaf nitrogen content) [Field *et al.*, 1983] that are all directly related to the value of leaf intercellular CO₂ concentration. In addition, several recent studies have documented how variations in environmental conditions cause changes in the ratio of photosynthetic capacity to stomatal conductance and associated changes in leaf $\delta^{13}\text{C}$ values [Farquhar *et al.*, 1989; Ehleringer *et al.*, 1993]. Leaf carbon isotope ratios are particularly useful therefore for examining subtle differences among species or environmental conditions that are difficult to separate using standard gas exchange techniques. The analysis of tree-ring carbon isotope ratios increases the period of temporal integration and allows the study of historical changes in the ratio of photosynthetic capacity to stomatal conductance associated with annual climatic variation. In addition, it is possible to estimate carbon isotope discrimination during photosynthetic gas exchange by a whole forest system, from diurnal changes in CO₂ concentration and $\delta^{13}\text{C}$ values of atmospheric CO₂ within forest canopies [Keeling, 1958, 1961; Lloyd and Farquhar, 1994].

As part of our involvement in the Boreal Ecosystem-Atmosphere Study (BOREAS), one major objective of our work was to provide measurements of physiological characteristics that can be used to help explain variation in ecosystem-level gas exchange processes. We have focused much effort on the measurement and analysis of carbon isotope ratios of leaf, tree-ring, and atmospheric CO₂ samples. In this paper we provide a general overview of our results in order to illustrate how stable isotope techniques can be used to scale up physiological information. As such, our measurements help to improve our understanding of the interactions between the atmosphere and the boreal forest, a major goal of the BOREAS project [Sellers *et al.*, 1995].

2. Methods

2.1. Study Sites

Two study areas were located at the northern and southern limits of the boreal forest in central Canada (see Sellers *et al.* [1995] and other papers in this issue for details on the study sites). The southern study area (SSA) was located 40 km north of Prince Albert, Saskatchewan, and the northern study area (NSA) extended from the town of Thompson, Manitoba. We conducted our research in both SSA and NSA in mature forests dominated by each of the following species: *Picea mariana* (spruce), *Pinus banksiana* (pine), and *Populus tremuloides* (aspen). Measurements were collected during three intensive field campaigns (IFC) during the 1994 growing season (May through September).

2.2. Photosynthetic Gas Exchange

Foliage gas exchange was measured with a portable photosynthesis system (LI-6200, Li-Cor Inc., Lincoln, Nebraska) with a 250 mL leaf chamber. All measurements were made under ambient conditions on upper canopy foliage. For the conifer sites, gas exchange was measured on mature 1-year-old foliage (foliage produced in 1993). For the aspen sites, gas exchange was measured on fully expanded leaves (foliage produced in 1994). A_{max} (photosynthesis at light saturation) and g_{max} (conductance at light saturation) values were calculated by averaging photosynthesis measurements when the photon flux density of photosynthetically active radiation (PAR; 400–700 nm wavelengths) was greater than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The A_{max} values were used as an indication of photosynthetic capacity of the leaves of the different boreal tree species. Leaf area for conifers was measured using the volume displacement method, and gas exchange data are presented using half the total surface area (BOREAS Experimental Plan, J. Norman, personal communication, 1996). Projected leaf area was used for aspen.

2.3. Plant Collection and Isotopic Analysis

Mature aspen leaves and current-year conifer foliage samples were collected from the dominant trees at all sites during September 1994. In addition to the major tree species, leaf samples were collected from an additional 10–15 abundant species at each site. From each of five individual plants, four to five mature leaves were collected from the top of the plant and bulked into a single sample. Foliage was dried at 65°C and ground to a fine powder with a tissue grinder or a mortar and pestle.

An increment borer was used to collect samples of tree growth rings at the pine site in the NSA during August 1993. Holocellulose was purified from the wood samples by a method described by Leavitt and Danzer [1993].

The leaf and tree ring organic tissue samples were prepared for measurements of carbon isotopic composition by combustion. A 1–2 mg subsample of ground tissue was sealed in a tin capsule and loaded into an elemental analyzer for combustion (Carla Erba). The carbon dioxide generated from the combustion was purified cryogenically and passed directly to the inlet of a gas isotope ratio mass spectrometer (Delta S, Finnigan Mat, San Jose, California) at the University of Utah.

Isotope ratios in delta notation are calculated as

$$\delta = \left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}} - 1 \right) \quad (1)$$

where R is the molar ratio of heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$), the international standard for atmospheric CO_2 samples and leaf organic samples is CO_2 from Pee Dee Belemnite (PDB) limestone [Ehleringer and Osmond, 1989]. The δ values are conveniently presented in parts per thousand (‰).

The leaf carbon isotope values were used to calculate the ratio of leaf intercellular (c_i) to ambient CO_2 concentration (c_a). These calculations were done with two models, a simple model that assumes no change in CO_2 concentration from the substomatal cavity to the chloroplast, and a more detailed model that includes mesophyll resistance and assumes that CO_2 concentration in the chloroplast is lower than that in the intercellular air spaces [Farquhar et al., 1989; Lloyd and Farquhar, 1994]. For the c_i/c_a calculations, leaf $\delta^{13}\text{C}$ values were first converted to carbon isotope discrimination values (Δ):

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \quad (2)$$

where δ_a is the isotope ratio of source atmospheric CO_2 (−7.5‰, based on our measurements presented elsewhere [Flanagan et al., 1996]) and δ_p is the isotope ratio of plant tissue. The c_i/c_a values were then calculated using the equations shown below [Farquhar et al., 1989; Lloyd and Farquhar, 1994]:

$$\Delta = a + (b - a) \frac{c_i}{c_a} \quad (3)$$

$$\Delta = a \left(1 - \frac{c_i}{c_a} + 0.025 \right) + 0.075(e_s + a_i) + b \left(\frac{c_i}{c_a} - 0.1 \right) - \frac{f\Gamma^*}{c_a} \quad (4)$$

where a is fractionation against $^{13}\text{CO}_2$ during diffusion in air (4.4‰), b is fractionation against $^{13}\text{CO}_2$ during carboxylation (27.5‰), e_s is equilibrium fractionation as CO_2 enters solution (1.1‰), a_i is fractionation against $^{13}\text{CO}_2$ during diffusion in water (0.7‰), f is fractionation associated with photorespiration (8‰), Γ^* is the CO_2 photocompensation point (taken

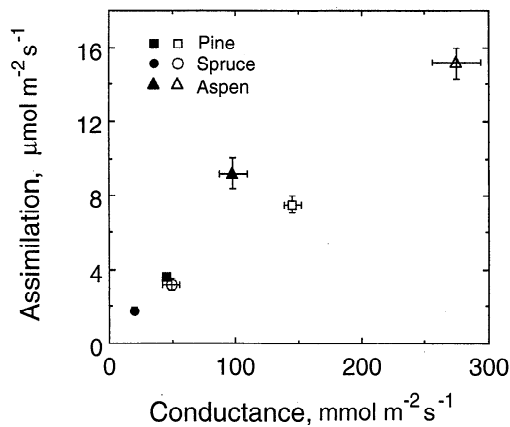


Figure 1. Mean values for maximal leaf CO_2 assimilation (A_{max}) and stomatal conductance (g_{max}) rates for the major tree species in the southern (open symbols) and northern (solid symbols) study sites. Measurements were made on foliage exposed to full sun (photon flux density for photosynthetically active radiation $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) at the top of the canopy in July 1994.

Table 1. Comparison of Leaf Carbon Isotope Ratio ($\delta^{13}\text{C}$) Among the Major Tree Species in the Northern and Southern Study Areas During 1994

	Spruce	Pine	Aspen
North sites	-26.6 ± 0.3 ab	-25.6 ± 0.2 a	-28.4 ± 0.4 c
South sites	-26.5 ± 0.3 ab	-26.6 ± 0.2 ab	-27.8 ± 0.2 bc

Values are in units of per mil (‰). Leaf samples were collected in September. Values are the mean \pm SE, $n = 5$, except for south aspen site, where $n = 4$. Values with different letters are significantly different based on Tukey multiple comparison tests after an analysis of variance.

as $40 \mu\text{mol mol}^{-1}$). In the calculations for (4) it is assumed that the reduction in CO_2 concentration from the substomatal cavity to the chloroplast is equal to $0.1c_a$ and that 25% of this reduction occurs from the substomatal cavity to the cell wall surface, and 75% occurs from the cell wall to the sites of carboxylation [Lloyd and Farquhar, 1994]. This drawdown in CO_2 concentration ($0.1c_a$) is conservative based on measurements made on a number of leaves at saturating light intensity that indicate the drawdown can be $0.16c_a$ – $0.20c_a$ when assimilation is maximal [von Caemmerer and Evans, 1991; Lloyd et al., 1992; Loreto et al., 1992].

3. Results and Discussion

3.1. Comparison of Photosynthetic Capacity and Stomatal Conductance

There were significant differences in photosynthetic capacity (A_{max}) among the major tree species, with aspen having the highest net CO_2 assimilation rates and spruce the lowest (Figure 1). This pattern of difference among species was consistent in both the NSA and the SSA. In addition, photosynthetic rates in the SSA were approximately twice those measured in the NSA. Variation in maximal stomatal conductance (g_{max}) was correlated to that observed for photosynthetic capacity, except that maximal stomatal conductance in the NSA was approximately 3 times lower than values measured in the SSA (Figure 1). The lower conductance resulted in higher stomatal limitation of photosynthesis and lower c_i/c_a values for tree species in the NSA (Tables 1 and 2). Further details of our photosyn-

Table 2. Comparison of the Ratio of Intercellular CO_2 to Ambient CO_2 Concentration (c_i/c_a) in the Major Tree Species From Short-Term Gas Exchange Measurements Made During ICF-2 (Mean \pm SE) and Calculations From Leaf Carbon Isotope Ratios (Data Shown in Table 1) Using the Simple Model (3) and a More Detailed Model That Includes Mesophyll Resistance (4)

	Spruce	Pine	Aspen
Gas exchange			
North sites	0.54 ± 0.018	0.58 ± 0.014	0.51 ± 0.017
South sites	0.65 ± 0.013	0.68 ± 0.011	0.63 ± 0.017
Simple model $\delta^{13}\text{C}$			
North sites	0.639	0.594	0.715
South sites	0.633	0.638	0.687
Mesophyll resistance model $\delta^{13}\text{C}$			
North sites	0.820	0.774	0.900
South sites	0.815	0.819	0.871

thetic gas exchange measurements are presented elsewhere [Brooks *et al.*, 1997a].

Our measurements of leaf photosynthetic characteristics were consistent with several previous reports that demonstrated low CO₂ assimilation and stomatal conductance rates in boreal coniferous species (see additional papers in this issue). The conifer species have low leaf nitrogen contents, while the broad-leaf aspen trees have significantly higher leaf nitrogen contents, consistent with the gas exchange measurements. However, differences in foliar nitrogen content were not sufficient to explain the observed reduction in maximal CO₂ assimilation and stomatal conductance rates in the NSA (H. Margolis and M. Ryan, unpublished data, 1996). Lower gas exchange capacity in the NSA was likely related to a variety of differences in climate between the NSA and SSA. In addition, during 1994 the northern sites were drier than the long-term average climatic conditions (200 mm in 1994 compared to 270 mm (1967–1994), mean precipitation during May–August for Thompson, Manitoba), while the southern sites received higher than average precipitation (255 mm in 1994 compared to 220 mm (1889–1994), during May–August for Prince Albert, Saskatchewan). Our observed differences in stomatal conductance, c_i/c_a values, and the implied differences in the degree of stomatal limitation of photosynthesis between trees in the NSA and SSA, were consistent with these patterns in precipitation.

3.2. Leaf Carbon Isotope Ratios: Integrated Values of c_i/c_a

Our short-term gas exchange measurements were useful for broad comparisons among species and sites but are of limited utility in obtaining information about the longer-term functioning of plants in these ecosystems. However, measurement of the carbon isotope ratio of leaf tissue provides an assimilation-weighted average of c_i/c_a [Farquhar *et al.*, 1982, 1989]. Aspen leaves collected at the end of the growth season (IFC 3) had significantly lower $\delta^{13}\text{C}$ values than the two conifer species, although all species had similar values (Table 1). Only pine showed any substantial difference between the NSA and SSA sites, with leaf $\delta^{13}\text{C}$ values 1‰ higher at the northern site. Calculations of c_i/c_a from leaf carbon isotope ratios indicated higher values than were observed during our short-term gas exchange measurements (Table 2). This was particularly true for calculations of c_i/c_a that included estimates of mesophyll resistance and a reduction in CO₂ concentration from the intercellular air spaces to the chloroplast.

In general, boreal tree species have low photosynthetic capacity because of the nutritionally poor soils associated with a short growing season and cold soil temperatures. Because of the strong correlation between photosynthetic capacity (A_{max}) and maximal stomatal conductance (g_{max}), the low photosynthetic capacity of boreal species results in low absolute rates of stomatal conductance. However, it is important to distinguish between low absolute values of stomatal conductance and strong stomatal limitation of photosynthesis [Farquhar and Sharkey, 1982]. The high values of c_i/c_a calculated from carbon isotope ratios indicated a relatively low degree of stomatal limitation of photosynthesis, despite the low absolute values of stomatal conductance in the boreal tree species. Gas exchange studies by other BOREAS investigators showed strong stomatal closure in response to increase in vapor pressure deficit in all tree species [Dang *et al.*, 1997]. Our leaf $\delta^{13}\text{C}$ data suggested that carbon assimilated during periods with low c_i/c_a contributed only a small fraction to total leaf carbon gain. Consistent with these measurements, Dang *et al.* [1997] have calculated

that the PAR-weighted average for the leaf-air vapor pressure difference (VPD) was 1.0 kPa during the 1994 growing season in the NSA, despite the fact that maximum VPD could reach 3.8 kPa on some days and the daily average VPD was greater than 1.0 kPa for 50% of the growing season. The seasonal average c_i/c_a values at 1.0 kPa, calculated from gas exchange measurements on pine, spruce, and aspen, were 0.77, 0.71, and 0.81, respectively [Dang *et al.*, 1997]. These seasonal average values were consistent with our calculations of c_i/c_a using the $\delta^{13}\text{C}$ data and the mesophyll resistance model (Table 2).

Carbon isotope discrimination patterns were similar at sites near both the northern and southern boundaries of the boreal forest in Canada (Table 1). In addition, tree leaf $\delta^{13}\text{C}$ values did not vary significantly along a transect between the northern and southern boundaries of the boreal forest, a transect which spanned over 600 km [Brooks *et al.*, 1997b]. The relatively constant leaf carbon isotope ratios were found in four different age classes of foliage, indicating that this consistency was robust over time.

Comparison of our leaf carbon isotope ratios with other published reports (Table 3), illustrates that conifer trees often have much higher $\delta^{13}\text{C}$ values than we have observed for the boreal conifer species. The leaf $\delta^{13}\text{C}$ values we have measured for the boreal tree species are similar to a variety of plants (including broad-leaf species from temperate areas), indicating that in general, stomatal limitation of photosynthesis is low for these boreal tree species, despite the low absolute leaf gas exchange rates that have been measured.

3.3. Tree Ring Carbon Isotope Ratios: Historical Variation in c_i/c_a

Measurements of the carbon isotope ratio of cellulose from individual tree growth rings provides information about changes in c_i/c_a and the ratio of photosynthetic capacity to stomatal conductance associated with annual climatic variation. We have observed significant variation in the ^{13}C content of tree rings at the old Jack pine site in the NSA during the past decade (Figure 2). Wet years, such as 1986, resulted in the most negative $\delta^{13}\text{C}$ values, indicating a reduced stomatal limitation of photosynthesis. In contrast, dry years, such as 1981, resulted in higher $\delta^{13}\text{C}$ values indicative of lower c_i/c_a and higher stomatal limitation of photosynthesis. There was a clear trend toward progressively lower $\delta^{13}\text{C}$ values from 1981 through 1986, followed by a progressive increase in growth ring $\delta^{13}\text{C}$ values from 1986 through 1990. In general, these trends were correlated with summertime growth conditions, with summer precipitation and temperature accounting for 44% of the interannual variation in tree ring carbon isotope ratios (Figure 2). Interannual variations in carbon isotope ratio appear to be buffered, such that significant differences arise only during those years that are unusually cold/hot or wet/dry. While the temporal variation in growth ring $\delta^{13}\text{C}$ values illustrates the potential influence of climatic variation on leaf and ecosystem photosynthetic gas exchange processes in boreal environments, current analyses explain just under one half of the total observed variance in isotopic composition. A more detailed analysis of growth ring $\delta^{13}\text{C}$ values including information on pine trees at other BOREAS sites is currently under way.

It is important to note that quantitative, absolute comparisons between leaf $\delta^{13}\text{C}$ values and the $\delta^{13}\text{C}$ values measured on cellulose extracted from tree growth rings should not be made. Such comparisons between whole leaf tissue and cellulose are complicated by differences in chemical composition and isoto-

Table 3. Comparison of Sun Leaf Carbon Isotope Ratios From Other Selected Studies of Boreal, Temperate, Arctic, and Tropical Plant Species

Species	$\delta^{13}\text{C}$, ‰	Location	Reference
Coniferous trees			
<i>Pinus edulis</i>	-21.5 ± 0.8	Utah	Flanagan et al. [1992]
<i>Juniperous osteosperma</i>	-22.9 ± 0.9	Utah	Flanagan et al. [1992]
<i>Pinus edulis</i>	-24.2	New Mexico	Lajtha and Barnes [1991]
<i>Juniperous osteosperma</i>	-24.3 ± 0.9	Utah	Ehleringer and Cerling [1995]
<i>Juniperous monosperma</i>	-24.5	New Mexico	Lajtha and Barnes [1991]
<i>Pinus ponderosa</i>	-25.5 ± 0.6	Utah	Ehleringer and Cerling [1995]
<i>Picea abies</i>	-25.9 ± 0.1	Sweden	Hogberg et al. [1993]
<i>Picea mariana</i>	-26.3 ± 0.7	Ontario	Flanagan and Johnsen [1995]
<i>Pinus massoniana</i>	-26.4 ± 0.6	Subtropical China	Ehleringer et al. [1986]
<i>Pinus resinosa</i>	-26.9 ± 0.7	Ontario	Flanagan and Varney [1995]
<i>Pinus taeda</i> , <i>P. echinata</i>	-27	Tennessee	Garten and Taylor [1992]
<i>Abies amabilis</i>	-27.6 ± 0.8	Washington	Buchmann et al. [1997]
<i>Pinus contorta</i>	-27.7 ± 0.4	Utah	Buchmann et al. [1997]
<i>Lagarostrobos franklinii</i>	-27 to -28	Tasmania	Francey et al. [1985]
<i>Picea abies</i>	-27.3 to -29.1	Bavaria	Gebauer and Schulze [1991]
<i>Picea mariana</i>	-28.6 to -30.4	Saskatchewan	Rask and Schoenau [1993]
Broad-leaf deciduous trees			
<i>Fagus sylvatica</i>	-24 to -26	Germany	Schleser [1990]
<i>Populus tremuloides</i>	-25.5 ± 0.3	Utah	Buchmann et al. [1997]
<i>Acer rubrum</i>	-26.3	Massachusetts	J. R. Ehleringer (unpublished data, 1996)
<i>Betula alligheniensis</i>	-27.05	Massachusetts	J. R. Ehleringer (unpublished data, 1996)
<i>Acer negundo</i>	-27.1 ± 1.0	Utah	Buchmann et al. [1997]
<i>Quercus rubra</i>	-27.15	Massachusetts	J. R. Ehleringer (unpublished data, 1996)
<i>Populus tremuloides</i>	-29.0	Utah	Flanagan et al. [1997a]
<i>Quercus sp.</i>	-29	Tennessee	Garten and Taylor [1992]
<i>Acer rubrum</i>	-29	Tennessee	Garten and Taylor [1992]
Arctic evergreen shrubs			
<i>Cassiope tetragona</i>	-27.5 to -28.1	Sweden	Michelsen et al. [1996]
<i>Dryas octopetala</i>	-29 to -30	Norway	Welker et al. [1993]

pic fractionation that occur during synthesis of different chemical components within a plant [Leavitt and Long, 1982; Berner et al., 1987]. In experiments with juniper trees, cellulose from growth rings was consistently more enriched in ^{13}C by 2–4‰ than the leaves produced by the tree during the same growth season [Leavitt and Long, 1982].

3.4. Variation in Carbon Isotope Ratios Among Plant Lifeforms

Grouping plants into similar functional categories has been suggested by several authors as a method to simplify scaling physiological processes from individual plants to larger areas [Chapin, 1993; Dawson and Chapin, 1993; Smith et al., 1993; Körner, 1994]. Chapin [1993] has argued that using life-forms as a sorting criteria would be useful because life-forms are easily recognized and different species within a life-form group should have similar physiological characteristics. In addition, 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. 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 [Brooks et al., 1997b]. We used carbon isotope discrimination values (Δ) to compare life-form groups because Δ values remove the influence of source CO_2 isotopic composition, a parameter that can differ among plants located at different heights within a forest [Berry et al., 1997; Brooks et al., 1997a]. Carbon isotope discrimination values illustrate the influence of changes in plant physiological characteristics on the carbon isotopic composition of leaf tissue, independent of confounding changes in the isotope ratio of source CO_2 .

Life-form groups explained a significant fraction of the variation in leaf carbon isotope discrimination data from 29 species sampled in six different forests; seven life-form categories explained 42% of the variation in Δ [Brooks et al., 1997b]. Species identity alone was only able to explain 64% of the variation. The life-forms were ranked in the following order based on their Δ values: evergreen trees < deciduous trees = evergreen and deciduous shrubs = evergreen forbs < deciduous forbs = mosses (Figure 3). This ranking of the life-forms differed slightly between deciduous (aspen) and evergreen (spruce and pine) ecosystems. Correlations between Δ and life-form were related to differences in plant stature and leaf longevity. Shorter plants had lower Δ values than taller plants, likely resulting from reduced light intensity at lower levels in the forest, and a low ratio of photosynthesis to stomatal conductance previously observed in understory plants [Percy and Pfitsch, 1991; Berry et al., 1997]. After height differences were accounted for, deciduous leaves had higher discrimination values than evergreen leaves, indicating that deciduous leaves maintained higher c_i/c_a values than did evergreen leaves in a similar environment within these boreal ecosystems (Figure 3). We found the same pattern of variation in carbon isotope discrimination values 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. We conclude that life-forms are robust indicators of functional groups for photosynthetic gas exchange characteristics in boreal ecosystems.

In addition to analyzing relationships among life-form groups, our measurements of leaf carbon isotope discrimina-

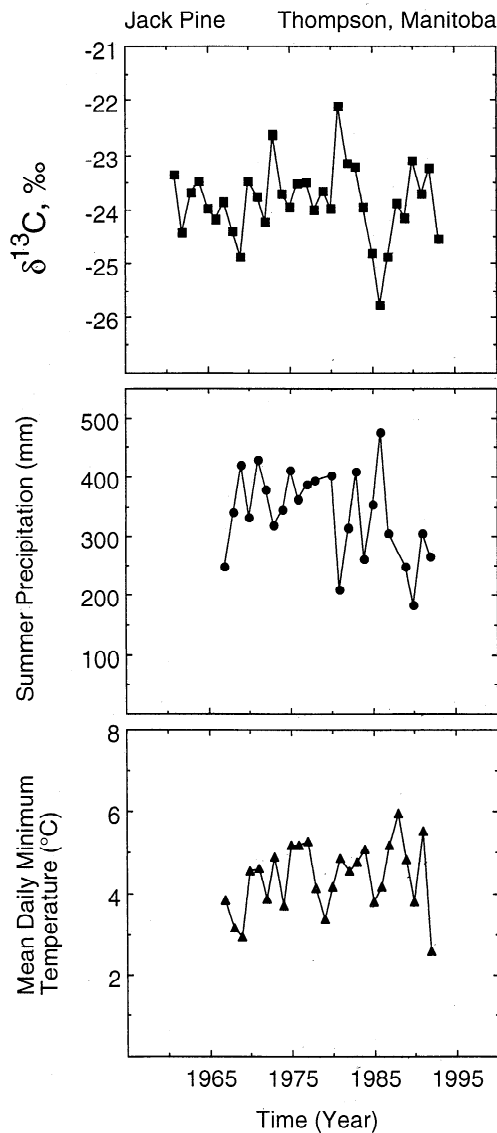


Figure 2. Changes in the carbon isotope ratio of cellulose extracted from tree growth rings from *Pinus banksiana* in the northern study area, and associated changes in summer precipitation (May–August) and mean daily minimum temperature at Thompson, Manitoba.

tion values on several species within different forest types can be used as an indicator of ecosystem characteristics. For example, plants in the pine ecosystem had, on average, lower discrimination values ($20.8‰ \pm 0.18$ SE) than plants in the spruce and aspen ecosystems ($22.4‰ \pm 0.22$ and $22.2‰ \pm 0.15$, respectively; $F = 19$, $P < 0.0001$). This was consistent with the more arid nature of the pine ecosystem and the generally lower evaporative fractions (ratio of latent heat flux to the sum of latent and sensible heat flux) measured in the pine ecosystems [Sellers *et al.*, 1995]. It is interesting that the discrimination value for the pine tree foliage alone (Table 1) was not as sensitive an indicator of the arid nature of the pine sites as the average discrimination value for several species at the site. This is likely related to the presence of relatively deep roots in the pine trees, which allows access to abundant groundwater supplies, as determined by stable isotope analysis of tree xylem water [Flanagan *et al.*, 1997b].

3.5. Whole Forest Carbon Isotope Discrimination

Analysis of net partitioning of CO_2 between ocean and terrestrial ecosystems using stable isotope techniques is dependent on knowledge of carbon isotope discrimination during photosynthetic gas exchange in terrestrial ecosystems, and the isotope ratio of CO_2 released from ecosystem carbon pools [Ciais *et al.*, 1995; Fung, 1995]. It is possible to estimate discrimination during photosynthetic gas exchange by the whole forest system, from diurnal changes in CO_2 concentration and $\delta^{13}\text{C}$ values of atmospheric CO_2 within forest canopies. This forest discrimination estimate was calculated by assuming that no isotope effect occurs during respiration by plants and soils [Lin and Ehleringer, 1997], so that the isotope ratio of CO_2 respired by the forest system (δ_r) at night represents an integrated measure of the isotopic composition of forest organic matter. Forest carbon isotope discrimination was then calculated as $\Delta_A = \delta_a - \delta_r$ [Lloyd and Farquhar, 1994]. Measurements of the concentration and stable isotope ratio of atmospheric CO_2 necessary for these calculations have been presented elsewhere [Flanagan *et al.*, 1996]. The spatial area integrated by the calculation depends on the footprint of the air sample mast (in our case, the air samples are affected primarily by sources approximately 140 m upwind of the mast during smooth surface conditions [Schuepp *et al.*, 1990]), while the temporal component integrated depends on the relative contribution that different aged carbon pools make to total system respiration (and to δ_r). If the majority of respired CO_2 comes from recently fixed carbon (within days), the calculated forest Δ_A could be expected to show seasonal changes associated with environmental influences on leaf-level gas exchange and isotopic discrimination.

Our data illustrate a seasonal change in discrimination in the aspen-dominated sites, with an increase in Δ_A occurring between the middle and the end of the growing season, possibly because of a reduction in photosynthetic capacity relative to stomatal conductance associated with leaf senescence (Figure 4). A decline in temperature and vapor pressure deficit experienced by leaves in the fall would also have contributed to a reduction in stomatal limitation of photosynthesis (and resulted in an increase in discrimination) in the aspen leaves during IFC-3. In contrast, the evergreen conifer canopies exhibited relatively constant discrimination values throughout the active growing season. The observed forest Δ_A values were

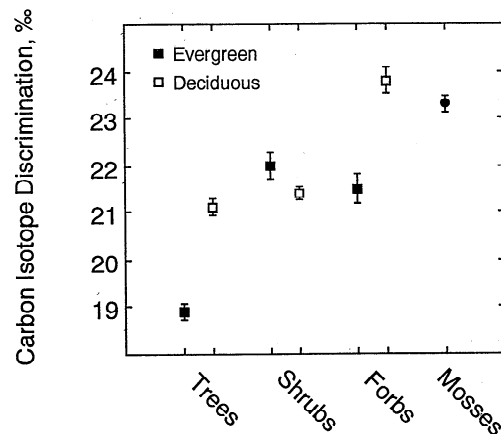


Figure 3. Comparison of mean values for carbon isotope discrimination (\pm SE) among life-form groups.

consistent with observations of the sun foliage $\delta^{13}\text{C}$ values of the dominant tree species (Table 1).

Our data illustrate that the three main types of mature forest in the boreal forest biome influence the carbon isotope ratio of atmospheric CO_2 in similar manners. Measurements of total system carbon isotope discrimination averaged $19.1\text{‰} \pm 0.5\text{‰}$, which is slightly higher than values calculated from δ_r measurements made by Lancaster [1990] in a lodgepole pine forest at Rock Lake, Alberta ($\delta_r = -25.3 \pm 0.4\text{‰}$, approximately $\Delta_A = 17.9\text{‰}$), and a large-scale modeling study estimate for boreal latitudes (approximately $\Delta_A = 17.5\text{‰}$ [Ciais et al., 1995]). Our total system isotopic discrimination values are also slightly higher than values predicted for boreal regions by the global model of Lloyd and Farquhar [1994] (northern black spruce forest, $\Delta_A = 16.3\text{‰}$; southern black spruce forest, $\Delta_A = 17.4\text{‰}$), although their estimates cover much larger areas of land than our measurements represent. Using an experimental approach similar to ours, Quay et al. [1989] and Lloyd et al. [1996] measured δ_r values slightly more negative (approximately -28‰ and -27.1‰ , respectively) for tropical forests in Amazonia, a difference that would be expected for comparison between tropical and boreal forests [Farquhar et al., 1989].

The ability to detect a seasonal change in aspen total forest ecosystem discrimination, which was correlated with expected environmental influences on leaf photosynthetic gas exchange, suggests that a large fraction of the respired CO_2 comes from recently produced carbohydrates in aboveground plant material and roots. In other forest systems, autotrophic respiration has been estimated to contribute 70% of the total respiratory flux, consistent with this suggestion [Edwards et al., 1989].

Our measurements of seasonal variation in aspen total forest carbon isotope discrimination (Figure 4) and annual variation in the $\delta^{13}\text{C}$ values of pine growth rings (Figure 2) support the cautionary note expressed by Lloyd and Farquhar [1994] for interpreting annual variations in the latitudinal gradient and rates of change in the isotope ratio of atmospheric CO_2 . Many previous studies attempting to partition net uptake of atmospheric CO_2 between the ocean and terrestrial biosphere have used a single, constant value for isotopic discrimination by land plants [e.g., Keeling et al., 1989; Francey et al., 1995]. Large environmental differences may occur within a season or between years in a given biome that strongly influence isotopic exchange processes between the terrestrial biosphere and the atmosphere. Global models attempting the use of stable isotopes in partitioning ocean and land uptake of CO_2 should incorporate realistic, dynamic models of biosphere physiological processes to deal with this temporal variation in isotopic discrimination [Ciais et al., 1995].

4. Conclusions

In this paper we compare measurements of photosynthesis and carbon isotope discrimination characteristics among plants from three mature boreal forest types (black spruce, Jack pine, and aspen) in order to help explain variation in ecosystem-level gas exchange processes. Measurements were made at the southern (SSA) and northern (NSA) ends of the boreal forest in central Canada as part of the Boreal Ecosystem-Atmosphere Study (BOREAS). In both the NSA and the SSA, there were significant differences in photosynthesis among the major tree species, with aspen having the highest CO_2 assimilation rates and spruce the lowest. Within a species, photosynthetic

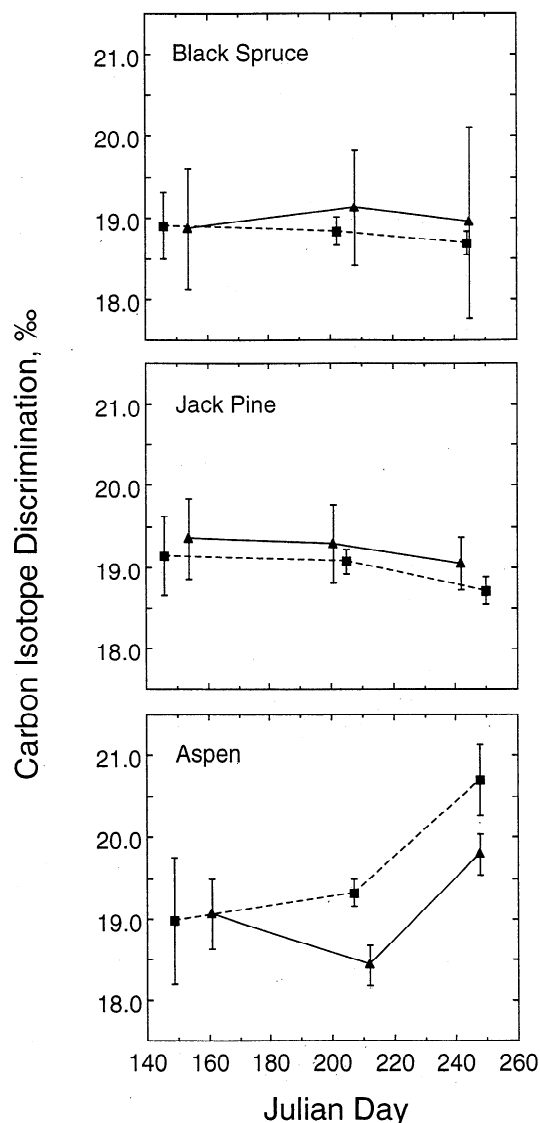


Figure 4. Seasonal variation in total ecosystem carbon isotopic discrimination. The square symbols and dashed lines represent measurements on forests in the southern study area. The triangle symbols and solid lines represent measurements on forests in the northern study area.

rates in the SSA were approximately twice those measured in the NSA, and this was correlated with similar variations in stomatal conductance. Calculations of the ratio of leaf intercellular to ambient CO_2 concentration (c_i/c_a) from leaf carbon isotope discrimination values indicated a relatively low degree of stomatal limitation of photosynthesis, despite the low absolute values of stomatal conductance in these boreal tree species. Within each ecosystem, leaf Δ values were strongly correlated with life-form groups (trees, shrubs, forbs, and mosses), and these differences are maintained between years. Although we observed significant variation in the ^{13}C content of tree rings at the old Jack pine site in the NSA during the past decade (indicating interannual variation in the degree of stomatal limitation), changes in summer precipitation and temperature accounted for only 44% of the isotopic variance. We scaled leaf-level processes to the ecosystem level through analyses of well-mixed canopy air. Differences observed at the individual species level, apparent with leaf-level sampling,

were melded into a single value that was largely determined by the major tree species at each respective forest. On average, all three forest types had similar ecosystem-level Δ values (average value (\pm SD), $19.1\text{‰} \pm 0.5\text{‰}$), calculated from measurements of change in the concentration and carbon isotope ratio of atmospheric CO_2 during a diurnal cycle within a forest canopy. However, there were seasonal changes in ecosystem discrimination for aspen forests, while the evergreen conifer forests exhibited relatively constant discrimination values throughout the active growing season. Ecosystem carbon isotope discrimination values scale to global carbon budget studies, and our results indicate that previous global modeling efforts may have underestimated discrimination in boreal forests by 1–2‰.

Acknowledgments. This work was supported by the Natural Sciences and Engineering Research Council of Canada through grants to L. B. F. and by grants to J. R. E. from NASA BOREAS. We thank Stephanie Berry, Nina Buchmann, Craig Cook, Dave Kubien, Kevin Rapp, Dan Skoda, Linda Sperry, Greg Varney, and Steve Veltman for help with the field work and preparation of isotope samples.

References

- Benner, R., M. L. Fogel, E. K. Sprague, and R. E. Hodson, Depletion of ^{13}C in lignin and its implications for stable carbon isotope studies, *Nature*, **329**, 708–710, 1987.
- Berry, S. C., G. T. Varney, and L. B. Flanagan, Leaf $\delta^{13}\text{C}$ in *Pinus resinosa* trees and understory plants: Variation associated with light and CO_2 gradients, *Oecologia*, **109**, 499–506, 1997.
- Brooks, J. R., L. B. Flanagan, G. T. Varney, and J. R. Ehleringer, Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO_2 within boreal forest canopies, *Tree Physiol.*, **17**, 1–12, 1997a.
- Brooks, J. R., L. B. Flanagan, N. Buchmann, and J. R. Ehleringer, Carbon isotope ratios of boreal forest life-forms: Functional grouping of plant physiological characteristics, *Oecologia*, in press, 1997b.
- Buchmann, N., J. R. Ehleringer, and W.-Y. Kao, Carbon dioxide concentrations within forest canopies—Variation with time, stand structure, and vegetation type, *Global Change Biol.*, **2**, 421–432, 1997.
- Chapin, F. S., Functional role of growth forms in ecosystem and global processes, in *Scaling Physiological Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 287–312, Academic, San Diego, Calif., 1993.
- Ciais, P., P. P. Tans, J. W. C. White, M. Troler, R. J. Francey, J. A. Berry, D. R. Randall, P. J. Sellers, J. G. Collatz, and D. S. Schimel, Partitioning of ocean and land uptake of CO_2 as inferred by $\delta^{13}\text{C}$ measurements from the NOAA Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network, *J. Geophys. Res.*, **100**, 5051–5070, 1995.
- Cowan, I. R., and G. D. Farquhar, Stomatal function in relation to leaf metabolism and environment, *Symp. Soc. Exp. Biol.*, **31**, 471–505, 1977.
- Dang, Q.-L., H. A. Margolis, M. R. Coyea, M. Sy, and G. J. Collatz, Regulation of branch-level gas exchange of boreal trees: Role of shoot water potential and vapor pressure difference, *Tree Physiol.*, **17**, in press, 1997.
- Dawson, T. E., and F. S. Chapin, Grouping plants by their form—Function characteristics as an avenue for simplification in scaling between leaves and landscapes, in *Scaling Physiological Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 313–319, Academic, San Diego, Calif., 1993.
- Edwards, N. T., D. W. Johnson, S. B. McLaughlin, and W. F. Harris, Carbon dynamics and productivity, in *Analysis of Biogeochemical Cycling Processes in Walker Branch Watershed*, edited by D. W. Johnson and R. I. Van Hook, pp. 20–95, Springer-Verlag, New York, 1989.
- Ehleringer, J. R., and T. E. Cerling, Atmospheric CO_2 and the ratio of intercellular to ambient CO_2 concentrations in plants, *Tree Physiol.*, **15**, 105–111, 1995.
- Ehleringer, J. R., and C. B. Osmond, Stable isotopes, in *Plant Physiological Ecology: Field Methods and Instrumentation*, edited by R. W. Pearcy et al., pp. 281–300, Chapman and Hall, New York, 1989.
- Ehleringer, J. R., C. B. Field, Z. Lin, and C. Kuo, Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline, *Oecologia*, **70**, 520–526, 1986.
- Ehleringer, J. R., A. E. Hall, and G. D. Farquhar, *Stable Isotopes and Plant Carbon-Water Relations*, Academic, San Diego, Calif., 1993.
- Farquhar, G. D., and T. D. Sharkey, Stomatal conductance and photosynthesis, *Annu. Rev. Plant Physiol.*, **33**, 317–345, 1982.
- Farquhar, G. D., M. H. O'Leary, and J. A. Berry, On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves, *Aust. J. Plant Physiol.*, **9**, 121–137, 1982.
- Farquhar, G. D., J. R. Ehleringer, and K. T. Hubick, Carbon isotope discrimination and photosynthesis, *Annu. Rev. Plant Physiol. Plant Mol. Biol.*, **40**, 503–537, 1989.
- Field, C. B., and J. R. Ehleringer, Introduction: Questions of scale, in *Scaling Physiological Processes: Leaf to Globe*, edited by J. R. Ehleringer and C. B. Field, pp. 1–4, Academic, San Diego, Calif., 1993.
- Field, C. B., J. Merino, and H. A. Mooney, Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens, *Oecologia*, **60**, 384–389, 1983.
- Flanagan, L. B., and K. H. Johnsen, Genetic variation in carbon isotope discrimination and its relationship to growth under field conditions in full-sib families of *Picea mariana*, *Can. J. For. Res.*, **25**, 39–47, 1995.
- Flanagan, L. B., and G. T. Varney, Influence of vegetation and soil CO_2 exchange on the concentration and stable oxygen isotope ratio of atmospheric CO_2 within a *Pinus resinosa* canopy, *Oecologia*, **101**, 37–44, 1995.
- Flanagan, L. B., J. R. Ehleringer, and J. D. Marshall, Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland, *Plant Cell Environ.*, **15**, 831–836, 1992.
- Flanagan, L. B., J. R. Brooks, G. T. Varney, S. C. Berry, and J. R. Ehleringer, Carbon isotope discrimination during photosynthesis and the isotope ratio of respired CO_2 in boreal forest ecosystems, *Global Biogeochem. Cycles*, **10**, 629–640, 1996.
- Flanagan, L. B., C. S. Cook, and J. R. Ehleringer, Unusually low carbon isotope ratios in plants from hanging gardens in southern Utah, *Oecologia*, in press, 1997a.
- Flanagan, L. B., J. R. Brooks, G. T. Varney, and J. R. Ehleringer, Discrimination against $\text{C}^{18}\text{O}^{16}\text{O}$ during photosynthesis and the oxygen isotope ratio of respired CO_2 in boreal forest ecosystems, *Global Biogeochem. Cycles*, **11**, 83–98, 1997b.
- Francey, R. J., R. M. Gifford, T. D. Sharkey, and B. Weir, Physiological influences on carbon isotope discrimination in huon pine (*Lagarostrobos franklinii*), *Oecologia*, **66**, 211–218, 1985.
- Francey, R. J., P. P. Tans, C. E. Allison, I. G. Enting, J. W. C. White, and M. Troler, Changes in oceanic and terrestrial carbon uptake since 1982, *Nature*, **373**, 326–330, 1995.
- Fung, I. Y., Perturbations to the biospheric carbon cycle: Uncertainties in the estimates, in *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?*, edited by G. M. Woodwell, and F. T. Mackenzie, pp. 367–374, Oxford Univ. Press, New York, 1995.
- Garten, C. T., and G. E. Taylor, Foliar $\delta^{13}\text{C}$ within a temperate deciduous forest: Spatial, temporal, and species sources of variation, *Oecologia*, **90**, 1–7, 1992.
- Gebauer, G., and E. D. Schulze, Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria, *Oecologia*, **87**, 198–207, 1991.
- Hogberg, P., C. Johansson, and J.-E. Hallgren, Studies of ^{13}C in the foliage reveal interactions between nutrients and water in forest fertilization experiments, *Plant Soil*, **152**, 207–214, 1993.
- Jarvis, P. G., Scaling processes and problems, *Plant Cell Environ.*, **18**, 1079–1089, 1995.
- Jones, H. G., *Plants and Microclimate*, Cambridge Univ. Press, New York, 1992.
- Keeling, C. D., The concentration and isotopic abundances of atmospheric carbon dioxide in rural areas, *Geochim. Cosmochim. Acta*, **13**, 322–334, 1958.
- Keeling, C. D., The concentration and isotopic abundances of carbon dioxide in rural and marine air, *Geochim. Cosmochim. Acta*, **24**, 277–298, 1961.

- Keeling, C. D., R. B. Bacastow, A. F. Carter, S. C. Piper, T. P. Whorf, M. Heimann, W. G. Mook, and H. Roeloffzen, A three-dimensional model of atmospheric CO₂ transport based on observed winds, 1, Analysis of observational data, in *Aspects of Climate Variability in the Pacific and the Western Americas*, *Geophys. Monogr. Ser.*, vol. 55, edited by D. H. Peterson, pp. 165–236, AGU, Washington, D. C., 1989.
- Körner, Ch, Scaling from species to vegetation: The usefulness of functional groups, in *Biodiversity and Ecosystem Function*, edited by E. D. Schulze and H. A. Mooney, pp. 117–140, Springer-Verlag, New York, 1994.
- Lajtha, K., and F. J. Barnes, Carbon gain and water use in pinyon pine–juniper woodlands in northern New Mexico: Field versus phytotron chamber measurements, *Tree Physiol.*, 9, 59–67, 1991.
- Lancaster, J., Carbon-13 fractionation in carbon dioxide emitting diurnally from soils and vegetation at ten sites on the North American continent, Ph.D. thesis, Univ. of Calif., San Diego, 1990.
- Leavitt, S. W., and S. R. Danzer, Method for batch processing small wood samples to holocellulose for stable carbon isotope analysis, *Anal. Chem.*, 65, 87–89, 1993.
- Leavitt, S. W., and A. Long, Evidence for ¹³C/¹²C fractionation between tree leaves and wood, *Nature*, 298, 742–744, 1982.
- Lin, G., and J. R. Ehleringer, No carbon isotopic discrimination during dark respiration in C₃ and C₄ plants, *Plant Physiol.*, in press, 1997.
- Lloyd, J., and G. D. Farquhar, ¹³C discrimination during CO₂ assimilation by the terrestrial biosphere, *Oecologia*, 99, 201–215, 1994.
- Lloyd, J., J. P. Syvertson, P. E. Kriedemann, and G. D. Farquhar, Low conductances for CO₂ diffusion from stomata to the sites of carboxylation in leaves of woody species, *Plant Cell Environ.*, 15, 873–899, 1992.
- Lloyd, J., et al., Vegetation effects on the isotopic composition of atmospheric CO₂ at local and regional scales: Theoretical aspects and a comparison between rain forest in Amazonia and boreal forest in Siberia, *Aust. J. Plant Physiol.*, 23, 371–399, 1996.
- Loreto, F., P. C. Harley, G. Di Marco, and T. D. Sharkey, Estimation of mesophyll conductance to CO₂ flux by three different methods, *Plant Physiol.*, 98, 1437–1443, 1992.
- Michelsen, A., S. Jonasson, D. Sleep, M. Havstrom, and T. V. Callaghan, Shoot biomass, δ¹³C, nitrogen and chlorophyll responses of two arctic dwarf shrubs to in situ shading, nutrient application, and warming simulating climatic change, *Oecologia*, 105, 1–12, 1996.
- Pearcy, R. W., and W. A. Pfitsch, Influence of sunflecks on the δ¹³C of *Adenocaulon bicolor* plants occurring in contrasting forest understory microsites, *Oecologia*, 86, 457–462, 1991.
- Quay, P., S. King, D. Wilbur, S. Wofsy, and J. Richey, ¹³C/¹²C of atmospheric CO₂ in the Amazon Basin: Forest and river sources, *J. Geophys. Res.*, 94, 18,327–18,336, 1989.
- Rask, H. M., and J. J. Schoenau, ¹³C natural abundance variations in carbonates and organic carbon from boreal forest wetlands, *Biogeochemistry*, 22, 23–35, 1993.
- Schlesler, G. H., Investigations of the δ¹³C pattern in leaves of *Fagus sylvatica* L., *J. Exp. Bot.*, 41, 565–572, 1990.
- Schuepp, P. H., M. Y. Leclerc, J. I. McPherson, and R. L. Desjardins, Footprint prediction of scalar fluxes from analytical solutions of the diffusion equations, *Boundary Layer Meteorol.*, 50, 355–373, 1990.
- Sellers, P., et al., The Boreal Ecosystem-Atmosphere Study (BOREAS): An overview and early results from the 1994 field year, *Bull. Am. Meteorol. Soc.*, 76, 1549–1577, 1995.
- Sellers, P. J., et al., Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate, *Science*, 271, 1402–1406, 1996.
- Smith, T. M., H. H. Shugart, F. I. Woodward, and P. J. Burton, Plant functional types, in *Vegetation Dynamics and Global Change*, edited by A. M. Solomon and H. H. Shugart, pp. 272–291, Chapman and Hall, New York, 1993.
- von Caemmerer, S., and J. R. Evans, Determination of the average partial pressure of CO₂ in chloroplasts from leaves of several C₃ plants, *Aust. J. Plant Physiol.*, 18, 287–305, 1991.
- Welker, J. M., P. A. Wookey, A. N. Parsons, M. C. Press, T. V. Callaghan, and J. A. Lee, Leaf carbon isotope discrimination and vegetative responses of *Dryas octopetala* to temperature and water manipulations in a High Arctic polar semi-desert, Svalbard, *Oecologia*, 95, 463–469, 1993.

J. R. Brooks, Department of Biology, University of South Florida, Tampa, FL 33620.

J. R. Ehleringer, Department of Biology, Stable Isotope Ratio Facility for Environmental Research, University of Utah, Salt Lake City, UT 84112.

L. B. Flanagan, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, Canada. (e-mail: lflana@ccs.carleton.ca)

(Received June 20, 1996; revised April 18, 1997; accepted April 21, 1997.)