A compartmental model of carbon allocation in the vegetative barley plant

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Abstract. The allocation of carbon in a vegetative barley plant is described as an open, three-compartment model; the three compartments are soluble (which exchanges material with the environment), storage, and structure (both of which exchange material with the soluble compartment). The model shows a good fit with data on \(^{14}\)C kinetics following \(^{14}\)CO\(_2\) feeding and some of its assumptions, properties and implications are discussed.

Key-words: Hordeum distichum; Gramineae; barley; compartmental; model; carbon.

Introduction

Models of plant growth developed by several groups of workers have been based on the assumption that the products of photosynthesis accumulate in an assimilatory pool, the size of which determines the rate at which materials are withdrawn from it and used for production of structural material (Loomis, Rabbinge & Ng, 1979; de Wit, 1978; Thornley, 1977; Charles-Edwards, 1979). Such models have proved useful in spite of the fact that this assumption has not been tested. This paper attempts such a test by applying a compartmental analysis, in which this assumption is implicit, to data on carbon allocation in the barley plant.

General accounts of compartmental analysis are available (e.g. Atkins, 1969; Shipley & Clark, 1972), and comparable compartmental models have previously been applied to export of carbon from leaves (Moorby & Jarman, 1975), carbon flow in photosynthesis (Pearlman & Lawlor, 1981), and carbon allocation in a lichen (Farrar, 1978). The present work has two particular features: firstly, the barley plants used are growing actively and thus compartment sizes are continually changing; and secondly, rather than examine isotope efflux data only, compartment specific activity is followed.

Model description

The model considers the plant to consist of three compartments, with the environment represented by a fourth. All exchange of material, both between compartments and with the environment, occurs through the soluble compartment. The environmental compartment is assumed to have constant mass equal to \(P_g/k_{g1}\), where \(P_g\) is gross photosynthesis less photorespiration. Transfer of material from the environment is therefore governed by zero-order rate kinetics. All other exchanges follow first-order rate kinetics and rates of change of mass for the three plant compartments are described by the following equations:

\[
\frac{dQ_1}{dt} = P_g + k_{13}Q_3 + k_{12}Q_2 - k_{01}Q_1 - k_{31}Q_1 - k_{21}Q_1
\]

\[
\frac{dQ_2}{dt} = k_{21}Q_1 - k_{12}Q_2
\]

\[
\frac{dQ_3}{dt} = k_{31}Q_1 - k_{13}Q_3
\]

(For symbols, see the legend to Fig. 1.) Similar equations can be written for the tracer in each compartment.

The data used have been discussed previously (Farrar, 1980b). Barley plants grown in constant environments were fed \(^{14}\)CO\(_2\) for 30 min when about 10 d old and harvested sequentially over the following 5–14 d. They were divided into three fractions (see below) and the weight and \(^{14}\)C content of each determined. These data are in substantial agreement with those of Gordon, Ryle & Powell (1977, 1979). The model compartments are derived experimentally as follows: \(Q_1\), soluble = neutral material soluble in 95% ethanol (mainly sucrose and free hexoses); \(Q_2\), storage = neutral material soluble in amylase/glucosidase at pH 4.5 (mainly starch and fructosans); \(Q_3\), structure = insoluble and charged material (including cell walls, lipids, and most amino-acids and proteins). Non-respiratory \(^{14}\)C loss from the roots never
the initial sample time. Different integration step-sizes were also used and a simplified two-compartment model was investigated in which soluble and storage were combined to give a single compartment, exchanging material with both the environment and the structural compartment.

Examples of the fit, given in Table 1 and Fig. 2, show good fit of the model to the experimental data. Results presented in Table 2 show that the values of rate constants were (except at 15°C in the light) relatively unaffected by step-size and insertion of an extra data point; errors for the two-compartment model were similar to those for the three-compartment model.

![Diagram](image)

Table 1. Rate constants (d⁻¹) generated by fitting the model to experimental data, using a step-size of 0.025 d. The error term is the sum of the square of differences between experimental and fitted values. The meaning of the rate constants is given in Fig. 1.

<table>
<thead>
<tr>
<th>Growth conditions</th>
<th>( k_{10} )</th>
<th>( k_{01} )</th>
<th>( k_{21} )</th>
<th>( k_{12} )</th>
<th>( k_{31} )</th>
<th>( k_{13} )</th>
<th>Error (×10⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10°C, light</td>
<td>0.0032</td>
<td>0.99</td>
<td>1.93</td>
<td>0.82</td>
<td>0.049</td>
<td>0.11</td>
<td>0.29</td>
</tr>
<tr>
<td>15°C, light</td>
<td>0.0009</td>
<td>0.57</td>
<td>11.29</td>
<td>14.66</td>
<td>0.19</td>
<td>0.38</td>
<td>0.014</td>
</tr>
<tr>
<td>20°C, light</td>
<td>0.0003</td>
<td>2.07</td>
<td>0.34</td>
<td>1.66</td>
<td>0.26</td>
<td>1.98</td>
<td>0.001</td>
</tr>
<tr>
<td>30°C, light</td>
<td>0.023</td>
<td>4.14</td>
<td>0.74</td>
<td>1.64</td>
<td>0.073</td>
<td>0.24</td>
<td>1.1</td>
</tr>
<tr>
<td>15°C, dark</td>
<td>0.0002</td>
<td>1.82</td>
<td>2.17</td>
<td>1.53</td>
<td>0.20</td>
<td>0.69</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Experiments were conducted in the light at four temperatures, and in the dark at one temperature. Rate constants for respiratory loss from the soluble compartment showed a general rise with temperature, but the other rate constants showed high variability and little pattern (Table 1). Thus movement to and from the storage pool at 15°C (\( k_{12} \) and \( k_{21} \)) is unaccountably higher than at other temperatures. The rate constants for loss of structural material (\( k_{13} \)) are particularly hard to interpret; they seem higher than the literature would suggest, since protein, which constitutes about 25% of this fraction (Farrar, unpublished), has a turnover rate of about 0.1–0.2 d⁻¹ (Penning de Vries, 1975).

Part of the variability may be due to the time course of the experiments being long in comparison with the main changes in isotope distribution between compartments, giving undue weighting to small and statistically insignificant changes in pool labelling towards the end of the experimental period.

Given this high variability, it would seem safest to believe that darkening has no major effect on the rate constants.

**Model predictions**

The model can be used to predict dark respiration rates; since these were not used in obtaining compartment sizes and rate constants, the degree of agreement between predicted and experimental data should provide an independent test of the model.
Figure 2. The model fitted to specific activity data collected for barley plants grown in continuous light at 10°C and fed 14CO2 for 30 min when 10 d old. The three-compartment model was simulated using a step size of 0.01 d. The data points are derived by experiment and the continuous lines are best fits offered by the model; each point is the mean of three replicates and the bars denote one standard error each side of the mean.

Table 2. The effects of changing step-size (s.s.), inserting extra initial values, and lumping soluble and storage compartments, on rate-constants (d⁻¹) generated by fitting the model to experimental data. The error term is the sum of the square of differences between experimental and fitted values.

<table>
<thead>
<tr>
<th>Model</th>
<th>Temperature °C</th>
<th>k₁₀</th>
<th>k₀₁</th>
<th>k₂₁</th>
<th>k₁₂</th>
<th>k₃₁</th>
<th>k₁₃</th>
<th>Error (× 10⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Three-compartment</td>
<td>10</td>
<td>0.0029</td>
<td>0.94</td>
<td>2.03</td>
<td>0.87</td>
<td>0.05</td>
<td>0.12</td>
<td>0.36</td>
</tr>
<tr>
<td>s.s. = 0.025 d</td>
<td>15</td>
<td>0.0005</td>
<td>0.46</td>
<td>6.83</td>
<td>8.31</td>
<td>0.17</td>
<td>0.32</td>
<td>0.16</td>
</tr>
<tr>
<td>Extra initial value</td>
<td>30</td>
<td>0.022</td>
<td>3.95</td>
<td>0.74</td>
<td>1.68</td>
<td>0.07</td>
<td>0.23</td>
<td>1.23</td>
</tr>
<tr>
<td>Three-compartment</td>
<td>10</td>
<td>0.003</td>
<td>0.95</td>
<td>2.03</td>
<td>0.87</td>
<td>0.049</td>
<td>0.12</td>
<td>0.32</td>
</tr>
<tr>
<td>s.s. = 0.01 d</td>
<td>15</td>
<td>0.0008</td>
<td>0.51</td>
<td>1.11</td>
<td>1.65</td>
<td>0.24</td>
<td>0.62</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>0.022</td>
<td>4.03</td>
<td>0.75</td>
<td>1.71</td>
<td>0.072</td>
<td>0.23</td>
<td>1.13</td>
</tr>
<tr>
<td>Two-compartment</td>
<td>10</td>
<td>0.007</td>
<td>0.54</td>
<td>0.017</td>
<td>0.13</td>
<td>1.41</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s.s. = 0.025 d</td>
<td>15</td>
<td>0.0006</td>
<td>0.25</td>
<td>0.078</td>
<td>0.3</td>
<td>0.12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Extra initial value</td>
<td>30</td>
<td>0.017</td>
<td>2.07</td>
<td>0.043</td>
<td>0.20</td>
<td>1.87</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Specific dark respiration rate \( R \) is given by

\[
R = \frac{(Q₁ \cdot k₀₁)}{(Q₁ + Q₂ + Q₃)}
\]

and \( R \) can be predicted for each temperature studied, using measured values of \( Q₁ \) and the value for the rate constant obtained as described above. The predicted values are encouragingly close to measured ones (Table 3).

There are other properties of this model common to a variety of multicompartment models. Thus the declining respiratory loss of 14CO2 in the light, or the net loss of CO2 in the dark, would be described as a sum of three (in this case) exponential terms. At least two such exponential terms are seen in the falling rate of 14CO2 evolution in barley (Ryle, Cobby & Powell, 1976; Farrar, 1980b). Similarly, a compartmental system of this kind can be shown, by straightforward simulation, to be capable of generating changes in pool sizes of the type observed, say after darkening barley plants.

Thus the ability to fit the model to data points, and the successful predictions of respiration rate, lend confidence to the general utility of the model, which can also account for observed changes in pool sizes and respiratory 14CO2 loss due to its compartmental nature.

Validity of model assumptions

The model proposed is such a gross oversimplification of the barley plant that it is clearly not completely valid; the proper question is whether its assumptions...
Table 3. Specific dark respiration rates as predicted by the model for 10-day-old barley, using the rate constants of Table 1, and as measured on whole plants. Respiration rates were measured as described by Farrar (1980b), and are for whole plants grown in solution culture.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Predicted (g plant dry weight⁻¹ h⁻¹)</th>
<th>Measured (g plant dry weight⁻¹ h⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>6.7</td>
<td>4.0</td>
</tr>
<tr>
<td>15</td>
<td>4.2</td>
<td>6.2</td>
</tr>
<tr>
<td>20</td>
<td>6.3</td>
<td>9.0</td>
</tr>
<tr>
<td>30</td>
<td>30.0</td>
<td>14.3</td>
</tr>
</tbody>
</table>

are sufficiently fulfilled to make it useful. The assumptions are these:

(1) The tracer is a ‘perfect’ tracer. Whilst plant metabolism can discriminate between C-14 and C-12 to some extent, this is normally assumed to be of little quantitative importance (Yemm & Bidwell, 1969).

(2) Each compartment is homogeneous. This is where the model simulates most drastically. Not only do these compartments consist of discrete chemical species, they also refer to the complex of roots, leaves, tissues and subcellular compartments that is the whole plant. At least for the soluble and storage pools, we are dealing with rather few major compounds—sucrose in the former case and starch and fructosans in the latter. There is evidence that the soluble compartment shows at least a two-component decay in specific activity (Farrar, 1980b) which is consistent both with this compartment being heterogeneous, and it being a homogeneous component in a two- or more compartment system.

(3) Each compartment is well mixed, that is, the mixing time is very small compared with the residence time of a molecule in the compartment. The compartment that should fit this criterion the most closely is the soluble one, since it is through this that all exchanges take place. The half-time of a molecule in this compartment can be estimated by $0.693/(k_{01}+k_{31}+k_{33})$, $\approx 0.3$ d; or the average residence time of a molecule by $1/(k_{01}+k_{31}+k_{33})$, $\approx 0.4$ d (Table 4). Mixing times thus need to be of the order of, say, 2 h at most; the slowest mixing process may be phloem transport, which proceeds at about 60 cm h⁻¹ (Moody, 1977) and as these plants never exceeded 50 cm from root to leaf tip, sucrose can travel the length of the plant in less than 1 h; at the end of a 30 min $^{14}$CO₂ feeding period, root apical meristems of 10 d barley plants contain $^{14}$C (Ower, Farrar & Whitbread, unpublished). However, it would be surprising if complete mixing of this compartment did occur. This is still more true for the storage and structural compartments.

(4) The transfer of material is governed by first-order rate kinetics (i.e. the rate of loss of material from a pool is proportional to the size of the pool). Since this assumption is central to several models of crop growth, it is discussed in more detail below.

Discussion

The model shows good fits to experimental data, some predictive ability, and the assumptions appear to be reasonable. It remains to explore its further properties and to compare it with related models.

It is difficult to determine whether a two- or three-compartment model is more appropriate. This would be far more difficult were efflux data alone available (Shipley & Clark, 1972); having data on compartment specific activity simplifies the problem considerably. Thus whilst a two-compartment model fits the data as well as a three-compartment model (Table 2) it is clear that, at short labelling times, soluble and storage material do behave differently, with the former the precursor of the latter (Fig. 2). At longer labelling times they show similar specific activities (Farrar, 1980b), presumably because they intercommunicate and both are turned over rapidly.

The rapid turnover of soluble material—mainly sucrose—is expected where all exchange of carbon between compartments, and the environment, takes place through this pool. The sum of rate constants for loss of material from this compartment is about 2–5 d⁻¹, giving a carbon atom a half-time of about 4–7 h in this compartment (Tables 1 & 4). Figures of 10 h for the half time of $^{14}$C remaining in whole barley plants, and of 3–4 h for the $^{14}$C in the soluble pool of barley, can be inferred from published data (Farrar, 1980b; in each case reference is to the first phase of a two-phase efflux) and support the rapid turnover of soluble material this analysis indicates. A similar half-time of 8.8 h for a soluble pool comes from data on $^{14}$C efflux from barley analyzed by Barnes & Hole (1978). A large proportion of the soluble carbohydrate in the young barley plants is in the leaves (Farrar, 1981; Gordon et al., 1977) and it can be shown to have a half-time of about 0.5 h (Ower, Farrar & Whitbread, unpublished); that this half time is small compared with that from whole plants is presumably due to its describing export, not metabolism, of soluble sugar.

Perhaps more surprising is the rapidity of turnover of storage material—a half-time of about 10–20 h in constant light (Table 4). There seem to be no estimates

Table 4. Effects of temperature on the half-times for C atoms in the three compartments and on the respiratory cost of manufacturing storage and structural material; these are based on the rate constants of Table 1 for 10, 20 and 30°C, and on those of Table 2 for a step-size of 0.01 d for 15°C.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Soluble (h)</th>
<th>Storage (h)</th>
<th>Structure (h)</th>
<th>Respiratory cost of manufacturing storage and structure, $k_{01}/(k_{31}+k_{33})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>5.8</td>
<td>20.4</td>
<td>151.0</td>
<td>0.50</td>
</tr>
<tr>
<td>15</td>
<td>8.9</td>
<td>10.0</td>
<td>26.8</td>
<td>0.38</td>
</tr>
<tr>
<td>20</td>
<td>6.8</td>
<td>10.1</td>
<td>8.4</td>
<td>3.46</td>
</tr>
<tr>
<td>30</td>
<td>4.0</td>
<td>10.0</td>
<td>69.3</td>
<td>5.10</td>
</tr>
</tbody>
</table>
of this figure in the literature, and indeed turnover of storage carbohydrate has been rather understudied, although work on net sucrose and starch levels in barley leaves (Gordon, Ryle & Webb, 1980) shows most leaf sucrose and starch to be lost during a 16 h photoperiod. Data showing turnover are given by Gordon et al. (1977) and Farrar (1980b). The figures given by the model for turnover of structural material (Table 4) are rather higher than estimates in the literature, especially when it is considered that both proteins and amino-acids are within the structural compartment. Thus Penning de Vries (1975) lists turnover rates of up to 0.22 d\(^{-1}\) for leaf protein and 0.1 d\(^{-1}\) for chlorophyll. The figures at 10 and 30°C are therefore in reasonable agreement, but that at 20°C is much higher than expected. However, Barnes & Hole (1978) obtain a figure of 0.41 d\(^{-1}\) from \(^{14}\)C work on barley.

A second property of the model is that it enables the respiratory cost of manufacture of structural plus storage material to be computed. The ratio (carbohydrate lost in respiration/carbohydrate incorporated into storage and structure) varies from 0.38 to 5.1 (Table 4). This compares with other values for barley of 1.0, obtained by respiration and dry weight measurements (Farrar, 1980a); 0.9–3.2 calculated crudely from \(^{14}\)C data for these experiments (Farrar, 1980b); and 0.36 from the \(^{14}\)C of Ryle et al. (1976) as analysed by Barnes & Hole (1978). The lower figures are in line with those for a variety of species (Raven, 1976).

Implicit in this model, as in several models of crop growth (Loomis et al., 1979) is the assumption that the rate of production of structural material is proportional to the size of the soluble carbohydrate pool, i.e. mass transfer is governed by first-order kinetics. This assumption has received some experimental support (Thornley & Hurd, 1974) but is not consistent with the observation that the carbohydrate content of young barley can vary whilst the relative growth rate of structural material remains constant (Farrar, 1980b). To maintain a constant relative growth rate of structural material with a soluble carbohydrate pool of varying size implies either that the latter is not involved in control of the former, or that the rate constant for transfer of material from soluble to structure varies inversely with carbohydrate pool size. Certainly no simple control, such as is commonly assumed by crop modellers, seems likely.

The model thus agrees with published as well as directly tested data and so it would seem to have some general validity. To some extent it represents an experimental verification of the similar model of Thornley (1977) and other such approaches (Loomis et al., 1979). Certainly the division of the plant into basic, although heterogeneous, chemical fractions seems a useful way to describe growth at least in young barley plants. However, the assumption that the size of the carbohydrate pool controls allocation to growth processes seems open to considerable question. Since most of the carbohydrate may be spatially separated from centres of growth this is perhaps not surprising. We feel that models of this type may be of more utility if applied to restricted parts of the plant.

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References
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