Predicting daytime carbon isotope ratios of atmospheric CO$_2$ within forest canopies

N. BUCHMANN,*† J. R. BROOKS‡ and J. R. EHLERINGER§

Max-Planck-Institut für Biogeochemie, Postfach 10 01 64, 07701 Jena, Germany, ‡US EPA, NHEERL/Western Ecology Division, 200 SW 35th St, Corvallis, OR 97333, USA, and §Department of Biology, University of Utah, 257 South 1400 East, Salt Lake City, UT 84112–0840, USA

Summary

1. While measurements of leaf carbon isotope ratios (^{13}C/^{12}C) in terrestrial ecosystems have become more frequent, interpreting these data can remain a challenge in well developed canopies: the variation in leaf δ^{13}C (δ^{13}C$_p$) values is influenced by both the variation in δ^{13}C of source air (δ^{13}C$_a$) and by photosynthetic carbon isotope discrimination (Δ). However, source air information is often unavailable, limiting the interpretation of δ^{13}C$_p$, particularly in dense stands.

2. In this synthesis we found that about 70% of the observed variation in δ^{13}C$_p$ values within the canopy was influenced by changes in Δ, and that about 30% was determined by source air effects. Significant shifts in δ^{13}C$_a$ occur in canopies with high leaf area, predominantly within 1 m above the forest floor. In complex canopies, particularly in the understorey, source air effects cannot be neglected if δ^{13}C$_p$ measurements are used to calculate Δ and c_i/c_a ratios [ratio of internal CO$_2$ concentration in the mesophyll airspaces (c_i) to the ambient atmospheric concentration of CO$_2$ (c_a)].

3. We modelled δ^{13}C$_a$ of daytime source air for deciduous and coniferous forests in boreal, temperate and tropical biomes. An inverse regression model with easily available input variables accounted for about 90% of the variation in daytime δ^{13}C$_a$ values throughout the canopy.

4. In open canopies with leaf area index (*L*) of <2·5 or at canopy heights ≥1 m, the within-canopy daytime δ^{13}C$_a$ differences are negligible, and variations in δ^{13}C$_p$ are associated primarily with changes in Δ. Then, one can use the easily available carbon isotope ratio of the troposphere (δ^{13}C$_{trop}$) as a substitute for δ^{13}C$_a$ to calculate Δ to within ±0·4‰.

5. In canopies with *L* values >2·5, and at canopy heights <1 m, our model is recommended for calculating canopy δ^{13}C$_a$ values when direct measurements are not feasible. Although δ^{13}C$_a$ is highly variable near the forest floor in those dense forests, our model is more accurate and precise for estimating δ^{13}C$_a$ within 1 m above the forest floor than using δ^{13}C$_{trop}$ throughout the canopy (–0·2‰ ± 1·5 versus –1·4‰ ± 1·1).

Introduction

Measurements of the carbon isotopic composition of foliage (^{13}C/^{12}C) have proved useful in ecological studies because they can give insights into the long-term ratio of carbon to water fluxes, integrated over the entire life span of a leaf or needle (Farquhar, Ehleringer & Hubick 1989). Two parameters are available in this respect: the measured carbon isotope ratios of leaves (δ^{13}C$_p$) and the derived carbon isotope discrimination (Δ). Although δ^{13}C$_p$ data are easily obtainable with a typical analytical precision of ±0·1‰, their interpretation to leaf discrimination requires additional information or assumptions.

Foliar δ^{13}C values are influenced by (1) the δ^{13}C of ambient CO$_2$, the source air for photosynthetic assimilation; and (2) carbon isotope discrimination (Δ) during photosynthesis (Farquhar *et al.* 1989):

$$\Delta = \left(\frac{\delta^{13}C_a - \delta^{13}C_p}{1 + \delta^{13}C_p} \right) \quad (1)$$

However, in many ecological studies Δ is the parameter of primary interest, because it relates directly

†Author to whom correspondence should be addressed. E-mail: buchmann@bgc.jena.mpg.de

to ecophysiological traits, such as c_i/c_a, the ratio of internal CO_2 concentration in the mesophyll airspaces (c_i) to the ambient atmospheric concentration of CO_2 (c_a) (Farquhar *et al.* 1989; Equation 2), and ultimately to potential water-use efficiency:

$$\Delta = a + (b - a) * \left(\frac{c_i}{c_a}\right) \quad (2)$$

which includes fractionation factors associated with CO_2 diffusion in air (*a*), and with photosynthetic carboxylation (*b*). However, before one can calculate and use Δ for addressing ecological questions, the isotopic composition of the source air must be known.

Canopy profiles of $\delta^{13}C_a$ and c_a are the result of interactions between the atmosphere and the biosphere. Photosynthesis and turbulent mixing of the air decrease canopy c_a and increase $\delta^{13}C_a$, while soil microbial and plant respiration increase c_a and lead to more negative $\delta^{13}C_a$ values of canopy CO_2 (e.g. Buchmann, Kao & Ehleringer 1997a; Francey *et al.* 1985; Lloyd *et al.* 1996; Sternberg, Mulkey & Wright 1989). These processes are affected by plant life form and stand structure, which affect the resistance to mixing of atmospheric and respired air. In dense canopies such as crop stands and most forests, air turbulence is reduced, soil CO_2 efflux can be high, and pronounced $\delta^{13}C_a$ profiles of daytime canopy CO_2 can develop (>3‰). Canopy $\delta^{13}C_a$ values near forest floors are more negative due to the amount of ^{13}C depleted (isotopically lighter) CO_2 from soil efflux (e.g. Broadmeadow *et al.* 1992; Buchmann *et al.* 1997b; Flanagan *et al.* 1996). In contrast, in open, well mixed canopies such as deserts, savannas and widely spaced tree stands, $\delta^{13}C_a$ remains almost constant throughout the canopy, close to tropospheric values ($\delta^{13}C_{trop}$) (Buchmann *et al.* 1997a). This variable effect of stand structure on the isotopic composition of canopy air makes ecophysiological interpretations of $\delta^{13}C_p$ values challenging. Without intensive $\delta^{13}C_a$ measurements, the selection of a source air value remains subjective and adds uncertainty in the estimation of Δ. Knowledge about $\delta^{13}C$ of source air seems most critical for calculating meaningful Δ values, particularly in complex and dense canopies and their understorey.

Our goal was twofold. First, using existing data sets of $\delta^{13}C_a$ and $\delta^{13}C_p$, we determined how much the variation in $\delta^{13}C_a$ contributes to the intracanopy variation in $\delta^{13}C_p$ in forest stands. Second, we developed and tested a model for calculating daytime $\delta^{13}C_a$ profiles within forest canopies. Several recent studies included extensive $\delta^{13}C$ measurements of canopy air as well as of tree and understorey foliage, providing the necessary data sets to model $\delta^{13}C$ in canopy air (e.g. Berry, Varney & Flanagan 1997; Brooks *et al.* 1997a; Brooks *et al.* 1997b; Buchmann, Hinckley & Ehleringer 1998a; Kruijt *et al.* 1996). Here we have compiled these data sets, and modelled daytime canopy $\delta^{13}C_a$ for a variety of deciduous and coniferous forests of boreal, temperate and tropical biomes. We aimed for a simple, widely applicable model that would predict daytime $\delta^{13}C$ of source air using easily available input parameters.

Materials and methods

We examined 34 data sets to evaluate the contribution of source air effects on $\delta^{13}C_p$. Each data set contained $\delta^{13}C_a$ and $\delta^{13}C_p$ values. Forests from three biomes (boreal, temperate and tropical) and both deciduous and evergreen life forms were represented, and leaf area indices (*L*) ranged from 1·5 to 9·2 (Table 1). Only summer $\delta^{13}C_a$ data were used to represent times with maximum CO_2 assimilation rates. When diurnals of $\delta^{13}C_a$ were available, data between 08.00 and 18.00 h were either photosynthetically weighted (diurnals of $\delta^{13}C_a$ were weighted by the rate of photosynthesis occurring at that time), or simply averaged over this period. Photosynthetic weighting of $\delta^{13}C_a$ emphasizes the mid-morning to mid-day period when most carbon gain occurs.

Using only those data sets where original data were available to us (*n* = 20), we tested six different linear and non-linear regression models that described the pattern of daytime canopy $\delta^{13}C_a$ profiles in forests (Table 2). We used a subset of these data sets (*n* = 16) for substituting the regression coefficients with easily obtainable and meaningful parameters (Table 3, data sets marked 'm'). We used the remaining independent data sets (*n* = 3) to evaluate the accuracy of our regression model for daytime $\delta^{13}C_a$ (data sets marked 'e' in Table 3). Finally, we used those 19 data sets to evaluate the precision of the model by determining the difference between predicted and measured $\delta^{13}C_a$ values for every data point.

Results and discussion

VERTICAL INTRACANOPY DIFFERENCES IN $\delta^{13}C_P$ AND $\delta^{13}C_A$

Using all data sets that provided both $\delta^{13}C_p$ and $\delta^{13}C_a$, we calculated the vertical intracanopy differences in $\delta^{13}C_p$ values between the lowest and the highest position within the canopy (Table 1). Mean intracanopy differences in $\delta^{13}C_p$ within forest canopies differed among biomes (*P* = 0·004); and were smaller in boreal and temperate forests (≈ 3‰) than in tropical forests (≈ 4·5‰). Table 1 reports only studies that included measurements of $\delta^{13}C_a$ and $\delta^{13}C_p$, but many others report $\delta^{13}C_p$ canopy profiles that fit within the given ranges. For instance, Vogel (1978) reported a 2·6‰ vertical intracanopy difference for $\delta^{13}C_p$ values within a temperate beech forest; Schleser & Jayasekera (1985) measured 2·5 and 5‰ within individual lime and beech trees. Investigating the source for variations in $\delta^{13}C_p$, Garten & Taylor (1992) found 2–3‰ differences in $\delta^{13}C_p$ within temperate deciduous and coniferous forests. Intracanopy variation in $\delta^{13}C_p$ values in tropical forests is generally larger than in temperate forests: Medina, Sternberg & Cuevas (1991) reported an average

Table 1. Vertical intracanopy differences in plant ($\delta^{13}C_p$) and air ($\delta^{13}C_a$) $\delta^{13}C$ values (‰) and the contribution (percentage) of $\delta^{13}C_a$ differences to $\delta^{13}C_p$ differences for ecosystems with different stand leaf area indices (L)

Biome	Ecosystem	L	h (m)	Intracanopy differences $\delta^{13}C_p$	$\delta^{13}C_a$	Contribution (%)	Reference
Boreal	*Picea mariana*	6·2	0·3–9	3·4	1·2	36	Flanagan *et al.* 1996
		8·4	0·3–9	3·8	1·0	26	Brooks *et al.* 1997b
	Pinus banksiana	1·4	0·3–9	2·8	0·0	–	
		2·3	0·3–9	2·9	0·3	9	
	Populus tremuloides	2·3	0·3–9	3·3	1·0	32	
		3·0	0·3–9	2·8	0·8	29	
Boreal mean				3·2 ± 0·2	0·7 ± 0·2	26 ± 5	
Temperate	*Abies amabilis*	6·4	0·7–35	4·0	0·7	17	Buchmann, Hinckley & Ehleringer 1998a
		8·8	0·5–8	3·7	1·0	26	
		9·2	0·5–21	4·5	0·7	16	
	Acer sp.	2·1	0·3–12	3·6	0·6	17	Buchmann, Kao & Ehleringer 1997a
		3·9	0·3–12	2·6	1·0	37	
		4·5	0·3–12	3·1	0·8	25	
	Pinus contorta	1·5	0·3–12	1·5	0·2	14	Buchmann *et al.* 1997a
		1·7	0·3–12	2·4	0·6	25	
		2·2	0·3–17	4·2	0·2	5	
	Pinus resinosa	na	0·3–16	4·5	1·0	22	Berry, Varney & Flanagan 1997
	Populus tremuloides	1·5	0·3–9	0·8	0·4	63	Buchmann *et al.* 1997a
		2·0	0·3–10	2·5	0·6	26	
		2·3	0·3–10	3·3	0·6	19	
	Ulmus americana	na	0·5–10	3·0	1·0	33	Berry *et al.* 1997
	Quercus sp.	na	1–13	2·4	1·0	42	Harwood 1997
	Mixed deciduous	na	1–20	4·0	2·0	50	Hanba *et al.* 1997
	Zea mays	2·5	0·2–1	1·7	0·7	41	Buchmann & Ehleringer 1998
Temperate mean				3·1 ± 0·3	0·8 ± 0·1	28 ± 4	
Tropical	Rainforest	na	1–13	3·5	0·8	24	Francey *et al.* 1985
		na	1–25	3·5	1·8	50	Sternberg, Mulkey & Wright 1989
		na	0–30	5·3	0·6	11	van der Merwe & Medina 1989
		na	0–20	4·4	0·8	18	Broadmeadow *et al.* 1992
				4·1	1·2	30	
		na	0·5–20	2·4	2·0	83	Harwood 1997
		≈ 9	1–26	5·2	2·8	30	Kruijt *et al.* 1996
				7·4	3·0	41	
		≈ 8	2–30	5·0	0·9	18	Buchmann *et al.* 1997b
			2–32	4·3	0·9	20	
		na	0·5–14	4·7	1·6	34	J.R.E., unpublished results
Tropical mean				4·5 ± 0·04	1·5 ± 0·3	33 ± 3	
Global mean				3·6 ± 0·2	1·0 ± 0·1	29 ± 2·8	

na, not available.
Summer daytime $\delta^{13}C_a$ data were photosynthetically weighted or averaged between 08.00 and 18.00 h (see text for details). Vertical intracanopy differences were calculated between the two heights (h) given in column 4.

difference between $\delta^{13}C_p$ high in the canopy and those of understorey plants of 5·1‰. Ehleringer *et al.* (1986) found $\delta^{13}C_p$ differences ranging between 2 and 7‰ for different plant species growing together within a mature tropical forest, indicating plasticity in the response of individual species to the same environmental conditions.

This general trend of vertical intracanopy differences in $\delta^{13}C_p$ among forest types was reflected in daytime canopy $\delta^{13}C_a$ data. Mean vertical intracanopy differences in $\delta^{13}C_a$ differed among biomes ($P = 0·008$), with smaller differences in boreal (≈ 0·7‰; Table 1) and temperate forests (≈ 0·8‰), and larger intracanopy differences in tropical forests (≈ 1·5‰). In an open stand, each tree can be considered a 'roughness element', creating turbulent flow and relatively uniform c_a and $\delta^{13}C_a$ canopy profiles (Denmead 1968; Jarvis &

McNaughton 1986; Raupach 1989). In contrast, dense canopies impede airflow (Fitzjarrald & Moore 1990), resulting in pronounced variation of c_a and $\delta^{13}C_a$. In addition, canopy and stand structure have feedback effects on canopy gas exchange (Norman 1989; Parker 1995).

The observed decrease of $\delta^{13}C_p$ values (becoming more negative) with decreasing height above the forest floor was primarily due to ecophysiological changes in the foliage (70%; i.e. by altering c_i/c_a) in all forest types in each of the three biomes. When the lowest 1 m in the canopy was excluded, almost all changes in $\delta^{13}C_p$ resulted from ecophysiological changes rather than from changes in $\delta^{13}C_a$ of source air. Nevertheless, source air effects were important in many cases. The contribution of intracanopy variations in $\delta^{13}C_a$ to $\delta^{13}C_p$ variations was similar among all three biomes ($P = 0·455$), and

Table 2. Regression models tested to predict canopy $\delta^{13}C_a$ profiles (independent variable x = height above ground, in m)

Biome	Ecosystem	L	Exponential models $y=\dfrac{1}{(a+b\cdot e^{-x})}$ r^2	F	P	$y=a+b\cdot e^{-x}$ r^2	F	P	Logarithmic models $y=a+b\cdot\ln(x)$ r^2	F	P	$y=\dfrac{1}{a+b\cdot\ln(x)}$ r^2	F	P	Inverse models $y=a+\dfrac{b}{x}$ r^2	F	P	$y=\dfrac{1}{a+\dfrac{b}{x}}$ r^2	F	P
Boreal	*Picea mariana*	6·2	0·96	94	***	0·94	61	**	0·95	74	***	0·97	124	***	0·77	14	*	0·75	12	*
	Pinus banksiana	8·4	0·99	265	***	0·97	151	***	0·97	117	***	0·98	155	***	0·71	10	*	0·68	9	*
		2·3	0·90	37	**	0·90	35	**	0·96	90	***	0·96	106	***	0·81	17	*	0·81	17	*
	Populus tremuloides	2·3	0·65	7	ns	0·63	7	ns	0·71	10	*	0·75	12	*	0·99	321	***	0·98	244	***
		3·0	0·77	13	*	0·72	10	*	0·81	17	*	0·88	28	**	0·96	99	***	0·94	60	**
Temperate	*Abies amabilis*	6·4	0·79	15	*	0·79	15	*	0·90	38	**	0·91	40	**	0·77	13	*	0·76	13	*
		8·8	0·99	202	***	0·99	210	***	0·95	41	***	0·96	52	**	0·99	190	***	0·99	188	***
		9·2	0·99	386	***	0·99	272	***	0·87	27	**	0·89	31	**	0·98	239	***	0·98	186	***
	Acer sp.	2·1	0·86	25	**	0·84	21	*	0·93	56	***	0·96	97	***	0·92	46	**	0·91	42	**
		3·9	0·81	17	*	0·78	14	*	0·92	47	***	0·96	93	***	0·94	60	**	0·93	54	**
		4·5	0·84	22	**	0·85	23	**	0·91	43	**	0·89	31	**	0·54	5	ns	0·53	5	ns
	Pinus contorta	1·5	0·59	6	ns	0·59	6	ns	0·79	15	*	0·80	16	*	0·88	31	**	0·88	30	**
		1·7	0·77	13	*	0·74	12	*	0·88	29	**	0·91	41	**	0·97	134	***	0·97	119	***
		2·2	0·91	43	**	0·91	39	**	0·97	134	***	0·98	195	***	0·87	27	**	0·87	26	**
	Populus tremuloides	1·5	0·70	9	*	0·69	9	*	0·81	17	*	0·83	19	*	0·99	381	***	0·99	354	***
		2·0	0·55	5	ns	0·54	5	ns	0·70	10	*	0·74	11	*	1·0	872	***	1·0	1092	***
		2·3	0·87	27	**	0·86	24	**	0·95	78	***	0·97	116	***	0·91	38	**	0·90	36	*
Tropical	Rainforest	≈ 8	0·97	115	***	1·0	1066	***	0·96	100	***	0·98	210	***	0·81	17	*	0·83	20	*
		≈ 8	0·97	114	***	0·98	212	***	0·96	103	***	0·99	288	***	0·81	17	*	0·78	14	*
		na	0·81	13	*	0·78	11	*	0·89	24	**	0·93	41	**	0·93	37	**	0·92	35	**
Number of data sets with																				
$P > 0{\cdot}05$					3			3			0			0			1			1
$P < 0{\cdot}05$											5			4			6			6
$P < 0{\cdot}01$											8			7			6			7
$P < 0{\cdot}001$											7			9			7			6
Number of data sets with best fit among models					3			3			1			11			7			1
Overall performance					rejected			rejected			rejected			accepted			accepted			rejected

Data from 20 original data sets were used (see Table 1).
ns, $P > 0{\cdot}05$; *, $P < 0{\cdot}05$; **, $P < 0{\cdot}01$; ***, $P < 0{\cdot}001$. For details on the selection of the best models see text.
na, not available.

Table 3 Results of curve fitting for 20 data sets of daytime $\delta^{13}C_a$ using the regression model $\delta^{13}C_a = a + (b/h)$

Site	L	a	b	F	r^2	
Tropical						
Rainforest	8	−8·04	−0·083	17	0·81	m
	8	−8·07	−0·276	17	0·81	e
Seasonal forest	na	−8·59	−0·027	37	0·93	na
Temperate						
Abies amabilis	6·4	−7·58	−0·196	13	0·77	m
	8·8	−7·09	−0·324	190	0·99	m
	9·2	−7·69	−0·254	239	0·98	m
Pinus contorta	1·5	−7·50	−0·013	31	0·88	e
	1·7	−7·70	−0·036	134	0·97	m
	2·2	−7·85	−0·018	27	0·87	m
Populus tremuloides	1·5	−7·46	−0·016	381	0·99	m
	2·0	−7·68	−0·033	872	1·00	m
	2·3	−7·72	−0·021	38	0·91	m
Acer sp.	2·1	−7·25	−0·035	46	0·92	m
	3·9	−7·80	−0·058	60	0·94	m
	4·5	−8·09	−0·021	5	0·54	m
Boreal						
Populus tremuloides	2·3	−7·59	−0·049	321	0·99	e
	3·0	−7·77	−0·166	99	0·96	m
Picea mariana	6·2	−8·02	−0·080	14	0·77	m
	8·4	−7·79	−0·058	10	0·71	m
Pinus banksiana	2·3	−7·66	−0·022	17	0·81	m

Regression coefficients, F values and coefficients of determinations are given ($n = 6$; for more details see text). For P see Table 2. e, evaluation data set; m, modelling data set. na, not available.

Fig. 1. Vertical intracanopy differences in $\delta^{13}C$ of leaves ($\delta^{13}C_p$) as a function of stand leaf area index, L ($P = 0·001$) of boreal, temperate and tropical forest stands (see Table 1 for data description).

averaged 29% (SE = 2·8%; calculated as intracanopy difference in $\delta^{13}C_a$/intracanopy difference in $\delta^{13}C_p \times 100$; Table 1). As the largest intracanopy differences for $\delta^{13}C_a$ were observed in canopies with high leaf area, these variations should be accounted for before extracting long-term ecophysiological information from $\delta^{13}C_p$ values.

EFFECT OF LEAF AREA INDEX ON VERTICAL INTRACANOPY DIFFERENCES IN $\delta^{13}C_P$

Stand structure strongly influences canopy c_a profiles and the isotopic composition of canopy air. Stand density, crown architecture and understorey vegetation influence turbulent mixing of air within canopies (Parker 1995; Raupach, Denmead & Dunin 1992). Therefore stand leaf area index (L) is considered a good surrogate for these effects. We observed a general trend of increasing vertical intracanopy differences in $\delta^{13}C_p$ values with increasing L for forests from boreal, temperate and tropical climates ($r = 0·75$, $P < 0·001$; Fig. 1). The largest vertical intracanopy differences in $\delta^{13}C_p$ (4–8‰) were reported for tropical forests with the highest L (≈ 8).

MODELLING DAYTIME CANOPY $\delta^{13}C_A$

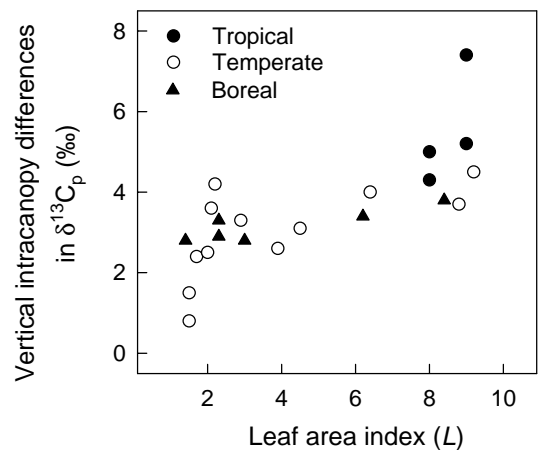Given the importance of source air effects on $\delta^{13}C_p$ in dense canopies, we tested different models for calculating daytime $\delta^{13}C_a$ profiles within forest stands. Among the six different models tested (Table 2), the two exponential models resulted in the largest number of insignificant ($P > 0·05$) relationships between height above the ground (h) and canopy $\delta^{13}C_a$, and therefore were excluded from further analyses. The remaining logarithmic and inverse models explained typically about 90% of the variance in daytime $\delta^{13}C_a$ profiles within canopies. Two equations, one for an inverse logarithmic and one for a simple inverse regression, resulted in the most 'best fits' (highest r^2 or F values) for those 20 data sets where original data were available (Table 2). The inverse logarithmic model explained slightly more of the variance in daytime $\delta^{13}C_a$ (mean $r^2 = 0·91$) than the simple inverse model (mean $r^2 = 0·88$). In a further step, we tested the potential to substitute the regression coefficients a and b of both accepted equations with easily obtainable and meaningful parameters such as L, $\delta^{13}C_{trop}$ and $\delta^{13}C_a$ at the top of the canopy ($\delta^{13}C_{a(top)}$). However, coefficients of the inverse logarithmic regression model correlated only weakly with these parameters ($-0·4 < r < 0·4$), whereas coefficients of the inverse regression (Equation 3) resulted in stronger, significant correlations ($r < -0·5$ and $r > 0·5$, $P < 0·025$). In addition, the more complex logarithmic model requires transformation of the data, whereas the inverse model is more appealing due to its simplicity. Thus we used the simple inverse regression model for all further analyses (Equation 3; Table 3):

$$\delta^{13}C_a = a + \frac{b}{h} \qquad (3)$$

where a and b are coefficients and h is height within the canopy. In theory, as height increases (e.g. >1000 m), the term (b/h) of Equation 3 will approach zero. Thus the model predicts that at great heights $\delta^{13}C_a = a$. Therefore we tested whether we could use $\delta^{13}C_{a(top)}$ (from direct measurements), $\delta^{13}C_{trop}$ (from international networks), or c_a at the top of the canopy (from direct
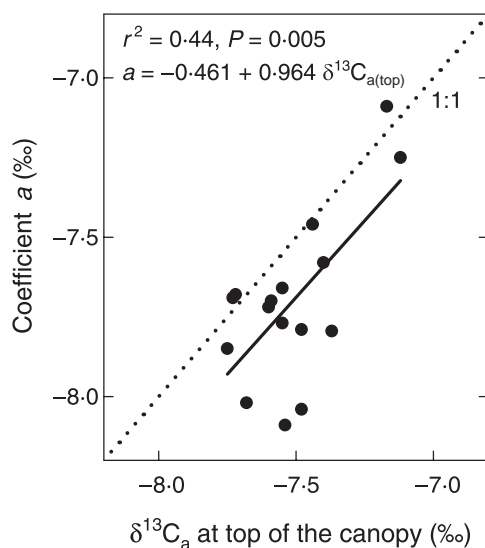
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Fig. 2. Relationships of the regression coefficient *a* from the empirical model (Equation 3; see Table 3) with the $\delta^{13}C$ of air ($\delta^{13}C_a$) at the top of the canopy.

Fig. 3. Relationship of the regression coefficient *b* from the empirical regression model (Equation 3; see Table 3) with the stand leaf area index, *L* ($P = 0.002$).

measurements) as potential substitutes for the empirical coefficient *a*. We found a significant linear relationship between *a* and $\delta^{13}C_{a(top)}$ ($P = 0.005$; Fig. 2). The intercept of the relationship was not significantly different from zero ($P = 0.836$), and the slope was equal to unity (0.96 ± 0.29 SE). Using $\delta^{13}C_{trop}$ or c_a as alternative substitutes for *a* resulted in weak relationships ($r^2 = 0.26$ and $r^2 = 0.081$, respectively). However, the variation in *a* is relatively small (Table 3), with a standard deviation of 0·32‰ and a mean of –7·75‰ for all 19 data sets. In comparison, the mean and standard deviation of $\delta^{13}C_{trop}$ is -7.77 ± 0.13‰, not significantly different from those of *a*. Given the ease of obtaining $\delta^{13}C_{trop}$ values compared to $\delta^{13}C_{a(top)}$, we tested further whether $\delta^{13}C_{trop}$ may be adequate in our model.

As the empirical coefficient *b* increases in our inverse regression model (Equation 3; Table 3), the term (*b*/*h*) increases as well (provided *h* remains constant), and $\delta^{13}C_a$ can become more negative than the intercept of Equation 3 (either $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$). However, if *b* decreases, $\delta^{13}C_a$ will approach the intercept. We found a significant negative relationship between *b* and *L* of all forest stands ($P = 0.002$; Fig. 3). Despite the spread in the data, the linear relationship resulted in the best fit ($r^2 = 0.49$, $F = 13.5$), whereas a cubic fit increased r^2 (0·57), but with a much smaller *F* value (5·2). This means, for stands with small *L*, the daytime $\delta^{13}C_a$ ratios will approach $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$, as usually observed in open stands (Buchmann *et al.* 1997a). For stands with high *L*, the daytime $\delta^{13}C_a$ will be more negative than $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$ as *b* was always negative (Table 2). This corresponds to the intracanopy CO_2 profiles typically found in dense temperate and boreal stands or tropical stands (Buchmann *et al.* 1998b).

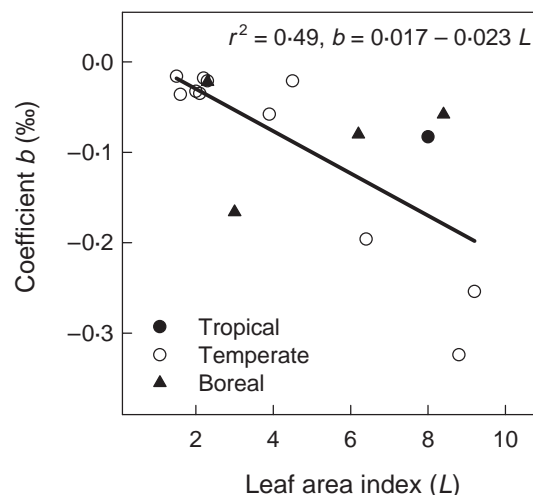We replaced both coefficients in Equation 3 (see Table 3) with the respective regression equations (Figs 2

and 3), and further simplified the equations obtained (e.g. by omitting insignificant regression coefficients). This resulted in Equation 4:

$$\delta^{13}C_a = (\delta^{13}C_{a(top)} \text{ or } \delta^{13}C_{trop}) - \frac{(0.023 \cdot L)}{h} \qquad (4)$$

VERIFICATION OF MODELLED CANOPY $\delta^{13}C_A$

We tested the accuracy of our model using measured $\delta^{13}C_a$ values from the original flask collections from three data sets not used to develop the above model (Fig. 4; Table 4). In addition, we tested whether the model was better than assuming $\delta^{13}C_a$ equals $\delta^{13}C_{trop}$ for all heights throughout the canopy (the standard assumption if no $\delta^{13}C_a$ data are available). Using the model with $\delta^{13}C_{a(top)}$ as the intercept, differences between original flask data and modelled $\delta^{13}C_a$ values averaged 0·03‰ (±0.06‰ SD) for the boreal forest, –0·12‰ (±0.11‰ SD) for the temperate forest and –0·63‰ (±0.63‰ SD) for the tropical forest. When using $\delta^{13}C_{trop}$ as the intercept, differences between measured and modelled values averaged 0·25‰ (±0.06‰ SD) for the boreal forest, 0·30‰ (±0.11‰ SD) for the temperate forest and –0·53‰ (±0.64‰ SD) for the tropical forest. Assuming a constant $\delta^{13}C_{trop}$ throughout the canopy resulted in mean differences of –0·90‰ (±1.21‰ SD) for the tropical forest, –0·04‰ (±0.81‰ SD) for the temperate forest and –0·02‰ (±0.42‰ SD) for the boreal forest. Differences >1‰ were only found at heights <1 m in the tropical forest, and just above the forest floor in the temperate forest (at 0·02 m). The overall accuracy of our model using $\delta^{13}C_{a(top)}$ as the intercept for predicting daytime canopy $\delta^{13}C_a$ values was significantly better than using $\delta^{13}C_{trop}$ as a constant throughout the canopy (paired *t*-test: $P = 0.047$), with accuracies of 0·26‰ for the model with $\delta^{13}C_{a(top)}$ as the intercept, compared to 0·41‰ for assuming constant $\delta^{13}C_{trop}$ throughout the canopy. Using $\delta^{13}C_{trop}$ as
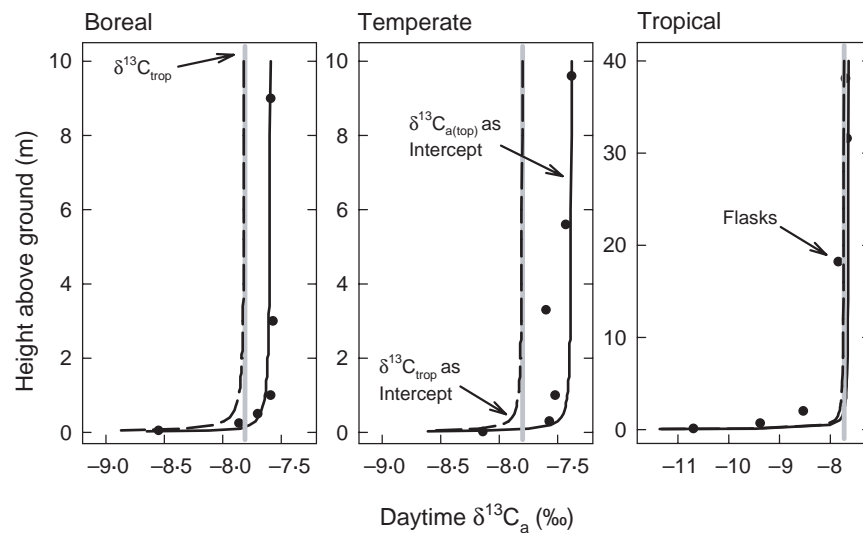
Fig. 4. Application of the regression model using either $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$ as the intercept to the observed canopy air data (flasks collected during the day) for three different forest stands (data for boreal, temperate and tropical forests from Brooks *et al.* 1997a; Buchmann *et al.* 1997a and Buchmann *et al.* 1997b, respectively). The grey line depicts a constant $\delta^{13}C_{trop}$ throughout the canopy.

Table 4. Evaluation of the model's accuracy using three independent data sets from boreal, temperate and tropical forest stands

Biome			Difference from measured $\delta^{13}C_a$ (‰)		
			Intercept		$\delta^{13}C_{trop}$
Ecosystem	L	h (m)	$\delta^{13}C_{a(top)}$	$\delta^{13}C_{trop}$	
Boreal	2·3	9·0	0·01	0·23	0·22
Populus tremuloides		3·0	0·04	0·26	0·24
		1·0	0·05	0·27	0·22
		0·3	−0·05	0·17	−0·05
		0·05	0·10	0·32	−0·74
mean ± SD			0·03 ± 0·06	0·25 ± 0·06	−0·02 ± 0·42
Temperate	1·5	10·0	0·00	0·42	0·42
Pinus contorta		5·6	−0·04	0·38	0·37
		3·3	−0·27	0·15	0·14
		1·0	−0·10	0·32	0·28
		0·3	−0·07	0·35	0·23
		0·02	−0·25	0·17	−1·67
mean ± SD			−0·12 ± 0·11	0·30 ± 0·11	−0·04 ± 0·81
Tropical	8	38·1	−0·06	0·09	0·09
rainforest		31·6	−0·02	0·07	0·06
		18·2	−0·19	−0·10	−0·11
		2·0	−0·80	−0·71	−0·80
		0·7	−1·48	−1·39	−1·65
		0·1	−1·21	−1·12	−2·96
mean ± SD			−0·63 ± 0·63	−0·53 ± 0·64	−0·90 ± 1·21

Measured $\delta^{13}C_a$ (‰) were taken from the original boreal, temperate and tropical data sets (Brooks *et al.* 1997a; Buchmann, Kao & Ehleringer 1997a; Buchmann *et al.* 1997b, respectively). Predicted $\delta^{13}C_a$ (‰) were calculated using two different intercepts in the model $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$, or using $\delta^{13}C_{trop}$ as a constant throughout the canopy (see text for details).

the intercept yielded intermediate accuracies (Table 4; Fig. 4). Thus, when the $\delta^{13}C_{trop}$ values did not closely match $\delta^{13}C_{a(top)}$, additional error was introduced into the modelled canopy $\delta^{13}C_a$ values.

The precision of the model was determined by calculating differences between measured and predicted $\delta^{13}C_a$ for every data point in the 19 data sets (Table 5). Above 1 m in height, all three approaches produced similar results for all the stands examined, independent

of stand L. The model with $\delta^{13}C_{a(top)}$ as the intercept predicted $\delta^{13}C_a$ values within −0·13‰ (±0·29‰ SD), the model using $\delta^{13}C_{trop}$ as the intercept predicted $\delta^{13}C_a$ values within 0·11‰ (±0·32‰ SD), and using $\delta^{13}C_{trop}$ throughout the canopy had the overall precision of 0·08‰ (±0·35‰ SD). The similarity of the three approaches above 1 m is not surprising given that during the day, strong turbulent mixing counteracts the development of intracanopy $\delta^{13}C_a$. Below 1 m, the

Table 5. Evaluation of the model's precision using 19 data sets in Table 3

			Difference from measured $\delta^{13}C_a$ (‰)		
			Intercept		$\delta^{13}C_{trop}$
L	h (m)	n	$\delta^{13}C_{a(top)}$	$\delta^{13}C_{trop}$	
<2·5	<1 m	19	0·22 ± 0·64	0·46 ± 0·63	−0·51 ± 0·62
	≥1 m	34	−0·04 ± 0·08	0·23 ± 0·20	0·22 ± 0·20
>2·5	<1 m	19	−0·24 ± 1·49	−0·003 ± 1·51	−1·41 ± 1·1
	≥1 m	39	−0·21 ± 0·37	0·00 ± 0·37	−0·05 ± 0·40
All	≥1 m	73	−0·13 ± 0·29	0·11 ± 0·32	0·07 ± 0·35

Predicted $\delta^{13}C_a$ (‰) were calculated with our model using either $\delta^{13}C_{a(top)}$ or $\delta^{13}C_{trop}$ as the intercept (see text for more details) or using $\delta^{13}C_{trop}$ as a constant throughout the canopy. The difference between predicted and measured values was calculated for each data point. Data are summarized (mean difference ± SD) for stands above and below $L = 2·5$, and for above and below 1 m canopy height.

three approaches showed similar precision for predicting $\delta^{13}C_a$ values in low leaf area stands ($L < 2·5$) (Table 5). However, in high leaf area stands ($L > 2·5$), the model using either intercept is much more precise in estimating $\delta^{13}C_a$ below 1 m than assuming a constant $\delta^{13}C_{trop}$ throughout the canopy (−0·2 ± 1·5‰ versus −1·4 ± 1·1‰ SD).

Conclusions

We have shown that, for many forest ecosystems, canopy profiles of $\delta^{13}C_p$ above 1 m height are not significantly affected by the variation in $\delta^{13}C_a$. In these cases, using $\delta^{13}C_{trop}$ from the international networks as a substitute for measured canopy $\delta^{13}C_a$ yielded similar accuracy and precision as using $\delta^{13}C_a$ values measured at the top of the canopy in our model. The accuracy of $\delta^{13}C_{trop}$ to predict $\delta^{13}C_{a(top)}$ depends on how closely tropospheric background measurements match upper canopy $\delta^{13}C_a$ values (as seen for the temperate and boreal forest in Fig. 4 and Table 4). These differences between $\delta^{13}C_{trop}$ and $\delta^{13}C_{a(top)}$ can be minimized if the distance between the study site and the nearest sampling location within the international networks is small, and if the tropospheric c_a from this network site is similar to the average daytime c_a at the top of the canopy.

However, for understorey vegetation in high leaf-area forest stands, isotopic variation in source air can be considerable and cannot be neglected. In these cases, the use of $\delta^{13}C_{trop}$ introduced considerable error (mean 1·4‰), and is not recommended. There are two options to overcome this problem: (1) measure $\delta^{13}C_a$ values at the study site, representative in time and space; or (2) predict $\delta^{13}C_a$ values using Equation 4 with either intercept (Table 5). The model constrains $\delta^{13}C_a$ estimates by including site leaf area index, thus accounting for biospheric–atmospheric interactions within the forest canopy. The model results in significantly better predictions for $\delta^{13}C_a$ than using $\delta^{13}C_{trop}$ to calculate leaf carbon isotope discrimination for understorey vegetation in dense stands.

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