REVIEW ARTICLE

Jon Lloyd · Graham D. Farquhar

^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere

Abstract Estimates of the extent of the discrimination against $^{13}CO_2$ during photosynthesis (Δ_A) on a global basis were made using gridded data sets of temperature, precipitation, elevation, humidity and vegetation type. Stomatal responses to leaf-to-air vapour mole fraction difference (D, leaf-to-air vapour pressure difference divided by atmospheric pressure) were first determined by a literature review and by assuming that stomatal behaviour results in the optimisation of plant water use in relation to carbon gain. Using monthly time steps, modelled stomatal responses to D were used to calculate the ratio of stomatal cavity to ambient CO_2 mole fractions and then, in association with leaf internal conductances, to calculate Δ_A. Weighted according to gross primary productivity (GPP, annual net CO_2 asimilation per unit ground area), estimated Δ_A for C_3 biomes ranged from 12.9‰ for xerophytic woods and shrub to 19.6‰ for cool/cold deciduous forest, with an average value for C_3 plants of 17.8‰. This is slightly less than the commonly used values of 18–20‰. For C_4 plants the average modelled discrimination was 3.6‰, again slightly less than would be calculated from C_4 plant dry matter carbon isotopic composition (yielding around 5‰). From our model we estimate that, on a global basis, 21% of GPP is by C_4 plants and for the terrestrial biosphere as a whole we calculate an average isotope discrimination during photosynthesis of 14.8‰. There are large variations in Δ_A across the globe, the largest of which are associated with the precence or absence of C_4 plants. Due to longitudinal variations in Δ_A, there are problems in using latitudinally averaged terrestrial carbon isotope discriminations to calculate the ratio of net oceanic to net terrestrial carbon fluxes.

Key words Carbon isotope discrimination Global carbon cycle · Stomata · Photosynthesi

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Introduction

Plants are depleted in ^{13}C relative to atmospheric CO_2 (Nier and Gulbransen 1939). There is considerable variation in plant carbon $^{13}C/^{12}C$ ratios (Wickman 1952) with this variation being attributable to differences in photosynthetic pathway (Bender 1968) as well as genotypic and environmental influences (for recent reviews see Farquhar et al. 1989; Ehleringer et al. 1993). The underlying physiological bases of these variations in plant carbon isotope fractionation are now reasonably well understood (Farquhar et al. 1989) and our purpose here is to use current theory of carbon isotope discrimination in plants to evaluate the extent of isotope discrimination by terrestrial vegetation on a global basis. As well as being of interest to ecologists and physiologists, an evaluation of the variation in carbon isotope discrimination on a global scale is of direct relevance to studies of the global carbon cycle: the assumed value for ^{13}C discrimination by the terrestrial plants affects the interpretation of temporal variations (Keeling et al. 1989a; Quay et al. 1992; Tans et al. 1993) and latitudinal gradients (Pearman and Hyson 1986; Keeling et al. 1989b; Ciais et al. 1994; Enting et al. 1994) in atmospheric $^{13}CO_2/^{12}CO_2$ ratios.

Theory

Isotope discrimination by C_3 plants

Total discrimination against $^{13}CO_2$ during CO_2 assimilation by C_3 plants (Δ_A) can be calculated by summing all discriminations associated by diffusion from the atmosphere to the sites of carboxylation within the chloroplast and weighting the discriminations according to the associated drawdown of CO_2, and then adding the discrimination associated with CO_2 fixation by the primary photosynthetic enzyme ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco) and subtracting the fractionations associated with the release of CO_2 via

photorespiration and respiration (Farquhar and Lloyd 1993), i.e.

$$\Delta_A = a_b \frac{C_a - C_s}{C_a} + a\frac{C_s - C_{st}}{C_a} + a\frac{C_{st} - C_w}{C_a}$$

$$+(e_s + a_1)\frac{C_w - C_c}{C_a} + b\frac{C_c}{C_a} - \frac{eR_d/k + f\Gamma^*}{C_a}, \qquad (1)$$

where a_b is the fractionation against $^{13}CO_2$ during diffusion across the laminar boundary layer (2.9‰; Farquhar 1983), a is fractionation against $^{13}CO_2$ during diffusion in free air (4.4‰; Craig 1953), e_s is equilibrium fractionation as CO_2 enters solution (1.1‰; Mook et al. 1974), a_s is the fractionation against $^{13}CO_2$ during diffusion in water (0.7‰; O'Leary 1984), b is the discrimination against $^{13}CO_2$ during photosynthetic fixation of CO_2, and e and f are the fractionations associated with respiration and photorespiration, respectively, C_a is the ambient mole fraction of CO_2 in the atmosphere surrounding the leaf, C_s is the mole fraction of CO_2 at the leaf surface, C_{st} is the mole fraction of CO_2 in the sub-stomatal cavity (often referred to as C_i, the "intercellular" mole fraction of CO_2), C_w is the mole fraction of CO_2 at the photosynthesising mesophyll cell wall surface, C_c is the equivalent gaseous mole fraction of CO_2 at the sites of carboxylation within the chloroplast, R_d is the rate of foliar respiration in the light, k is the carboxylation efficiency and Γ^* is the CO_2 photocompensation point. For further discussions see Farquhar et al. (1982), Evans et al. (1986), Farquhar et al. (1989), Lloyd et al. (1992) and Farquhar and Lloyd (1993).

Roeske and O'Leary (1984) observed ^{13}C discrimination during fixation of CO_2 by Rubisco to be 29‰ with respect to dissolved CO_2, which, allowing for the isotope effect for diffusion against $^{13}CO_2$ in water (e_s=1.1‰), makes discrimination by this enzyme, b_3, approximately 30‰. Guy et al. (1993) also found b_3 to be about 29‰. To calculate the effective fractionation of CO_2 during photosynthesis (b in Eq. 1) carboxylation by phospho-enolpyruvate carboxylase (PEP-c) also needs to be considered. Discrimination by this enzyme, b_4, can be expressed as (Farquhar 1983)

$$b_4 = e_s + e_b + b_4^* \qquad (2a)$$

where e_b is the equilibrium discrimination effect accompanying the hydration of CO_2 (−9.0‰ at 25° C; Mook et al. 1974) and b_4^* is the discrimination of PEP-c against $H^{13}CO_3^-$ (2.0‰: O'Leary et al. 1981). Using the temperature dependence of e_b (Mook et al. 1974), b_4 can be calculated as (Henderson et al. 1992)

$$b_4 = \left(26.19 - \frac{9483}{273.2 + T_l}\right) \times 10^{-3} \qquad (2b)$$

(which has the value of −5.6‰ at 25° C) and using β to denote the ratio of PEP to RuBP carboxylation, b can then be calculated as (Farquhar and Richards 1984).

$$b = b_3 - \beta(b_3 - b_4) \qquad (3)$$

Available estimates of β suggest a value of 0.05 to 0.10 (see Farquhar and Richards 1984; Raven and Farquhar 1990; von Caemmerer and Evans 1991 for more discussion) which at 25° C corresponds to b varying from 26.4 to 28.2‰.

The difference between the diffusional fractionations in the laminar boundary layer (a_b) and free air (a) are small (for discussion see Kays 1966; Farquhar 1983) and the associated drawdown of CO_2 (C_a-C_s), is normally much smaller than that across the stomatal pore (C_s-C_{st}). That is, the boundary layer conductance, g_a, is much greater than the stomatal conductance, g_s. Therefore there is only a small error in ignoring the different fractionation factors in the boundary layer and stomatal cavity and in substituting $[a(C_a-C_{st})/C_a]$ for $[a_b \ (C_a-C_s)/C_a +a(C_s-C_{st})/C_a]$ in Eq. 1.

Depending on leaf anatomy the drawdown of CO_2 from stomatal cavity to the site of carboxylation, (C_{st}-C_c), ranges from about 0.16 C_a to 0.20 C_a at saturating photon irradiance (von Caemmerer and Evans 1991; Lloyd et al. 1992; Loreto et al. 1992). The associated internal conductance is probably physical in nature and hence independent of the net CO_2 assimilation rate of the leaf, A. This means that (C_{st}-C_c) will approach 0 as $A{\to}0$. A value corresponding roughly to leaves operating on average at about 50% of their maximum (light-saturated) photosynthetic capacity (Schulze and Hall 1982) is (C_{st}-C_c)=0.1 C_a. It is also necessary to partition this drawdown into that from the stomatal cavity to the cell wall surface, and that from the cell wall surface to the sites of carboxylation within the chloroplast. Based on a recent analysis for leaves of woody species (Syvertsen et al. 1994) a reasonable estimate is (C_{st}-C_w)=0.025 C_a and (C_w-C_c)=0.075 C_a. Eq. 1 can then be re-expressed as

$$\Delta_A = a\left(1 - \frac{C_{st}}{C_a} + 0.025\right) + 0.075(e_s + a_1)$$

$$+b\left(\frac{C_{st}}{C_a} - 0.1\right) - \frac{eR_d/k + f\Gamma^*}{C_a} \qquad (4)$$

Carbon isotope discrimination by C_4 plants

From the theoretical treatment of isotope discrimination during C_4 photosynthesis presented by Farquhar (1983) and Henderson et al. (1992),

$$\Delta_A = a_b \frac{C_a - C_s}{C_a} + a\frac{C_s - C_{st}}{C_a} + a\frac{C_{st} - C_w}{C_a}$$

$$+(e_s + a_1)\frac{C_{st} - C_w}{C_a} + [b_4 + (b_3 - s)\phi]\frac{C_m}{C_a} \qquad (5)$$

where ϕ is the ratio of the rate of CO_2 leakage from the bundle sheath cells to the rate of PEP carboxylation (termed the "leakiness"), s is the fractionation during leakage and C_m is the equivalent gaseous mole fraction of CO_2 at the site of carboxylation within the mesophyll cytoplasm. Measurements of "on-line" $^{13}CO_2$ discrimination by C_4 species suggest a value for ϕ of around 0.2

whilst s can be taken as equal to (e_s+a_1) (Henderson et al. 1992). We do not know the magnitude of the drop in CO_2 mole fraction from the stomatal cavity to the sites of carboxylation in the mesophyll cytoplasm in C_4 plants but guess here that $(C_{st}-C_m)$ is on average $0.050\ C_a$, half the value assumed for C_3 plants. As for C_3 plants the internal conductance can be divided into an intercellular air space component and a mesophyll component. Taking $(C_{st}-C_w)=0.0125\ C_a$ and $(C_w-C_c)=0.0375\ C_a$, Eq. 5 can then be expressed as

$$\Delta_A = a\left(1-\frac{C_{st}}{C_a}+0.0125\right)+0.0375(e_s+a_1)$$
$$+\left[b_4+(b_3-e_s-a_1)\phi\right]\left(\frac{C_{st}}{C_a}-0.05\right) \qquad (6)$$

Materials and methods

Calculations were done using the $1°\times1°$ global data set of primary and secondary terrestrial vegetation cover of Wilson and Hender-

Table 1 Land cover classes distinguished by Wilson and Henderson-Sellers and their allocation to biomes for calculations of $^{13}CO_2$ discrimination during photosynthesis

Biome name	Wilson and Henderson-Sellers (1985) land cover class
Tropical rain forest	50: Equatorial rainforest 52: Tropical broadleaf forest
Tropical seasonal forest	25: Dense drought deciduous forest 26: Open drought deciduous woodland
Tropical savannah (50% grasses)	23: Open tropical woodland 37: Tropical savannah (grass+tree)
Evergreen warm mixed forest ($T_c>5°$ C)	12: Dense mixed needleleaf and broadleaf, evergreen and deciduous forest 13: Dense mixed needleleaf and broadleaf, evergreen and deciduous woodland
Cool/cold mixed forest ($-15\leq T_c\leq5°$ C) Taiga ($T_c<15°$ C)	14: Evergreen broadleaf woodland 17: Open deciduous needleleaf woodland 18: Dense deciduous needleleaf forest 19: Dense evergreen broadleaf forest
Cool/cold deciduous forest	20: Dense deciduous broadleaf forest 21: Open deciduous broadleaf woodland
Cool/cold conifer forest	10: Dense needleleaf evergreen forest 11: Open needleleaf evergreen woodland
Xerophytic woods and shrub (30% grasses)	24: Woodland+shrub 28: Thorn scrub
Grasslands and shrub (70% grasses)	32: Tropical grasslands+shrub 34: Rough grazing+shrub 35: Pasture+tree 39: Pasture+shrub
Grasslands	30: Temperate meadow and permanent pasture 31: Temperate rough grazing 33: Tropical pasture
Dryland agronomy	15: Evergreen broadleaf cropland 40: Arable cropland 41: Dry farm arable
Irrigated agronomy/horticulture	22: Deciduous tree crops (temperate) 42: Nursery and market gardening 45: Cotton 47: Vineyard 48: Irrigated cropland
Dryland tropical horticulture	46: Coffee 49: Tea 51: Equatorial tree crop
Tundra	61: Tundra 62: Dwarf shrub (tundra transition and high altitude wasteland)
Desert (no plants)	70: Sand desert and barren land
Semi-desert (plants)	71: Scrub desert and semi-desert 73: Semi-desert and scattered trees
Paddy rice	4: Paddy rice
Mangroves	5: Mangrove
C_4 crops	43: Cane sugar 44: Maize

son-Sellers (1985), 1°×1° gridded elevations (Gates and Nelson 1975), monthly 0.5°×0.5° surface temperature and precipitation fields of Leemans and Cramer (1991) and monthly 2.5°×2.5° wet and dry bulb temperatures generated from European Centre of Medium Range Weather Forecasting (ECMWF) data by Ian Watterson at CSIRO Division for Atmospheric Research in Melbourne, Australia. Calculations were carried out using the Fujitsu VP2200 supercomputer located at the Australian National University and mapping of data sets was undertaken on a SUN workstation using the GMT-SYSTEM (Smith and Wessel 1990; Wessel and Smith 1991).

Vegetation data

The archive of land cover data of Wilson and Henderson-Sellers (1985) was originally constructed for use in a general circulation model (GCM) and the classification of vegetation is based more on surface energy and moisture balance characteristics than on plant ecophysiological attributes. Therefore, using the principles developed in the global biome model of Prentice et al. (1992) we regrouped the Wilson and Henderson-Sellers (1985) archive. This procedure consisted of amalgamating some Wilson and Henderson-Sellers categories and also sub-dividing some groups based on cold tolerance and chilling requirements. Non-tropical forest types were divided into different groups according to the mean temperature of the coldest month, T_c (Prentice et al. 1992). The equivalences between the classification used here and that of Wilson and Henderson-Sellers (1985) are shown in Table 1.

In order to distinguish between the C_3 and C_4 photosynthetic modes we specified the proportion of total photosynthesis undertaken by grasses for biomes in which they co-occur with woody plants. Our vegetation class "xerophytic woods and scrub" was assumed to have 30% of its annual photosynthesis attributable to grasses (C_3 and C_4), "grasslands+shrub" was assigned 70% photosynthesis by grasses whilst "grasslands" was taken as 100%.

Photosynthetic mode

Studies examining the distribution of C_4 grasses all indicate a strong relationship between the proportion of total species observed with the C_4 pathway (p_4) and temperature (Teeri and Stowe 1976; Hattersley 1983; Cavagnaro 1988). The proportion of aboveground C_4 biomass in a grassland should be well correlated with p_4 (Hattersley 1992). We therefore assumed that the proportion of total photosynthesis carried out by C_4 plants is also well represented by p_4. We used the relationship between p_4 and mean annual temperature (T) first presented for South America by Cavagnaro (1988), viz.

$$p_4 = \begin{cases} 0 & \text{for} \quad T < 5.94°C \\ 0.0848T - 0.504 & \text{for} \quad 5.94 \le T \le 17.80°C \\ 1 & \text{for} \quad T > 17.80°C \end{cases} \tag{7}$$

We also incorporated the constraint on the distribution of C_4 grasses pointed out by Collatz and Berry (in Berry 1994) who noted that the mean rainfall had to be at least 25 mm in a month of the year where temperature was in excess of 22° C in order for C_4 dominated grasslands to occur. This precipitation requirement was modified in proportion to p_4, ie for 50% C_4 grasses from Eq. 7 the precipitation requirement was the occurrence of 12.5 mm in a month of the year where the mean monthly temperature was greater than 11° C.

As well as occurring in grasslands, woody C_4 plants can also occur in semi-desert regions. Eq. 7 was also used to estimate p_4 for semi-deserts, but as plant life in these regions may be supported by ground water (e.g. Winter 1981) the Collatz and Berry moisture constraint was not included.

The C_4 crops, maize and sugar cane, are independently identified in the Wilson and Henderson-Sellers (1985) land cover archive.

Atmospheric pressure

Elevation fields were used to calculate P according to the standard meteorological formula

$$P = 1013(1 - E_v/44308)^{5.2568} \tag{8}$$

where P is in mbar and E_v is the elevation in metres (Diehl 1925).

Leaf temperatures

Average leaf temperatures (° C) during photosynthesis (T_l) were estimated from monthly mean air temperatures (T_m) as $T_l = 1.05$ ($T_m + 2.5°$). The 2.5° C addition accounts for a daytime increase in air temperature over monthly mean air temperature and the 5% increase allows for sensible heat flux from the canopy to the atmosphere.

Leaf-to-air vapour mole fraction difference

Atmospheric vapour pressure (e_a) was calculated from wet and dry bulb temperatures using standard formulae and leaf-to-air vapour mole fraction difference, v, was calculated as the difference between the saturated vapour pressure at T_l (e_i the subscript referring to the intercellular air spaces) and e_a. Leaf-to-air vapour mole fraction difference (D) was then calculated as v/P).

Estimation of the ratio of stomatal cavity to ambient CO_2 mole fraction (C_{st}/C_a)

The model of optimal stomatal behaviour of Cowan (1977) and Cowan and Farquhar (1977) was used to calculate C_{st}/C_a. Based on the premise that optimal stomatal behaviour is that for which the average evaporation rate is minimal for a given average rate of CO_2 assimilation, Cowan and Farquhar showed that as long as there is positive curvature in the relationship between rate of transpiration, E, and A i.e. $\partial^2 E/\partial A^2$ is everywhere >0 (as is the case for the majority of plants and environments), optimal stomatal behaviour is that which maintains the sensitivity of E to stomatal conductance (g_s) in constant ratio, λ, to that of A to g_s:

$$\frac{\partial E/\partial g_s}{\partial A/\partial g_s} = \frac{\partial E}{\partial A} = \lambda \tag{9}$$

By linearising the curvilinear relationship between carboxylation efficiency (k) and chloroplastic mole fraction of CO_2 and ignoring both leaf boundary layer and leaf internal conductances to CO_2 diffusion Lloyd (1991) showed that a constant λ was associated with a stomatal response of the form

$$g_s = 1.6k\left(\sqrt{\frac{\lambda(C_a - \Gamma)}{1.6D}} - 1\right) \tag{10}$$

where D is the leaf-to-air vapour mole fraction difference and Γ is compensation mole fraction of CO_2.

Rather than responding to humidity directly, it is E to which stomata respond (Nonami et al. 1990; Mott and Parkhurst 1991). Nevertheless, as E is related almost directly by D this means that it is the leaf-to-air vapour mole fraction difference rather than the leaf-to-air vapour pressure difference to which stomata are responsive. This distinction is important when considering the relationship between isotope discrimination and altitude. Re-arrangement of Eq. 10 yields (Farquhar et al. 1993).

$$\frac{C_{st}}{C_a} = 1 - \sqrt{\frac{1.6D(C_a - \Gamma)}{\lambda C_a^2}} \tag{11}$$

In order to characterise λ for the C_3 plants of different biomes, we reviewed the literature of laboratory and field studies on leaf gas

Table 2 Estimated values for the average biome marginal water cost of plant carbon gain (λ), the proportion of photosynthesis lost in plant respiration (ϕ_c), gross primary productivity (GPP), leaf temperature during photosynthesis (T_1), leaf-to-air vapour mole fraction deficit during photosynthesis (D) and discrimination against $^{13}CO_2$ during photosynthesis (Δ_A) for the different biome types

Biome	λ (mol mol⁻¹)	ϕ_c	GPP (Pmol yr⁻¹)	T_1 (°C)	D (mmol mol⁻¹)	Δ_A (‰)
Tropical rain forest	750[a]	0.75	3.46	28.3	13.0	18.4
Tropical seasonal forest	1500[b]	0.65	0.77	27.5	18.7	18.9
Tropical savannah	1200[c]	0.55	1.28(C_3) 1.28 (C_4)	27.9	17.9	18.6 (C_3) 3.6 (C_4)
Evergreen warm mixed forest	1000[d]	0.50	0.14	21.5	13.4	19.0
Cool/cold deciduous forest	1250[e]	0.50	0.28	16.8	10.9	19.6
Cool/cold mixed forest	500[f]	0.50	0.20	14.5	11.4	18.3
Cool/cold conifer forest	250[g]	0.45	0.47	13.0	9.4	15.4
Taiga	300[h]	0.38	0.12	13.8	10.7	15.6
Xerophytic woods and scrub	500[i]	0.40	0.07 (C_3) 0.01 (C_4)	26.3	23.3	12.9 (C_3) 3.6 (C_4)
Grasslands and shrub	700[j]	0.40	0.51 (C_3) 0.27 (C_4)	23.4	19.6	15.5 (C_3) 3.5 (C_4)
Grasslands	700[k]	0.40	0.82 (C_3) 0.83 (C_4)	21.0	17.0	17.4 (C_3) 3.5 (C_4)
Dryland agronomy	700[l]	0.45	0.80	21.2	15.8	17.0
Irrigated agronomy/horticulture	900[m]	0.45	0.07	26.4	24.1	16.4
Dryland tropical horticulture	400[n]	0.45	0.05	29.0	15.4	15.0
Tundra	250[o]	0.35	0.25	9.7	8.0	16.1
Semi-desert	1000[p]	0.45	0.06 (C_3) 0.13 (C_4)	24.9	37.1	14.2 (C_3) 3.7 (C_4)
Paddy rice	800[q]	0.45	0.33	27.6	13.6	18.0
Mangroves	300[r]	0.45	0.05	30.8	10.5	15.5
Maize and sugarcane	N/A	0.45	0.07	19.9	15.8	3.3

[a] Average value derived from leaf gas exchange studies of Pearcy 1987 (*Toona australiis* and *Argyrodendron peraltum*), Ziska et al. 1991 (*Tabebulia rosea* and *Psycotria limonensis*), Riddoch et al. 1991 (*Entandrophrama antogense*), Thompson et al. 1992 (*Toona australis*) and Kwesiga et al. 1986 (*Terminalia superba*, *Triplochiton scleroxylon* and *Terminalia ivorensis*)

[b] Average value derived from leaf gas exchange studies of Sobrado 1991 (*Humboldtiella arbrea*, *Mansoa verricifera*, *Lonchocarpus dipteromeurus*, *Beureria cumanensis*, *Pithecellobium ligustrinum*, *Memora* sp., *Capparis verrucosa*, *Capparis arstigueleae*, and *Morisonia americana*) and Ziska et al. 1991 (*Acacia mangium*)

[c] Based on climatological data and measurements of carbon isotopic composition of over 50 woody savannah species from South America (Miranda, Miranda and Lloyd unpublished data)

[d] Average value derived from leaf gas exchange studies of Meinzer et al. 1984 (*Podocarpus deifolius* and *Podocarpus rospiliosii*), Teskey et al. 1986 (*Pinus taeda*), Kirschbaum and Tomkins 1990 (*Eucalyptus grandis*), Wong et al. 1978 (*Eucalyptus pauciflora*), Sun and Ehleringer 1986 (*Schima superba*) and Lloyd 1991 (*Macadamia integrifolia*)

[e] Average value derived from leaf gas exchange studies of Bassman and Zwier 1991 (*Populus trichocarpa* and *Populus deltoides*), Norby and O'Neill 1991 (*Liriodendron tulipifera*), Taylor and Dobson 1989 (*Fagus sylvatica*), Pezeshki 1987 (*Nyssa aquatica*) and Pezeshki and Chambers 1986 (*Fraxinus pennsylvanica*)

[f] From values derived for conifer and summergreen trees (see footnotes e and g) assuming that 1/3 of photosynthesis in such forests is by conifers and 2/3 by summergreen trees

[g] Average value derived from leaf gas exchange studies of Conroy et al. 1988 (*Pinus radiata*), Delucia 1986 (*Picea engelmanii*), Eamus and Fowler 1990 (*Picea rubens*), Matyssek and Schulze 1988 (*Larix×leptolepis*) and Meinzer 1982 (*Pseudotsuga menziesii*)

[h] From values derived from conifer and summer-evergreen trees (see footnotes e and g) assuming the bulk of photosynthesis to be done by conifers

[i] From values derived from leaf gas exchange studies of Atkinson and Winner 1987 (*Heteromeles arbutifolia*) Badger et al. 1982 (*Nerium oleander*), Collatz et al. 1976 (*Eucalyptus socialis*) and Gollan et al. 1985 (*Nerium oleander*) and also allowing for some photosynthesis by grasses

[j] From values derived for grasses (footnote k), also allowing for some photosynthesis by evergreen or drought deciduous trees

[k] From values derived from leaf gas exchange studies of Larigauderie et al. 1988 (*Bromus mollis*), McVetty et al. 1989 (*Moricandia moricandoides*), Monson et al. 1986 (*Agropyron smithii*), Ryle et al. 1992 (*Trifolium repens*) and Woledge et al. 1989 (*Lolium perenne*)

[l] From values derived for grasses (see footnote k)

[m] Average value derived from gas exchange studies on well-watered agronomic plants by Evans 1983 (*Triticum aestivum*), Lloyd et al. 1992 (*Prunus persica*) and Wong et al. 1985a, b (*Gossypium hirsutum* and *Phaseolus vulgaris*)

[n] From leaf gas exchange studies of Batten et al. 1992 (*Litchi sinensis*), Lloyd et al. 1987 (*Citrus sinensis*) and Meinzer et al. 1992 (*Coffea arabica*)

[o] From a comparison on carbon isotopic composition of tundra herbs, conifers and deciduous trees (see text)

[p] From leaf gas exchange studies of Mooney and Chu (1983) and leaf gas exchange and carbon isotopic composition studies of desert plants (Ehleringer 1993)

[q] From leaf gas exchange study of Caemmerer and Evans (1991)

[r] From leaf gas exchange study of Ball et al. (1988)

exchange where concurrent values of A, g_s and D were given. Based on these results, values of λ were allocated to each of the biomes listed in Table 1 (see Results section and Table 2) and C_{st}/C_a then calculated for each grid square on a monthly basis with Γ (ppmv) taken as 2.0 T_1. For some biomes for which few reliable gas exchange data could be found, measurements on leaf carbon isotopic composition were used to deduce λ. These deductions required either meteorological data (woody savannah vegetation) or concurrent dry matter isotopic measurements of other plant types, for which λ was known, growing in the same location.

Observed stomatal responses to vapour pressure deficit in C_4 plants (Morison and Gifford 1983) were simulated by an empirical modification to Eq. 11. The equation used was

$$\frac{C_{st}}{C_a} = 0.5 - \sqrt{\frac{1.6D}{\lambda_4 C_a}}$$ (12)

with λ_4 taken as 2500 mol mol^{-1}.

Isotope discrimination

Isotope discrimination by C_3 plants was calculated using Eq. 4 with b taken as 27.5‰, f taken as 8‰ (Rooney 1988) and e taken as 0‰. Based on a recent determination of 38.6 μmol mol^{-1} at 25° C (von Caemmerer et al. 1994) the temperature dependence of Γ^* was modelled as $1.54\ T_1$. The ambient mole fraction of CO_2, C_a, was taken as 350 μmol mol^{-1}.

For C_4 plants isotope discrimination was calculated using Eq. 6 with the value of b_4 varying with T_1 according to Eq. 3.

Calculation procedure

Where applicable, separate calculations were made for C_3 and C_4 plants. Each month two calculations were done for each grid square, once each for the primary and secondary vegetation types. The overall discrimination for each month was calculated assuming that the primary vegetation type occupied 75% of the area of the grid square and the secondary vegetation type 25%.

The altitudinal dependence of $^{13}CO_2$ discrimination by C_3 plants has been found to average a reduction of about 1‰ per 1000 m elevation (Körner et al. 1988). After including the associated environmental parameter (D) we found that only a small empirical correction was required, a reduction of 0.3‰ per 1000 m elevation. This is equivalent to a slight reduction in λ with increasing elevation. No correction was applied for C_4 plants.

Annual mean discriminations for each grid square were obtained by weighting monthly discriminations according to the monthly gross primary productivity (GPP, equivalent to the net rate of CO_2 assimilation by foliage expressed on a ground area basis), obtained as NPP/$(1-\phi_c)$ where NPP is the net primary productivity estimated using a simple model dependent on temperature and precipitation (Friedlingstein et al. 1992) and ϕ_c is the proportion of GPP lost as plant respiration (Table 2). Latitudinal and global averages of all parameters listed here are also weighted by estimated GPP. Thus for each grid square, the average annual isotope discrimination was calculated as

$$\Delta_{A(i,j,y)} = \frac{\sum\limits_{m=1}^{m=12} \Delta_{A(i,j,m)} GPP_{(i,j,m)}}{\sum\limits_{m=1}^{m=12} GPP_{(i,j,m)}}$$ (13a)

where the subscripts i and j denote the latitude and longitude coordinates of the grid square and y and m denote year and month respectively. Similarly for latitudinal or global averaging

$$\Delta_{A(y)} = \frac{\sum\limits_{i}\sum\limits_{j} \left[\Delta_{A(i,j,y)} GPP_{(i,j,y)}\right]}{\sum\limits_{i}\sum\limits_{j} GPP_{(i,j,y)}}$$ (13b)

where

$$GPP_{(i,j,y)} = \sum\limits_{m=1}^{m=12} GPP_{(i,j,m)}$$ (13c)

Model verification

Modelled discrimination was compared with values from the literature for the isotopic composition of CO_2 emitted from soils and vegetation (δ_R). These estimates of δ_R are typically obtained by concurrent measurements of ambient mole fraction of CO_2, C_a, and its isotopic composition, δ_a. Provided that sufficient diurnal variation in C_a and δ_a is obtained, then δ_R can be estimated from a plot of δ_a against $1/C_a$ (see Keeling 1958, 1961). We then assumed that $\delta_R \sim \delta_a - \Delta_A$, δ_a here being a mean global value and estimated allowing for changes in δ_a that have occurred over the last 35 years (Keeling et al. 1989a). Estimates of δ_R were obtained from Keeling (1958, 1961), Lancaster (1990), Quay et al. (1989) and from our own unpublished data. The resulting values of Δ_A were then compared with modelled values of Δ_A for the grid squares corresponding to the longitude and latitude where those estimates of δ_R were obtained.

Results

Global distribution of C_3 and C_4 photosynthesis

The modelled extent of C_4 photosynthesis is shown in Fig. 1. Notable features include the assignments of a small proportion of annual GPP to C_4 at latitudes above 45°N on the edges of the Kara-Kum and Turanian deserts as well as in Wales, and the large areas of maize in the United States mid-west and east of the Black Sea. Much of the vegetated land area between 15°S and 35°S is modelled to have at least some C_4 photosynthesis occurring. Using our simple model of GPP, C_4 plants are predicted to assimilate 2.6 Pmol CO_2 year^{-1} compared to 9.9 Pmol year^{-1} by C_3 plants (1 Pmol=10^{15} mol). On a global scale about 50% of C_4 photosynthesis occurs in each hemisphere.

Stomatal responses to leaf-to-air vapour mole fraction difference

Comparison on a common scale readily revealed large and systematic differences between different C_3 plant types in stomatal response to D. For example, comparison of data for cool- and cold-zone conifers with summergreen deciduous trees from the same climatic zone shows that, at any given D, summergreen trees consistently have a greater C_{st}/C_a, i.e. a higher λ (Fig. 2a). There is also a difference in stomatal responses between warm-temperate-zone conifers and conifers from colder areas (Fig. 2b): warm-temperate-zone conifers (such as are typically found in the south-eastern United States, at the higher altitudes in the tropics and in Oceania) have an average λ of around 1000 mol mol^{-1}. Their colderzone relatives have values more typically around 250 mol mol^{-1}. All values of λ used in the global analysis and the bases of their derivation are listed in Table 2. Figure 2c shows the different modelled stomatal responses for the C_3 trees and C_4 grasses that co-exist in savannas.

Despite numerous gas exchange studies using tundra species (e.g. Oberbauer and Oechel 1989) we could find no studies where the ambient vapour pressure at the time of measurement was also reported. From foliage carbon isotopic composition of tundra herbs (25 species; $\delta^{13}C=$
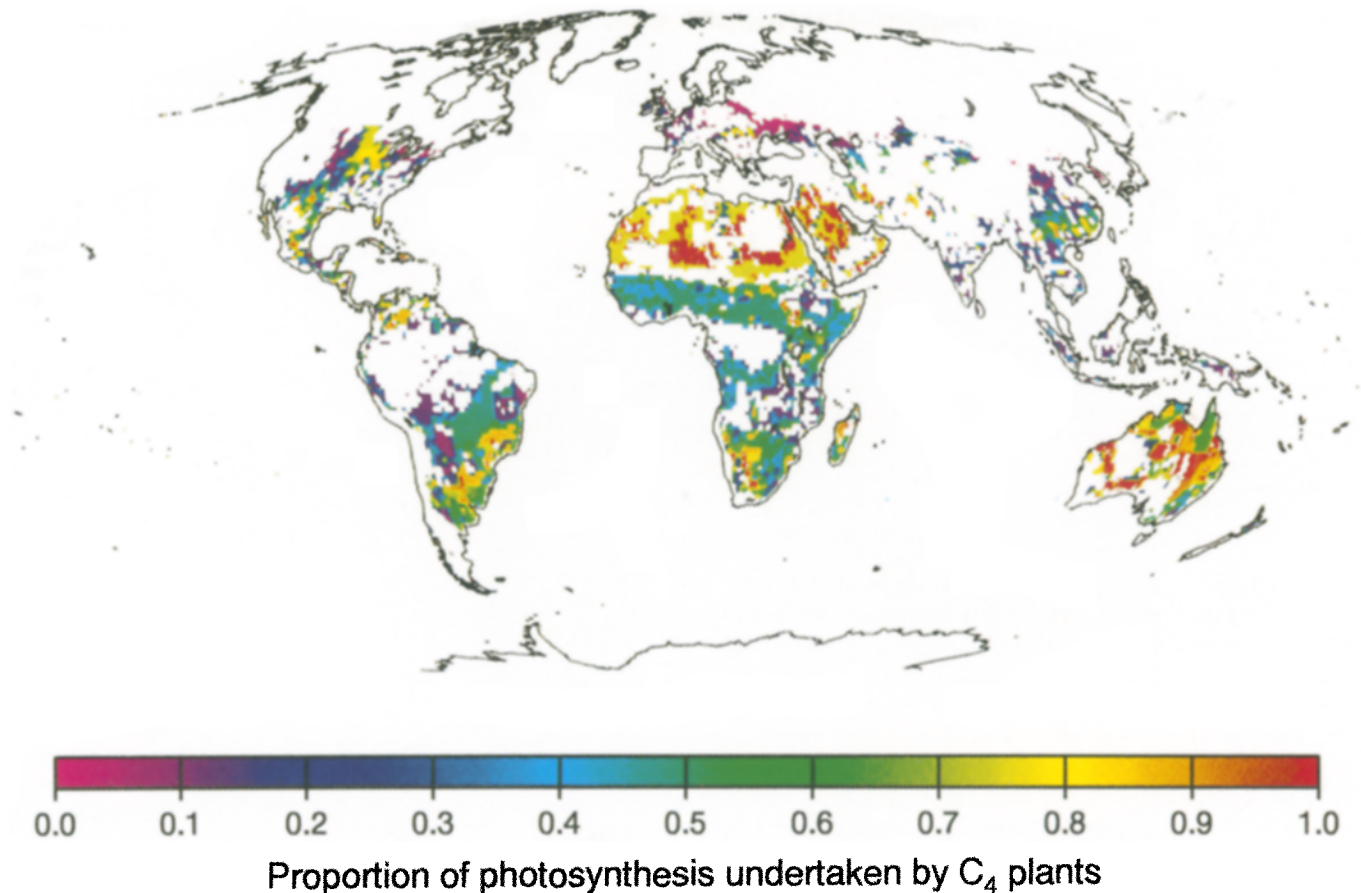
Proportion of photosynthesis undertaken by C$_4$ plants

Fig. 1 Estimated values for the proportion of annual gross primary productivity (GPP) undertaken by C$_4$ plants. Empty areas are modelled to have no C$_4$ plants present

odic rainfall events) seem to fall close to, but not on the same line as, the other forest and tundra biomes.

$-27.0‰$, $n=29$), coniferous trees (*Pinus sylvestris* and *Picea abies*; $\delta^{13}C=-26.9‰$, $n=5$) and summergreen trees (*Betula pendula*, *B. nana* and *B. pubescens*, $\delta^{13}C=-28.6‰$, $n=6$), all sampled near Abisko ($68.3°N$) in northern Sweden (J. Lloyd, G. D. Farquhar and K. Palmqvist, unpublished data) we conclude that little difference in λ exists between cold-zone conifers and tundra herbs. On this basis we assign the same value of λ as for cool/cold zone conifers, 250 mol mol^{-1}, to the tundra biome.

Table 2 also lists estimated GPP and average leaf temperatures and leaf-to-air vapour mole fraction differences encountered during photosynthesis. A simple plot of estimated λ versus modelled D (Fig. 3) reveals an interesting relationship. For biomes characterised by a regular or periodic water supply there is a close correlation between λ and D on a global scale, with tropical forests, drought-deciduous forests, temperate evergreen forests and tundra all falling on the same line. The only exceptions to this are cool/cold deciduous forest trees which have an exceptionally high λ. Plants whose water supply is episodic (semi-desert and xerophytic woods and shrub) deviate significantly from that relationship, as do cultivated plants growing outside their naturally occurring environment. C$_3$ grasslands (subject to mostly peri-

Global patterns in ^{13}C discrimination

Mean annual ^{13}C discrimination as predicted by the model is shown in Fig. 4. On a global basis most of the spatial variation in terrestrial isotope discrimination is due to the different fractionations of C$_3$ versus C$_4$ plants (compare Fig. 4 with Fig. 1). Nevertheless, there are large differences in ^{13}C discrimination between different biomes, even when only the C$_3$ mode occurs. Average values are listed for all biomes in Table 2. Globally averaged and weighted according to GPP, we obtain a mean global isotope discrimination of $17.8‰$ for C$_3$ plants, $3.6‰$ for C$_4$ plants and $14.8‰$ for the planet as a whole.

Table 2 shows that for natural vegetation consisting of woody C$_3$ plants a large range in average discrimination is observed, ranging from $12.9‰$ for xerophytic trees and shrubs to $19.6‰$ in cool/cold deciduous forests. Despite few differences in T_1 or D between the various cool and cold forests of the northern hemisphere, large variations in Δ_A occur with cool/cold coniferous forests having an average discrimination of only $15.4‰$. Comparison of the different herb-dominated biomes shows that differences in average discrimination are relatively small compared with those arising as a consequence of the presence of C$_4$ grasses in warmer regions.

Fig. 2a–c The relationship between the ratio of stomatal cavity to ambient mole fractions of CO_2 (C_{st}/C_a) and leaf-to-air vapour mole fraction differences for different plant types. Also shown are the relationships predicted by Eq. 11 for a leaf temperature of 25° C with an ambient mole fraction of CO_2 of 350 μmol mol^{-1} for different values of λ. **a** A comparison of summergreen deci-duous trees and cool/cold zone conifers. **b** A comparison of cool/cold zone conifers and warm temperate zone conifers. **c** A comparison of the modelled relationships for C_3 trees and C_4 grasses (Eq. 12) in savannah regions. For data sources see Table 2

Leaf-to-air vapour mole fraction difference (mmol mol^{-1})
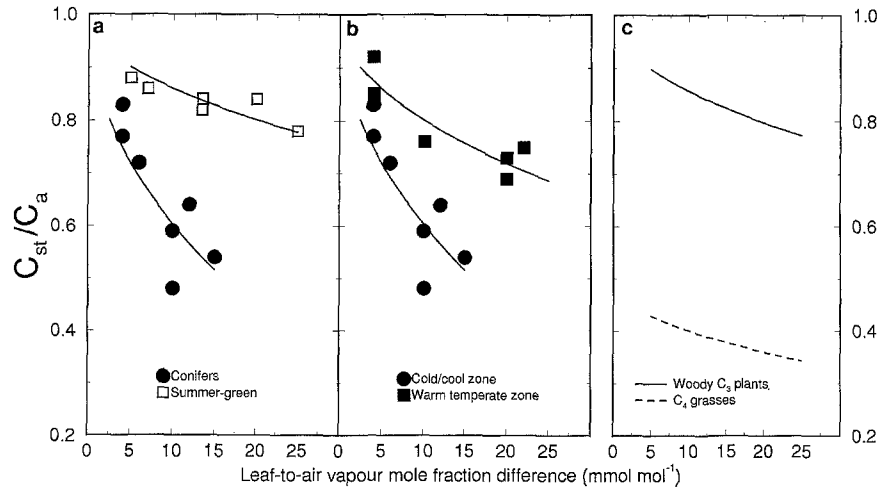
Variation in average discrimination with latitude is shown in Fig. 5 which details discrimination for both C_3 plants only and the terrestrial biosphere as a whole. This shows that in both hemispheres there is a decline in average Δ_A of C_3 plants north or south of the equator but that the average Δ_A of C_3 plant increases again as one approached the poles. Such gradients are however relatively small compared with the effect of C_4 plants, especially in the mid-latitudes of the southern hemisphere where sharp gradients in average terrestrial carbon isotope discrimination occur.

Latitudinally averaged values of C_c/C_a (C_3 and C_4 plants) are shown in Fig. 6 along with values obtained from a previous study modelling discrimination against ^{18}O in CO_2 on a global scale (Farquhar et al. 1993). Agreement between the two studies is close except at the higher latitudes.

Model validation

Modelled values of Δ_A are plotted against ($\delta_R - \delta_a$) from a range of souces in Fig. 7. This shows a significant correlation between terrestrial organic matter isotopic composition as inferred from atmospheric CO_2 measurements and the model predictions with a slope close to 1.0. Figure 7 contains data obtained from a wide range of biomes, viz. tropical rainforest, conifer forest, cool deciduous forests, schrub, grassland and tundra.

Discussion

In the analysis here, the differences in isotope discrimination on a global scale (Fig. 4) arise because of:

1. differences between C_3 and C_4 species in extent of discrimination against $^{13}CO_2$ during photosynthesis

2. differences between different C_3 plant types in stomatal response to vapour mole fraction difference (expressed here as differences in λ)
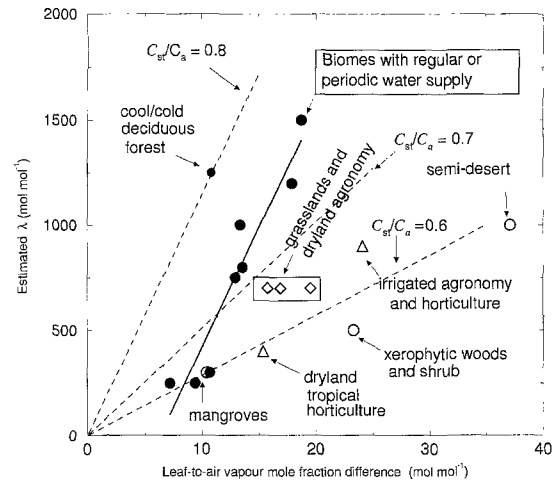

Fig. 3 The relationship between estimated values of λ (taken from Table 2) and the mean leaf-to-air vapour pressure deficit experience during photosynthesis (weighted according to GPP) for the different biome types

3. spatial and seasonal variation in vapour mole fraction differences

To differentiate between different photosynthetic modes on a global scale we modelled the abundance of C_4 plants according to the simple empirical relationship between mean annual temperature and the proportion of C_4 species present in grasslands (Cavagnaro 1988). Despite being based on a limited altitudinal transect in Argentina, this relationship seems to predict the distribution of C_4 plants on a global scale with reasonable accuracy. For example, Fig. 1 shows that the model simulates the presence of C_4 plants at reasonably high northern latitudes on the edges of the Kara-Kum and Central Asian deserts (Winter 1981) as well as in other colder regions such as Wales (e.g. *Cynodon dactylon*). It also correctly predicts the presence of some C_4 grasses in the temperate grasslands of North America (Teeri and Stowe 1976) and a decline in the proportion of C_4 grasses with increasing latitude along the east coast of Australia (Hattersley
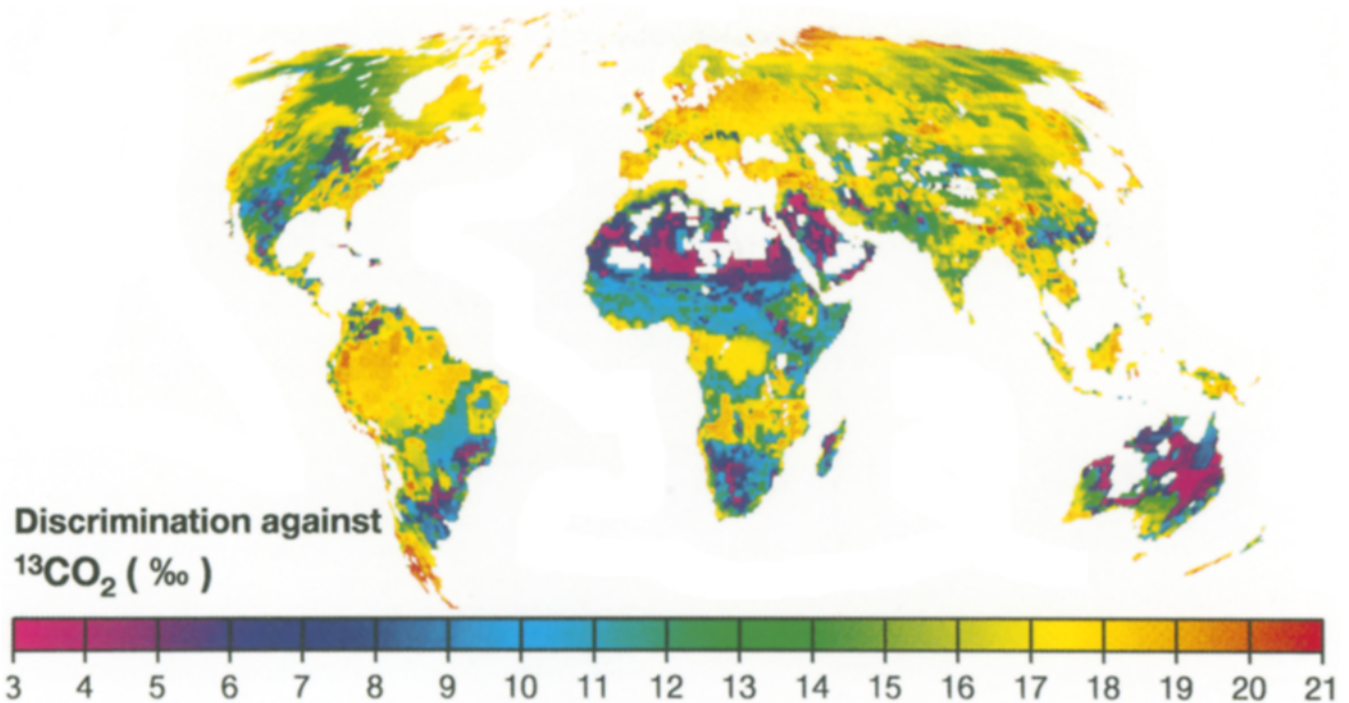
Discrimination against
$^{13}CO_2$ (‰)

Fig. 4 Modelled average annual values for discrimination against ^{13}C in CO_2 during photosynthesis
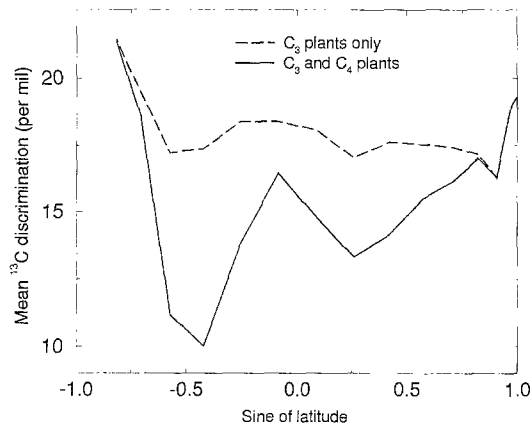

Fig. 5 The modelled latitudinal variation in discrimination against ^{13}C in CO_2 during C_3 photosynthesis and by the terrestrial biosphere as a whole (C_3 and C_4 photosynthesis)
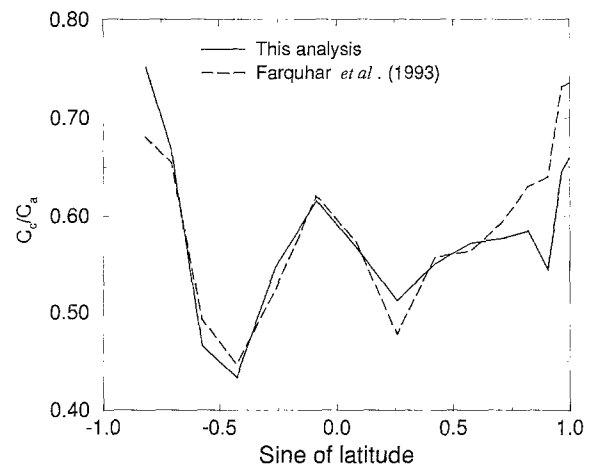

Fig. 6 Comparison between the current study and Farquhar et al. (1993) of the modelled latitudinally averaged values for ratios of the mole fraction of CO_2 in the chloroplast to the ambient mole fraction of CO_2 (C_c/C_a)

1983). Including the moisture limitation pointed out by Berry (1994) correctly excludes C_4 grasses from very arid regions (Syvertsen et al. 1976).

For C_4 species the average discrimination was only 3.6‰, compared with an average discrimination by C_3 plants of 17.8‰. Model simulations replacing all areas of C_4 plants by C_3 plants from the same biome show that an all-C_3 biosphere would have a mean discrimination of 17.5‰. This is slightly less that 17.8‰ because C_4 plants are generally found in more arid areas with higher than average vapour mole fraction differences. Thus photosynthesis by C_4 plants (estimated here at about 25%

that of C_3 plants) serves to reduce discrimination against $^{13}CO_2$ on a global scale by 2.7‰ below that which would occur if there were C_3 plants only. Our estimate of 21% of the total global GPP being undertaken by C_4 plants is slightly higher than a previous estimate which ignored the presence of C_4 grasses in temperate grasslands and in open scrubland (Farquhar et al. 1993) but is still less than the recent estimate of 30% given by Berry (1994). The extent of this estimate is dependent upon the vegetation database used, the proportion of photosynthesis assigned to grasses in savanna regions and the means by which GPP is estimated.

Although maize and sugar cane are modelled here to account for only about 3% of all C_4 photosynthesis, the conversion of C_3-dominated grasslands to these crops, as
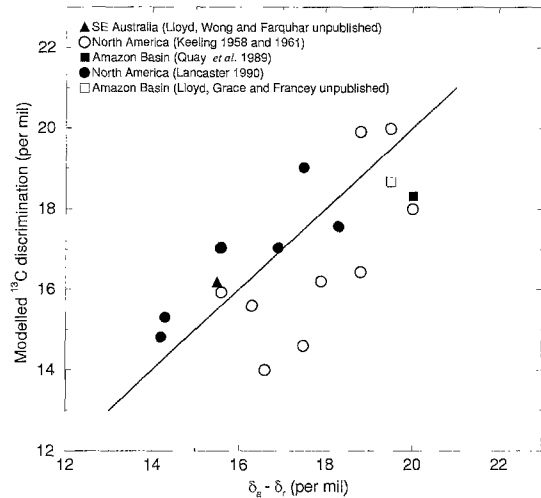
Fig. 7 Comparison of observed values for the difference in isotopic composition of respired versus mean atmospheric CO_2 ($\delta_a-\delta_R$) and modelled prediction of discrimination against ^{13}C in CO_2 during photosynthesis for the corresponding grid square in the current study. The *solid line* shows the 1:1 relationship

well as the extensive use of maize in shifting cultivation (Ruthenberg 1980) and the recent replacement of C_3 forests by C_4 pastures in tropical regions (Houghton et al. 1987) have all have contributed to anthropogenically induced changes in carbon isotope discrimination by the terrestrial biosphere. Conversion of 1% of global GPP from C_3 to C_4 decreases global discrimination by about 0.1‰. Future changes in the proportion of global photosynthesis undertaken by C_4 plants have been predicted as a consequence of possible future global warming (Henderson et al. 1994).

Our model of stomatal response and hence the dependence of isotope discrimination upon leaf-to-air vapour mole fraction difference was based on the model of optimal stomatal behaviour of Cowan (1977) and Cowan and Farquhar (1977). Although there have been occasional reports, especially with conifers, of $\partial E/\partial A$ varying widely (Meinzer et al. 1984: *Podocarpus rospiglkosii;* Guehl and Aussenac 1987; Fites and Teskey 1988; Grieu et al. 1988), the majority of studies attempting to test this hypothesis have shown $\partial E/\partial A$ to be reasonably constant for a given plant over a period of a day or so (Farquhar et al. 1980; Hall and Schulze 1980; Field et al. 1982; Mooney and Chu 1983; Mooney et al. 1983; Williams 1983; Hunt et al. 1985; Sandford and Jarvis 1986; Ball et al. 1988; Lloyd 1991; Berninger and Hari 1993). It is interesting to note that even in studies where $\partial E/\partial A$ varies widely the stomata usually respond to D in a curvilinear fashion, close to that predicted by the model. Examination of such data suggests an apparent inhibition of mesophyll photosynthetic capacity with increasing D. We consider it likely that this apparent depression in photosynthetic capacity at high D arises as a consequence of non-uniform stomatal closure (Terashima et al. 1988). Farquhar (1989) and Lloyd et al. (1992) have modelled the effects of stomatal heterogeneity on carbon isotope discrimina-

tion and showed that the effect on ^{13}C discrimination by the leaf as a whole is less than that which would be inferred by estimation of C_{si}/C_a from gas exchange measurements.

Calculation of λ from concurrent measurements of A, g_s and D in the literature showed considerable variation between the various C_3 plant types. One of the most striking contrasts was the difference between summergreen trees and conifers in the boreal and cool temperate zones (Fig. 2a). This difference in stomatal responses is reflected by the differences we observed in leaf carbon isotope composition between the two plant types when compared in northern Sweden (see Results). These differences is carbon isotopic composition have also been reported by other workers (Lowden and Dyck 1974; Leavitt 1993).

For plants growing in environments characterised by a regular water supply (tropical forests, drought-deciduous forests, temperate, cool and cold conifer, deciduous and mixed forests, tundra and mangroves) there was a strong positive relationship between the modelled average leaf-to-air vapour mole fraction deficit encountered during photosynthesis and the average value of λ as inferred from the literature (Fig. 3). On the other hand, xerophytic C_3 plants of semi-arid and arid areas are characterised by a more conservative water use strategy (i.e. a lower λ for a given leaf-to-air vapour mole fraction difference). This suggests that where evaporative demand is high, if water supply is periodic (tropical seasonal forest or tropical savannah), the most successful plants are those which have a non-conservative water-use strategy (i.e. a high λ). On the other hand, where water use is episodic, plants with a conservative water use strategy (low λ) seem to be the most successful. We note, however, that within the one desert community there may be substantial variations in λ (as evidenced by differences in Δ_A), with such differences being related to plant growth strategy. In such cases perennial species with a short life expectancy have considerably higher Δ_A than longer-lived species (Ehleringer and Cooper 1988; Ehleringer 1993, 1994). Similar differences have also been observed in grassland communities (Smedley et al. 1991). Combined with our global observations and previous work by Schulze (1982), this suggests that plants with a rapid phenological development but only over a short time period (such as is dictated by a regular seasonal water supply) are characterised by a less conservative efficiency of water use then those with a slower phenological development but over a longer period. For the case of growth dictated by water supply, this relationship is evident on the time scale of months (the short leaf longevity and non-conservative water use of dry tropical forest trees) and years (the relationship between conservative water use and long whole-plant longevity of desert perennials).

Differences in λ between summergreen deciduous trees and evergreen conifers (Fig. 2a) follow the same pattern, but in this case seasonality in growth and associated differences in survival strategy seem to be influenced by temperature rather than water availability. For

cold- and temperate-zone trees, another important feature would be the low hydraulic conductivity of conifers compared with summer-green deciduous trees (Wang et al. 1992). This could make conifers prone to xylem embolisms at high transpiration rates. Indeed, across a wide range of temperate tree species there is a relationship between hydraulic conductivity, susceptibility to xylem embolism at low temperatures and foliar phenology (Wang et al. 1992). The deciduous habit of some conifers such as *Larix* species which dominate the taiga of northern Eurasia and some of North America may be more a consequence of nutrient requirements than water relations (Tyrell and Boemer 1987; Schulze et al. 1994).

The model for ^{13}C discrimination described here, and that for discrimination against ^{18}O in CO_2 during photosynthesis (Farquhar et al. 1993) use a similar strategy for calculating C_c/C_a. This version differs from Farquhar et al. (1993) in that some values of λ have been altered (in particular λ has been reduced for tundra and increased for summergreen trees as a result of the survey outlined in Table 2.). The current model also has stomata responding to leaf-to-air vapour mole fraction difference rather than leaf-to-air vapour pressure difference (the distinction being important at high altitudes) and uses a more sophisticated procedure to evaluate the proportion of photosynthesis undertaken by C_4 plants. Nevertheless, on a global basis, the current model estimate of C_c/C_a varies by less than 0.01 from our previous estimate (Farquhar et al. 1993). Differences between the two models in C_c/C_a at high northern latitudes (Fig. 6) do however have consequences for modelling the strong latitudinal gradient in ^{18}O in atmospheric CO_2 in this region (Francey and Tans 1987).

Despite large differences in both λ and D on a global scale the relationship between λ and D for C_3 plants (Fig. 3) results in only a small modelled latitudinal variation in Δ_A for C_3 plants (Fig. 5). Nevertheless, the small decline in average Δ_A for C_3 plants as one moves away from the equator (~1‰ from the equator to 65°N) is in agreement with recent observations on the latitudinal variation in dry matter carbon isotopic composition of C_3 plants (Körner et al. 1991).

We tested the validity of the model by taking advantage of estimates of the isotopic composition of respired CO_2 being obtainable by concurrent sampling of mole fraction and carbon isotopic composition of atmospheric CO_2 within the nocturnal boundary layer. This reflects average ecosystem dry matter carbon isotopic composition on the scale of tens or hundreds of square kilometers. Even though the global simulation here is at a scale several orders of magnitude larger, the relationship between modelled isotopic composition of individual grid squares and observations at some point on those grid squares (Fig. 7) provides encouraging support for the validity of the modelling approach used. It was expected that the modelled Δ_A would be somewhat lower than $(\delta_a - \delta_R)$ as some re-fixation of respired CO_2 must occur (Keeling 1962). The extent to which this occurs is a function of canopy structure, height of the nocturnal boundary layer and night-time respiration rate, the rate of subsequent convective boundary layer growth and the rate of respiration by soil and branches relative to photosynthesis during the day, as well as the frequency with which the atmospheric boundary layer is disturbed by fronts or by deep cumulus convection. It is therefore almost impossible to predict on a global scale. If only 5% of respired CO_2 is re-assimilated (rather than passing to the troposphere) then for C_3 plants this would serve to deplete plant dry matter by, on average, about 0.9‰ (compared to what would happen if it was only tropospheric CO_2 that was being assimilated). On the other hand, Fig. 7 does not take into account the seasonal variations in the isotopic composition of atmospheric CO_2 associated with different seasonalities of photosynthesis versus respiration. During the growing season atmospheric CO_2 is typically enriched in ^{13}C, particularity at high northern latitudes (Keeling et al. 1989a).

The average value for the terrestrial biosphere estimated here (14.8‰) is markedly lower than other estimates (17.6‰, Keeling et al. 1989; 20.0‰, Quay et al. 1992; 18.0‰, Tans et al. 1993). These other estimates appear to be based solely on dry-matter isotopic composition of C_3 plants and the isotopic composition of atmospheric CO_2 and they are not far from our C_3 average of 17.8‰. In many of these studies, the difference between the assumed isotopic discrimination by the terrestrial biosphere and that of the ocean has been used to partition net fluxes of CO_2 between the ocean and the land. To a first approximation the approach leads to the estimated net flux into the terrestrial biosphere being inversely proportional to the estimate used for Δ_A. Thus, if net uptake of CO_2 by plant communities were to be currently occurring in proportion to GPP, assuming a value of around 18‰ for discrimination by the terrestrial biosphere will have underestimated the net terrestrial carbon flux by about 25%.

Nevertheless, rather than being dependent on GPP, a positive net ecosystem productivity (NEP, defined as the difference between GPP and ecosystem respiration) that would occur as a consequence of enhanced photosynthesis under conditions of increasing mole fractions of CO_2 in the atmosphere, is more dependent on the magnitude of plant growth responses and mean residence times of carbon in plant and soil carbon pools (Taylor and Lloyd 1992). There is considerable interspecific variation in CO_2 growth response among both C_3 and C_4 plants (for a recent summary see Poorter 1993) as well as variation between different biome types in mean carbon residence time (see for example Taylor and Lloyd 1992). Thus the isotopic signature associated with a *net* flux of CO_2 into the terrestrial biosphere (a positive NEP as a result of CO_2 "fertilisation") will probably not be the GPP weighted isotopic signature calculated here. Similarly although latitudinal variation in Δ_A will be critical in inversion studies where latitudinal variations in atmospheric isotopic composition are combined with atmospheric tracer transport models in order to deduce the global distribution of terrestrial versus oceanic sinks for anthropogenic

CO_2 (e.g. Ciais et al. 1994) there is considerable longitudinal variation in Δ_A within individual latitudinal bands (Fig. 4). This is particularly true for the mid-to-high northern latitudes where grasslands, deciduous forests, mixed forests and conifer forests all occur. If there are differences in the ratio of NEP to GPP for these different biomes, then the mean zonal latitudinal discriminations calculated here would not be the appropriate values for partitioning fluxes between the ocean and the land, i.e. substituting NEP for GPP in Eqs. 13a–c would give a different result. This is also an important consideration for calculations in the tropics and southern hemisphere where there is even larger variability in Δ_A.

We would anticipate that temporal variability in surface temperatures, precipitation and atmospheric vapour pressure would also result in substantial variations in Δ_A from year to year. For example, the model presented here predicts that increasing atmospheric vapour pressure by only 1 mbar results in an increase in global Δ_A of about 0.5‰. There is little doubt that, even for irrigated plants, substantial inter-annual variation in Δ_A is observed (e.g. Rundel and Sharifi 1993). Whether the cause in temporal variations in terrestrial plant productivity is a consequence of changes in mesophyll capacity for photosynthesis or via changes in stomatal conductance, these changes will almost certainly result in variations in Δ_A. Hence extreme care needs to be exercised in the interpretation of year-to-year variations in both latitudinal gradients and rates of change in the isotopic composition of atmospheric CO_2.

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