δ^{13}C-variations of leaves in forests as an indication of reassimilated CO_2 from the soil

G.H. Schleser and R. Jayasekera

Institut für Chemie 2, Kernforschungsanlage Jülich GmbH, P.O. Box 1913, D-5170 Jülich, Federal Republic of Germany

Summary. An attempt has been made to evaluate the contribution of soil respired CO_2 to the total assimilation of a forest tree, by heeding the ^{13}C-concentrations of CO_2 from the free atmosphere and from mineralization processes within the soil respectively. An expression has been derived, according to which the assimilated fraction of CO_2 from the soil at a particular height of a tree is given by the δ^{13}C-value of the corresponding leaves, δ^{13}C of atmospheric CO_2, δ^{13}C of soil respired CO_2 and the physiological state of the leaves expressed as the ratio of total respiration over gross photosynthesis and internal over external CO_2-concentration. In the particular case investigated, a δ^{13}C-difference of 5⁰/₀₀ has been determined from bottom to top of a beech tree which results in a CO_2 contribution from the soil of about 22% for the lower forest strata, while the total contribution of soil respired CO_2 accounts for about 5% of the overall assimilation.

During the process of photosynthesis the carbon isotope ^{13}C is strongly discriminated against the isotope ^{12}C. Therefore organically bound carbon is depleted in ^{13}C relative to the carbon of atmospheric CO_2. The CO_2 liberated from organically bound carbon during mineralization reflects approximately the ^{13}C-content of organic material and therefore represents a differently labelled ^{13}C-source compared to the ^{13}C of atmospheric CO_2. In forests or agricultural stands, where a certain stratification pattern of soil respired CO_2 can be expected, photosynthetically active leaves should fix differently labelled CO_2 depending on the position of the leaves. In fact it has been shown that leaves which are positioned more closely to the soil exhibit more negative δ^{13}C-values than those which are exposed to the free atmosphere, i.e. those which are growing on top of a canopy (Vogel 1978, Medina 1980).

Leaves at different positions of a tree are exposed to different environments which undoubtedly leads to different physiological states. Therefore different ^{13}C-contents of leaves may reflect not only different ^{13}C-sources as assumed by Vogel 1978 and Medina 1980 but also different physiological states of leaves. Model calculations (Schleser and Jayasekera 1984) show that the δ^{13}C-value of leaves depends on the source of ^{13}C, the ratio of total respiration R over gross photosynthesis P and the internal concentration of CO_2 expressed as C_i over the external concentration of CO_2 of a leaf C_{atm} (see also Francey and Farquhar 1982). The latter two quantities should be different from top to

bottom of a canopy since neither illuminance conditions nor temperature or humidity conditions are the same. This should be evident from the strong differences found for the leaf area weight of nitrogen and carbon and the distinct differences of minerals such as Mg and K. In fact the determination of δ^{13}C-values of leaves from a solitary standing tree, where strong turbulent conditions prevailed, also exhibited δ^{13}C differences with height. Since the ^{13}C-source is supposed to have been the same for all leaves of the solitary standing tree, the δ^{13}C-differences could only have originated in different physiological states.

It is shown that different results for reassimilated soil respired CO_2 are obtained, depending on whether differences of leaf state are considered or not. The δ^{13}C investigations have been performed with leaves from a beech tree (*Fagus sylvatica* L.) growing in a forest near Jülich, while the solitary standing lime tree (*Tilia tomentosa Moench*), which has been used for comparison is growing in a plain at a somewhat elevated position.

Theoretical considerations

The source of photosynthetically fixed CO_2 represents a mixture of CO_2 from the free atmosphere above the canopy and CO_2 emanating from the soil as a result of mineralization processes (Fig. 1). The ^{13}C-content of this mixture depends on the mixing ratio. Since the ^{13}C-content of the two sources is very different, the ^{13}C-content of atmospheric CO_2 within a forest stand depends very much on the stratification pattern of soil respired CO_2.

The contribution of CO_2 from the soil to the total CO_2 amount at any height within the forest stand is designated by $M_s(h)$. The corresponding contribution of the free atmosphere is $M_{atm}(h)$ and γ_s, γ_{atm} and γ'_s, γ'_{atm} represent the fractions of ^{12}C and ^{13}C respectively. Therewith the following relations hold

$$\gamma = {}^{12}C/({}^{12}C + {}^{13}C); \qquad \gamma' = {}^{13}C/({}^{12}C + {}^{13}C); \qquad (1\,a, b)$$

$$\gamma + \gamma' = 1; \qquad M_s + M_{atm} = M_{l,a} \qquad (1\,c, d)$$

where ^{12}C and ^{13}C are the concentrations of the isotopes of each source if the appropriate subscripts are heeded and $M_{l,a}(h)$ is the total amount of CO_2 in the vicinity of leaves at height h.

The fraction of ^{12}C in the vicinity of any leaf of a forest tree $\gamma_{l,a}$ is given by

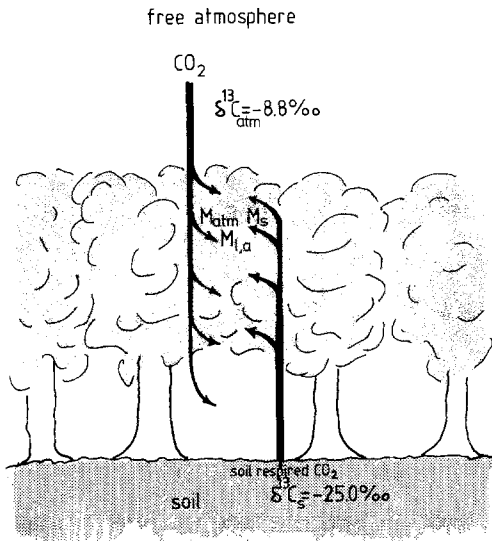$$\gamma_{l,a} = \frac{M_s \gamma_s + M_{atm} \gamma_{atm}}{M_s + M_{atm}}. \qquad (2)$$

Fig. 1. Schematic flux distribution of CO_2 in a forest. M_{atm} and M_s represent the contributions of CO_2 from the free atmosphere and the soil respectively. $M_{l,a}$ stands for the actual CO_2 concentration in the vicinity of leaves, i.e. the mixture of CO_2 from the free atmosphere and the soil

Since the same relation holds for $\gamma'_{l,a}$, the ratio of the two fractions is

$$\frac{\gamma'_{l,a}}{\gamma_{l,a}} = \frac{M'_s \gamma'_s + M'_{atm} \gamma'_{atm}}{M_s \gamma_s + M_{atm} \gamma_{atm}} = \frac{^{13}C_{l,a}}{^{12}C_{l,a}} = R_{l,a}. \tag{3}$$

From Eqs. (1 d) and (3) follows

$$\frac{M_s}{M_{l,a}} = \frac{R_{atm} - R_{l,a}}{(R_{atm} - R_{l,a}) + (R_{l,a} - R_s)\, \gamma_s/\gamma_{atm}} \tag{4}$$

Heeding Eqs. (1 b, c) and keeping in mind that $\gamma'_{atm} \ll 1$ and $\gamma'_s \ll 1$, γ_s/γ_{atm} can be expressed to a good approximation by

$$\frac{\gamma_s}{\gamma_{atm}} = \frac{1 - \gamma'_s}{1 - \gamma'_{atm}} \simeq (1 - \gamma'_s)(1 + \gamma'_{atm}) \simeq (1 - R_s + R_{atm}). \tag{5}$$

In plant physiology ^{13}C values are normally expressed in terms of the δ-notation, by which the unknown ^{13}C value, stated as carbon isotope ratio $^{13}C/^{12}C$, is compared with the $^{13}C/^{12}C$ standard as given by the PDB-formation (Craig 1957).

$$\delta^{13}C(^o/oo) = \left[\frac{R_{sample} - R_{PDB}}{R_{PDB}} \right] \cdot 10^3. \tag{6}$$

Equation (4) can then be rewritten by using Eqs. (5, 6)

$$\frac{M_s}{M_{l,a}} \simeq \frac{(\delta^{13}_{atm} - \delta^{13}_{l,a})}{(\delta^{13}_{atm} - \delta^{13}_s) + 10^{-3} \cdot (\delta^{13}_{l,a} - \delta^{13}_s) \cdot (\delta^{13}_{atm} - \delta^{13}_s) \cdot R_{PDB}}. \tag{7}$$

For simplicity reasons the symbol C has been dropped from the δ-notation. The second term of the denominator from Eq. (7) represents only a negligible contribution to the first term. For the present investigations the following relations hold

$$-30^o/oo \leqq \delta^{13}_s \leqq -24^o/oo$$

$$-10^o/oo \leqq \delta^{13}_{atm} \leqq -7^o/oo$$

$$-15^o/oo \leqq \delta^{13}_{l,a} \leqq -10^o/oo$$

which lead to

$$(\delta^{13}_{l,a} - \delta^{13}_s) \cdot (\delta^{13}_{atm} - \delta^{13}_s) \cdot 10^{-3}) \cdot R_{PDB} \leqq 0.46 \cdot R_{PDB}$$
$$\leqq 0.00518.$$

This is far less than the experimental error of δ-values and can be discarded in Eq. (7). Therefore the contribution of soil respired CO_2 to the total amount of CO_2 which is photosynthetically fixed within a forest stand at a particular height is given by

$$\frac{M_s}{M_{l,a}} \simeq \frac{\delta^{13}_{atm} - \delta^{13}_{l,a}}{\delta^{13}_{atm} - \delta^{13}_s} \tag{8}$$

where $\delta^{13}_{l,a}$ is a function of height. The knowledge of δ^{13}_{atm}, $\delta^{13}_{l,a}$ and δ^{13}_s therefore allows an estimate of the reassimilated CO_2 from the soil and this may also apply to any agricultural stand.

There is no problem in determining δ^{13}_{atm} and δ^{13}_s because they can easily be deduced from direct measurements. The evaluation of $\delta^{13}_{l,a}$ however causes problems because directly determined ^{13}C values at a particular height may not be representative. Turbulent and stagnant air conditions may frequently change and therefore only a large number of measurement might offer an estimate of $\delta^{13}_{l,a}$.

An indirect approach seems to be more appropriate for the present problem. It is known that the ^{13}C content of leaves reflects an averaged ^{13}C content of their immediate surrounding. If the physiological state of the leaves considered is fairly constant, this may reflect an averaged value over weeks.

According to Schleser and Jayasekera (1984) the relation between the ^{13}C content of leaves δ^{13}_b and the ^{13}C values of the surrounding atmosphere $\delta^{13}_{l,a}$ can be stated as

$$\delta^{13}_b = \delta^{13}_{l,a} + \varepsilon_D \cdot \left(1 - \frac{C_i}{C_{atm}}\right) + \left(\varepsilon_p - \varepsilon_R \cdot \frac{R}{P}\right) \cdot \frac{C_i}{C_{atm}}$$
$$- \varepsilon_t \cdot \frac{R}{P} \cdot \frac{C_i}{C_{atm}} \tag{9}$$

(see also Francey and Farquhar 1982).

In Eq. (9) ε_D represents the fractionation for diffusion from the surface of a leaf through the stomata and the membranes into the chloroplasts. ε_p is the kinetic fractionation for the process of CO_2 fixation by ribulose-1,5-bisphosphate carboxylase, ε_R the kinetic fractionation for total respiration and ε_t is the fractionation value of the carbon isotopes during the export of organic material out of a leaf. R represents the respiration of a leaf, P stands for gross photosynthesis and C_i and C_{atm} represent the internal and external CO_2 concentration of a leaf respectively.

The last term of Eq. (9) is of minor importance and will be discarded for the present evaluations (Schleser and Jayasekera 1984). Inserting $\delta^{13}_{l,a}$ of Eq. (9) into Eq. (8) results in

$$\frac{M_s}{M_{l,a}} \simeq \frac{\delta^{13}_{atm} - \delta^{13}_b + \varepsilon_D \left(1 - \frac{C_i}{C_{atm}}\right) + \left(\varepsilon_p - \varepsilon_R \frac{R}{P}\right) \frac{C_i}{C_{atm}}}{\delta^{13}_{atm} - \delta^{13}_s}. \tag{10}$$

If the physiological state of the leaves is known, i.e. C_i/C_{atm}, R/P and δ^{13}_b has been measured, the contribution of soil respired CO_2 to the total amount of photosynthetically fixed CO_2 at any height can be deduced, provided the fractionations ε are known.

In order to evaluate the total contribution of soil re-

spired CO_2 of a forest tree, its total assimilation has to be known as a function of height. For the present problem the normalized assimilatory performance $A_n(h)$ of the tree will suffice if the following conditions are met

$$A_n(h) = \begin{cases} 0; & \text{below the lowest reaching leaves} \\ & \quad \text{(boundary } l) \\ A(h); & \text{heeding sun and shade leaves} \\ 0; & \text{above the highest reaching leaves} \\ & \quad \text{(boundary } t) \end{cases}$$

and

$$\int_l^t A_n(h) \cdot dh = 1.$$

The total amount of reassimilated CO_2 from the soil, $A_{s,t}$, as related to the overall assimilation of CO_2 within a forest stand is then given by

$$A_{s,t} = \int_l^t \{A_n(h) \cdot [M_s/M_{l,a}]\} \cdot dh \tag{11}$$

which finally leads to

$$A_{s,t} = \int_l^t \left[A_n(h) \frac{\delta_{atm}^{13} - \delta_b^{13} + \varepsilon_D \left(1 - \frac{C_i}{C_{atm}}\right) + \left(\varepsilon_p - \varepsilon_R \cdot \frac{R}{P}\right) \frac{C_i}{C_{atm}}}{\delta_{atm}^{13} - \delta_s^{13}} \right] \cdot dh. \tag{12}$$

where δ_b^{13} is a function of height. In general it has to be assumed that the physiological state of the leaves as given by C_i/C_{atm} and R/P is also a function of height.

Material and methods

The experiments have been performed during the growing season of 1982. A beech tree (*Fagus sylvatica L.*) from the forest of Hambach near Jülich, Federal Republic of Germany, served as research object. A solitary lime tree (*Tilia tomentosa Moench*), growing in a plain near Jülich at a somewhat elevated position, was used for comparative studies.

Roughly 200 leaves from each height of a tree were pooled for a sample. After careful cleaning of the leaf surfaces, 50 from each sample, selected at random, served for specific leaf weight determinations. Afterwards the material was dried in a vacuum oven at 60° C.

The carbon content of each sample was analyzed by combusting the material in an oxygen gas stream at 1000° C and measuring the liberated CO_2 amount coulometrically. Nitrogen was determined according to the method of Dumas. Mg and K were measured by ICP emission spectroscopy. Relative errors amount to $\pm 0.5\%$ for C, $\pm 1\%$ for N, $\pm 2\%$ for Mg and about 3% for K.

Dried leaf material was combusted in an excess of oxygen and the resulting CO_2 was taken for isotope analysis using a MAT 250 mass spectrometer (Schleser and Pohling 1980). Air samples were collected in evacuated 2.5 l flasks. CO_2 was separated from the other air components in a vacuum line and then measured on the mass spectrometer. Soil respired CO_2 was daily collected in glass flasks via stainless steel cylinders which are permanently inserted in the soil. The CO_2 of these flasks has likewise been separated in a vacuum line from the other components and then been

isotopically analyzed. Results are reported in terms of $\delta^{13}C$ relative to PDB (Craig 1957). Sample replication, including all errors of sample preparation, amounted to $\pm 0.12\%_{oo}$.

Results and discussion

$\delta^{13}C$ variations of leaf material from different heights of two beeches and a solitary standing lime are shown in Fig. 2. The forest trees exhibit a strong correlation between $\delta^{13}C$ values and the corresponding tree heights, with correlation coefficients r^2 of 0.968 and 0.935 respectively, while the correlation for the lime tree is less pronounced ($r^2 = 0.736$). The leaves of the beech harvested in 1982 reveal a difference of about $5\%_{oo}$ from bottom to top of the tree (slope $\simeq 4.5$ m/$\delta^{13}C$) and the leaves of the lime show a difference of $2.5\%_{oo}$ (slope $\simeq 5.5$ m/$\delta^{13}C$).

While the forest trees exhibit a continuous increase of the ^{13}C concentration with height, the corresponding increase of the solitary standing lime seems to proceed stepwise. Since it has to be assumed that the source for the lime tree, i.e. the ^{13}C concentration of atmospheric CO_2, has been identical for all heights, except for leaves at 0.5 m height, near constancy of $\delta^{13}C$ data for particular height segments may indicate near constancy of the physiological state of leaves from these heights (see Eq. (9)), thus probably indicating similar microclimatological conditions. Contrary thereto it can be argued that the observed differences in $\delta^{13}C$ are solely indications of different physiological states of leaves. In forests these effects could be masked by a certain stratification pattern of soil respired CO_2 which leads to different ^{13}C sources for the leaves.

In view of the relationship for $A_{s,t}$, as expressed by Eq. (12), four points have to be considered:
1. $^{13}C/^{12}C$ composition of the free atmosphere, i.e. δ_{atm}^{13}
2. δ_s^{13} values of soil respired CO_2
3. the physiological state of the leaves, and
4. the assimilatory performance of the tree, i.e. $A_n(h)$.

1. $^{13}C/^{12}C$ composition of CO_2 above the canopy

The $\delta^{13}C$ value of atmospheric CO_2 has been determined above the canopy and resulted in a value of $\delta_{atm}^{13} = -8.8\%_{oo}$. Since changes of the averaged atmospheric daytime $\delta^{13}C$ value for a restricted time period are not expected to be large, δ_{atm}^{13} has only once been determined. For the interpretation of the following results it is assumed that atmospheric CO_2 did not alter its ^{13}C content for a number of weeks.

2. δ_s^{13} values of soil respired CO_2

Degradation of soil organic matter resulted in a CO_2 flux of about 120 mg/m^2h. This value prevailed for well over 2 weeks with slight fluctuations of about ± 15 mg CO_2/m^2h and at the end of this period leaves from different heights were harvested. The corresponding $\delta^{13}C$ value of the respired CO_2 was $\delta_s^{13} = -25\%_{oo}$. It should be noted, however, that δ_s^{13} values are not constant over the growing season. Differences of more than $2\%_{oo}$ have been measured from May to October. Therefore it is necessary to correlate δ_s^{13} values with leaf δ_b^{13} values of about the same time.

3. Physiological state of leaves

It would be easiest to deduce the contribution of soil respired CO_2 to the total assimilation, if the leaves of a tree
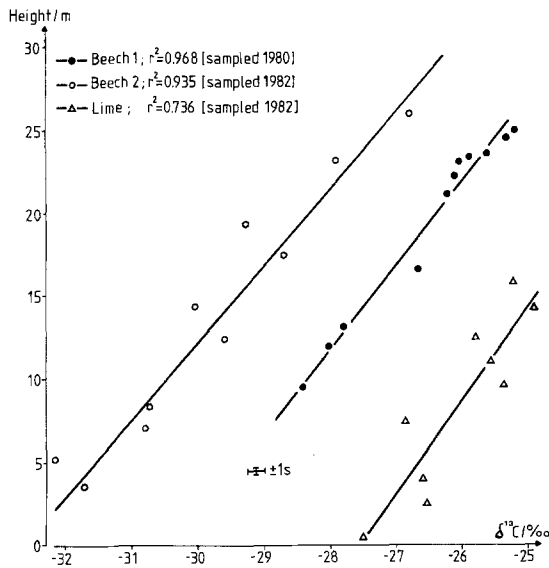
Fig. 2. $\delta^{13}C$ values of leaf material from different heights. Two beeches of a forest and a solitary standing lime have been analyzed
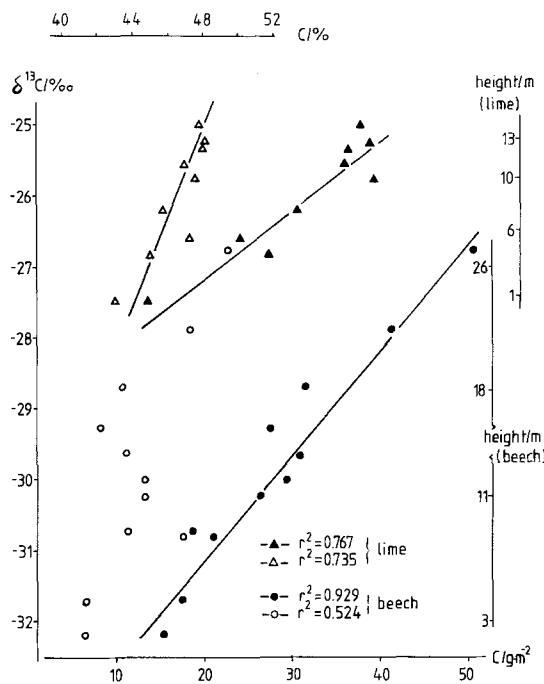

Fig. 3. Carbon concentration (open symbols) and area weight (solid symbols) related to $\delta^{13}C$ and tree height. A forest beech and a solitary standing lime have been analyzed (r^2 refers to $\delta^{13}C$)

Fig. 4. Nitrogen concentration (open symbols) and area weight (solid symbols) related to $\delta^{13}C$ and tree height. A forest beech and a solitary standing lime have been analyzed (r^2 refers to $\delta^{13}C$)

would photosynthetically behave identically, independent of their position. In this case differences in δ_b^{13} would directly reflect changes of the carbon source, i.e. changes of $^{13}C_{atm}$ because the physiological parameters such as C_i/C_{atm} and R/P of leaves from different heights would cancel (Eq. (9)).

However this assumption, which has implicitly been made by Vogel (1978) and Medina (1980), is unlikely to be correct, though it is open at present to what extent such a supposition might affect the results. The data of the soli-
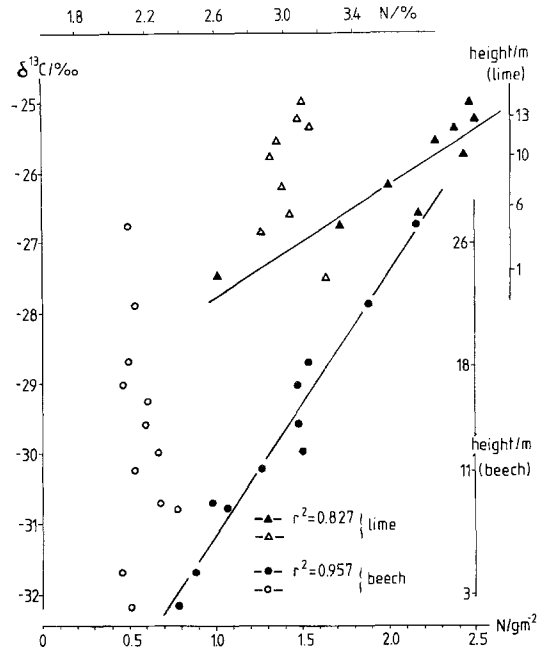
tary standing lime, as shown in Fig. 2, clearly demonstrate that $\delta^{13}C$ variations may also occur in case of a constant ^{13}C source for all leaves. In fact leaves from different positions of a tree do not behave identically, since they exhibit strong structural and compositional differences (e.g. Jackson 1966; Björkman 1981). Figures 3 and 4 show that the concentrations of carbon and nitrogen per unit area increase by a factor of 3 with height, though the corresponding amount per unit weight is almost constant. This implies variable mesophyll cell surface areas for differently positioned leaves which should lead to variable mesophyll resistances. A greater surface area most likely promotes a better transfer of CO_2 to the reaction sites in the chloroplasts. Consequently the internal concentration of CO_2, i.e. C_i, should be affected and hence δ_b^{13}, independent of δ_{atm}^{13}.

Nitrogen occupies a special position among the elements involved in photosynthesis. Its importance is indicated by the rather high nitrogen content of chloroplasts (Stocking and Ongun 1962) and it is known that the nitrogen content correlates with the rate of photosynthesis (Ojima and Kawashima 1968; Oda and Kawata 1970; Mooney et al. 1978). From Fig. 4 it therefore follows that the rate of photosynthesis per unit area should increase about threefold from bottom to top of the beech tree. This agrees quite well with measurements by Schulze (1970) who determined net assimilation rates of $\approx 4{,}150$ mg $CO_2/$ $dm^2 yr^{-1}$ for sun leaves compared to $\approx 1{,}730$ mg $CO_2/$ $dm^2 yr^{-1}$ for shade leaves of a forest beech. In principle this is to be expected on the basis of leaf area if the composition of components inside the leaves that determine the capacity of photosynthesis increases with increasing leaf thickness. Since the diffusion resistance to CO_2 increases with leaf thickness the internal CO_2 concentration of leaves should decrease with tree height especially for high photosynthetic rates.

The stomatal resistance to CO_2 could however be similar for leaves of different heights because the potassium
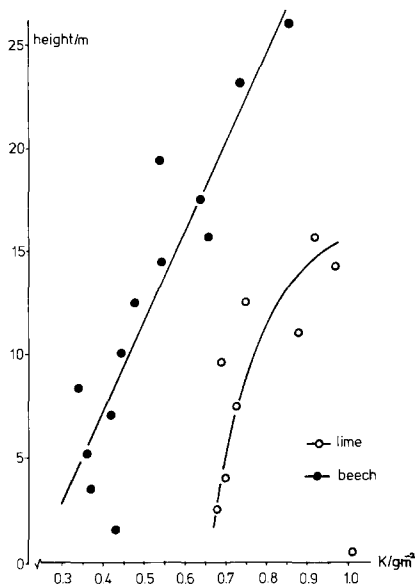
Fig. 5. Tree height vs. area weight of potassium in leaf material from a beech and a lime
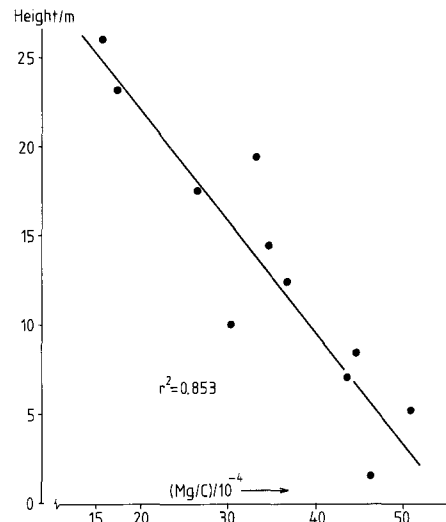

Fig. 7. Tree height vs (Mg/C) of leaf material from a forest beech
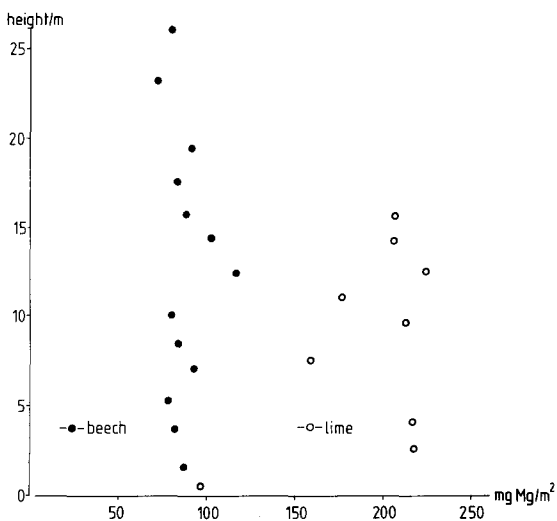

Fig. 6. Tree height vs. area weight of Mg in leaf material of a forest beech and a solitary standing lime

concentration per unit area increases by about the same factor as nitrogen (Fig. 5) and potassium seems to be essential for stomatal opening (cf. e.g. Humble and Hsia 1969).

Mg^{2+} is essential as a cofactor for the activation of RuBP carboxylase (Lorimer 1981) and exerts a strong influence on the kinetic isotope effect of the enzyme (Winkler et al. 1982; Estep et al. 1978). In vitro experiments showed an increasing discrimination of ^{13}C during CO_2 fixation with rising Mg^{2+} concentrations. It is noteworthy however to realize that Mg per unit area remains practically constant (Fig. 6), with deviations of roughly ±10% from the mean. The same is true for the lime tree, though scatter and magnitude of the Mg concentration are much larger. Related to C a strong decrease of Mg results from bottom to top of the beech tree (Fig. 7) which might indicate that δ_b^{13} changes are to be expected from bottom to top of the investigated tree irrespective of changes of the atmospheric ^{13}C concentration.

In summary it can be concluded that differences in the physiological state of the foliage exist as a function of height and these differences are likely to contribute to the variations of $\delta^{13}C$ from leaf material.

From Eq. (12) it is evident that the ratios of R/P and C_i/C_{atm} have to be known as a function of tree height. However no approach could be made to deduce these ratios. Therefore the following assumptions have been made for the subsequent calculations:

a) $C_i/C_{atm} = 0.65$ at medium height of the beech tree (Whiteman and Koller 1967; Wong et al. 1979) and

b) $R/P = 0.3$ likewise at medium height of the tree.

Higher rates of photosynthesis and transpiration on top of the canopy are likely to reduce C_i relative to leaves from the lower strata. Furthermore the assimilatory performance per unit of area of sun leaves is much higher than the corresponding value for shade leaves (Schulze 1970). Therefore it will be assumed that the stated values decrease from bottom to top of the tree varying linearly by ±5% around the medium height values.

4. The contribution of soil respired CO_2

The normalized assimilatory function $A_n(h)$ of the beech has been deduced from the shape of the tree and the observations by Schulze (1970) that the ratio of the assimilation rates of sun and shade leaves varies with the growing season. Figure 8 shows the corresponding assimilatory performance of the beech tree. (The analytical form is given in the appendix.)

C_i/C_{atm} and R/P had to be estimated. Nevertheless it is of interest to compare the corresponding results with evaluations which assume that C_i/C_{atm} and R/P are independent of tree height.

4.1. Assumption of constant physiological values. According to Eq. (9), discarding the last term, the $\delta_{l,a}^{13}$ value in the vicinity of the leaves is given by
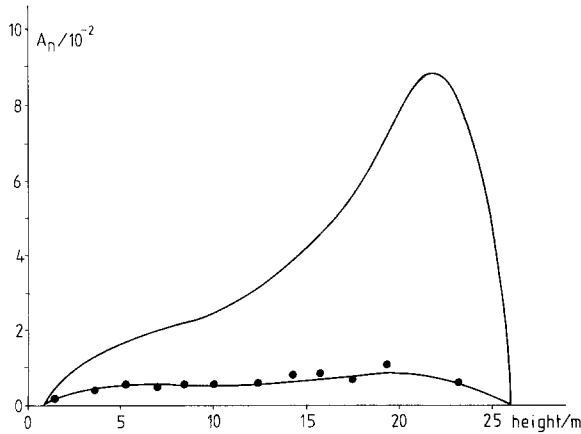
Fig. 8. Normalized assimilatory performance A_n of a forest beech. The points and the corresponding curve represent the soil respired contribution of assimilated CO_2, neglecting physiological differences of the leaves with height. For details cf. text

$$\delta_{l,a}^{13} = \delta_b^{13} - \varepsilon_D \left(1 - \frac{C_i}{C_{atm}}\right) - \left(\varepsilon_p - \varepsilon_R \cdot \frac{R}{P}\right) \frac{C_i}{C_{atm}}. \quad (13)$$

On top of the canopy the source of ^{13}C will very nearly be the free atmosphere. With Eq. (13) the ratio of $M_s/M_{l,a}$ as given by Eq. (8) will therefore result in

$$\frac{M_s}{M_{l,a}} \simeq \frac{\delta_{bo}^{13} - \delta_b^{13}(h)}{\delta_{atm}^{13} - \delta_s^{13}}. \quad (14)$$

With δ_{bo}^{13} being the value of leaf material from the top of the canopy. Introducing Eq. (14) into Eq. (11) results in

$$A_{s,t} \simeq \int_1^{26} A(h) \cdot \frac{\delta_{bo}^{13} - \delta_b^{13}(h)}{\delta_{atm}^{13} - \delta_s^{13}} dh. \quad (15)$$

Since $\delta_b^{13}(h)$ is a linear function with height, the same is true for the second factor in the integral of Eq (15). The corresponding linear regression analysis leads to the following form for $A_{s,t}$

$$A_{s,t} \simeq \int_1^{26} A(h) \cdot \{0.352 - 0.0123\,h\}\, dh. \quad (16)$$

The argument of this integral represents the contribution of soil respired CO_2 to the total assimilation as a function of height.

Integration of Eq. (16) finally results in

$$A_{s,t} \simeq 0.14$$

which implies that under the preceding assumptions the contribution of soil respired CO_2 to the total assimilation of the investigated beech tree amounts to 14%. The contribution of soil respired CO_2 as a function of height is given in Fig. 8. From Eq. (16) also follows that in the region of 1 to 5 m height, i.e. the lowest strata of the canopy, 35% of the assimilated CO_2 originate from the soil.

4.2. Influence of C_i/C_{atm} and R/P. The evaluation of Eq. (12) requires a knowledge of the fractionations ε. According to Vogel (1980) a value of $-4.2^o/oo$ has been used for ε_D, while ε_p has been fixed at $-30^o/oo$ (Winkler et al. 1982). Up to now the question has not been satisfactorily answered what isotope fractionation occurs with respiration. For the present calculations a value of $-7^o/oo$ has been used (Schleser 1984).

With these data the integration of Eq. (12) leads to

$A_{s,t} \simeq 0.05.$

From this result follows that a consideration of physiological variations of leaves may considerably change the expected assimilatory contribution of soil respired CO_2. Under the assumptions made the contribution drops by almost 65%. These figures may not be reliable because of the uncertainty of the data base, however they are in line with the fact that the solitary standing lime also exhibits $\delta^{13}C$ variations with height which can only be due to physiological differences of the leaves.

For the lower part of the canopy, i.e. from 1–5 m height, the corresponding contribution amounts to 22% which is also much lower compared to calculations in which constancy of the physiological parameters of leaves was assumed.

Conclusions

$\delta^{13}C$ variations in tree leaves of a forest may be an indication of atmospheric ^{13}C changes within a forest stand, provided the corresponding physiological parameters of the leaves are known and exact fractionation values ε are at hand.

The results obtained suggest that neglecting differences of leaves from bottom to top of a tree leads to an overestimation of the contribution of soil respired CO_2. Values that have been worked out on the basis of constant physiological parameters may at best provide an upper limit of the assimilatory contribution of soil respired CO_2.

It is difficult to value the exactness of the differences obtained because the consideration of the physiological state of leaves is connected with a number of assumptions that may be too crude. In addition the fractionations ε are not yet very reliable either, except for ε_D.

Once these difficulties have been overcome, $\delta^{13}C$ values of leaves could even be used for a characterization of the physiological state of leaves if the ^{13}C source is kept constant.

Appendix

The analytical form of the assimilatory performance as shown in Fig. 8, heeding the condition

$$\int_1^{26} A_n(h) \cdot dh = 1$$

is given by

$$A_n(h) = \begin{cases} 0; & 0 \leq h \leq 1 \text{ m} \\ 0.0080\sqrt{(h-h_1)/h_1}, & 1 \leq h \leq 9 \text{ m} \\ 0.0233[(h-h_2)/h_2]^2 + 0.0126[(h-h_2)/h_2] \\ \quad + 0.0226; & 9 \leq h \leq 18 \text{ m} \\ -2.877[(h-h_3)/h_3]^3 + 0.718[(h-h_3)/h_3]^2 \\ \quad + 0.118[(h-h_3)/h_3] + 0.0585; & 18 \leq h \leq 26 \text{ m} \\ 0; & h \geq 26 \text{ m} \\ h_1 = 1 \text{ m}; \quad h_2 = 9 \text{ m}; \quad h_3 = 18 \text{ m}. \end{cases}$$

In order to receive a smoothed curve for $A_n(h)$ the following conditions had to be met:

$$dA_n/dh\|_i = dA_n/dh\|_j \quad (i = 1, 2; j = i+1).$$

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