Source–sink partitioning. Do we need Münch?

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Abstract

The simulation of phloem translocation by the Münch theory commonly uses resistances from sources to sinks: the resistances are therefore regarded as important in partitioning. Although resistance is generally a set constant, it is in fact strongly affected by viscosity, and thus the concentration of the transported solute. In this paper, the model of partitioning proposed by Minchin et al. was first corrected for variations in viscosity. The model was further modified, with the source considered as an activity of solute production rather than as a compartment concentration. When so defined, the source cannot differ from the sum of sink activities, largely outdating the source- or sink-limitation concepts. The corrected model confined the effect of resistances on the partitioning to low source activities. In the example of wheat grain filling analysed, such activities would be so low that they would correspond only to pathological conditions. In that case, the use of resistances in modelling is therefore just a mathematical burden, not even easily quantifiable since they are related to anatomical traits that are difficult to access. Leaving out resistances, it becomes easy to calculate the sink activities directly from the source activities, using an intuitive, accessible parameterization. The conditions for such a simplification are discussed.

Key words: Dry matter distribution, model, sink priority, sink size, sink strength.

Introduction

Although attention has been given to partitioning for a long time, for example, wheat breeding for yield was improved by selecting for this character, the first crop simulation models were mostly directed to the study of nutrient capture, and led to the concept of non-limiting production. Only in a second step were so-called limiting factors (such as nutrient deficiencies, water stress or pest attack) considered in these early models (Moulin and Beckie, 1993). However, for both economic and environmental reasons, farmers are obliged to limit the inputs in crops, i.e. to grow their crops with limiting factors. High productivity is still required, with the addition that quality criteria for crops are now demanded. In consequence, greater attention has been paid recently to the partitioning of assimilates between sources and sinks, in order to explain how the plants manage when resources are limited. Older experiments indicated that the partitioning could vary with the overall level of nutrition, and may even lead to switches in sink priorities. The extensive shoot/root literature provides the best known examples of such a priority switch.

Among the first models for plant growth, one proposed by Thornley (1972) had already simulated the partitioning of assimilates using two physiological mechanisms: phloem translocation and assimilate use by the sinks. Phloem translocation is generally modelled according to Münch’s theory on the formation of a solution flow by an osmotically generated pressure gradient, so that the mass flow $U_1$ to sink 1 may be obtained as following:

$$U_1 = S_0 \times (S_0 - S_1)/R_1$$

(1)

where $S_0$ and $S_1$ are the local concentrations of assimilate in source 0 and sink 1, respectively, and $R_1$ is the hydraulic resistance from 0 to 1.

The transported assimilates are thereafter used by the sink, according to the Michaelis theory of enzyme kinetics,

$$U_1 = V_1 \times S_1/(K_1 + S_1)$$

(2)

where $V_1$ is the maximum rate and $K_1$ the affinity constant of the reaction.
Combining equations (1) and (2), the concentration $S_1$ of the sink compartment, and then the flow $U_1$, can thus be deduced from the concentration $S_0$ of the source compartment and the three parameters $R_1$, $V_1$, and $K_1$. Minchin et al. (1993) analysed the competition between two sinks, 1 and 2, respectively, for the assimilates exported by one source 0. They demonstrated that the flow rates, $U_1$ and $U_2$ to the sink compartments 1 and 2, respectively, can be calculated:

$$
\frac{S_0[R_2(S_0 - S_1) + R_0(S_2 - S_1)]}{R_0(R_1 - R_2) + R_1 \times R_2} = U_1 = \frac{V_1 \times S_1}{K_1 + S_1} \quad (3a)
$$

$$
\frac{S_0[R_1(S_0 - S_1) + R_0(S_1 - S_2)]}{R_0(R_1 - R_2) + R_1 \times R_2} = U_2 = \frac{V_2 \times S_2}{K_2 + S_2} \quad (3b)
$$

where $R_0$ is the resistance associated with the common pathway from the source compartment to both sink compartments, and $R_1$ and $R_2$ are the resistances associated with the specific pathways to sink compartments 1 and 2, respectively. $S_0$, $S_1$ and $S_2$ are the local concentrations of assimilate in source and sink compartments, while $K_1$, $V_1$, and $K_2$, $V_2$ are the Michaelis constants for sinks 1 and 2, respectively. The equations (3a) and (3b) must be solved using numerical techniques for a given set of parameters: $R_0$, $R_1$, $R_2$, $K_1$, $V_1$, $K_2$, and $V_2$; with $S_0$ as a variable.

Minchin et al. (1993) reproduced qualitatively some physiological results reported in the literature. Hence sink priority can be affected by girdling, as reported by Grusak and Lucas (1985), or a sink may be unable to profit from the suppression of its competitor, as indicated by Farrar and Minchin (1991). Unfortunately, the model of Minchin et al. (1993) often appeared limited to such qualitative applications, for two reasons. First, the variable $S_0$ is as difficult to measure as it is to model. Moreover, the model of Minchin et al. (1993) could wrongly suggest that a source is adequately characterized as producing a stable concentration $S_0$, whereas $S_0$ is likely to vary as a result of the interaction between source and sink activities. Second, the hydraulic resistances are not easy to measure. Comparing the phloem to an impermeable tube, of radius $x$ and length $L$, its resistance is often estimated by the Poiseuille law

$$
R = \frac{8L\eta}{\pi \mathcal{K} T \pi x^4} \quad (4)
$$

where $\mathcal{K}$ is the gas constant, $T$ is the absolute temperature and $\eta$ is the viscosity of the transported solution. This means that the resistance, although specific to a source–sink pathway, is not a constant, because it will change in accordance with temperature as well as with viscosity, i.e. the solute concentration! Surprisingly, however, variation in viscosity is generally not taken into account in the papers dealing with resistance..

The present paper presents a revised version of the model of partitioning proposed by Minchin et al. (1993). Calculations are therefore made for a 1 source/2 sinks system (Fig. 1), but could easily be extended further. First, the original model is corrected for the effect of viscosity on resistance. It is then transformed with the source and sinks considered as activities, rather than compartments. The source is indeed much more intuitively characterized through its activity $U_0$ of assimilate production than through its compartment concentration $S_0$, which then becomes a result of the simulation, instead of input data. The resulting model is then tested for the sensitivity of its parameters, using either arbitrarily chosen parameters or the parameterization of partitioning during grain filling in wheat. In this example, it is suggested that the model may be further simplified by the useful omission of the resistances.

**Materials and methods**

**Model correction**

The way in which viscosity varies with temperature or concentration has not been fully determined. However, much data on this can be found in the reference literature. According to Weast (1972), the viscosity of water decreases as temperature increases. The effect on resistance is further amplified because temperature is also directly involved in the resistance calculation as reported in equation (4). For convenience, the variation of resistance with temperature is plotted in Fig. 2a using a relative scale: 100% represents $20R$, the resistance at 20 °C. The variations remain moderate (about ±30%) in the 10–
the resistance is twice that at 20 °C. Within a temperature range of [0–42 °C], the resistance \( R \) fits the following cubic relationship:

\[
R_{20} = R_0 (1.208 \times 10^{-5} \theta^3 + 1.432 \times 10^{-3} \theta^2 - 0.07318 \theta + 2.07)
\]  

(5a)

This fit is by no means a physical explanation for the effect of temperature on hydraulic resistances, but it does correct for the effect with a resulting error of less than 1% within the physiological range of temperatures.

While phloem sap is a complex and variable mixture, sucrose is by far its main component. Data on pure sucrose solutions can thus be used to extrapolate the effect of sap concentration on viscosity and resistance (Fig. 2b). For sucrose concentrations that are physically possible, viscosity varied over several magnitudes. However, physiological concentrations are unlikely to increase beyond 1.5 M, still leading to a 10-fold variation in viscosity and, consequently, to variations in resistance. The variation of resistance with concentration is shown in Fig. 2b using a relative scale: 100% represents \( R \) for a viscosity of 3 mPa s. This viscosity, used in Minchin et al. (1993), roughly corresponds to a 1 M sucrose concentration (B). The resistance \( R \) at 3 mPa s, roughly corresponding to a 1 M sucrose concentration (B), is constant from source to sink compartments. Resistivity dramatically increases at the end of each sieve tube when passing through the pores, and it is unlikely that this effect could be described by a simple equation for the pathway from source to sink compartments.

Instead, the corrected value \( R \) of a resistance will be calculated in this paper, using the mean concentration between the start and the end of this resistance. For \( R_0 \) in \( R_1 \) and \( R_2 \), the mean concentrations used will be \((S_0 + S_1)/2; (S_0 + S_2)/2\) and \((S_0 + S_1)/2; (S_0 + S_2)/2\), respectively, where \( S \) is the concentration at the end of the common phloem pathway from source to sink compartments (Fig. 1). According to equation (1),

\[
U_0 = S_0 (S_0 - S_2)/R_0
\]

(6)

where \( U_0 \) is the flux exported by the source, i.e. \( U_1 + U_2 \). Because the concentrations \( S_1 \) and \( S_2 \), as well as the fluxes \( U_1 \) and \( U_2 \), must be numerically obtained, obtaining \( S_0 \) together with the resulting corrections for \( R_0 \), \( R_1 \), and \( R_2 \) does not add any difficulty.

### Parametrization for numeric simulations

Because equations (3a) and (3b) must be solved using numerical techniques, the parameters \( [R; K; V] \) of the sinks should be set before calculating the sink activities, varying the concentration \( S_0 \) of the source compartment. These parameters are arbitrarily chosen for Figs 3 and 4, whereas wheat (Triticum aestivum) parameters are used as a quantitative example in Figs 5 and 6. The following section thus deals with the problems related to obtaining a fair parameterization, an important consideration in model development. The parameters were obtained from field assays using the variety Térome in 1998 and 1999 at the INRA station, Grignon (France) during the fourth week after anthesis. The first sink \( {{\left[ K_1; V_1 \right]} \}} \) parameters; see Fig. 1) is the ear at the grain-filling stage and the second sink \( {{\left[ K_2; V_2 \right]} \}} \) parameters) is the polymerization of sucrose into fructans, forming temporary reserves in the stem internodes. Such reserves are eventually degraded to sustain grain-filling, and can thus be defined as a source activity. However, regardless of the net balance between storage and remobilization, fructan polymerization can be observed throughout the grain-filling period, either by measurements of enzyme activity (Bancal and Triboi, 1993) or by CO2 labelling (Gent, 1994). This activity is thus as a second sink, competing with grain-filling for sucrose. The source of carbohydrates (mostly net photosynthesis) will not be detailed in this paper. In the wheat example, the source activity \( U_0 \) will be the flux out of the source compartment, regardless of any eventual internal regulation of this activity within the source compartment itself. Nevertheless, as a general rule, the model could work with source activities more strictly defined as the production of solutes to be used by the sinks.

The resistance \( R_0 \) (common pathway from the source to both sink compartments) and \( R_1 \) (specific pathway to the sink compartment 1) were those of the leaves and the stem, respectively. The resistance \( R_2 \) is associated with the pathway from the sieve tubes to the fructan storage sites, both of them situated in the stem.
During the fourth week after anthesis, grain-filling was in the so-called linear phase, which meant that no change in its rate could be attributed to plant ageing. If one half of the plants were removed from the field, the net photosynthesis rate of the remaining plants largely increased, but the rate of grain-filling only slightly increased, suggesting that this process was not far from saturation. This recorded grain-filling rate was corrected for 25% growth respiration to obtain an estimate of \( V_f \) (125 mg of dry mass \( \text{d}^{-1} \), or 4.3 nmol of sucrose \( \text{s}^{-1} \) per culm). According to Jenner et al. (1991), the grain-filling rate, mainly due to starch deposition, is regulated through sucrose import by the ear. Numerous studies using in vitro cultures of wheat ears have been published (Jenner, 1970; Jenner and Ratjen, 1978; Gifford and Brenner, 1981; Armstrong et al., 1987). The in vitro growth rates published for grain were fitted to the corresponding sucrose concentrations in the culture medium through Michaelis equations with affinity ranging from 30 mM to 100 mM. The average value, 65 mM, will be used for \( K_s \), using a 500 mM sucrose concentration; if \( K_s=3000 \text{mM} \), is used so that \( S_2 \) always remains much lower than \( K_s \). The sucrose consumption rate for 6kestose formation by cell-free extracts of plant stems was then used to estimate \( V_f \). This rate was measured at 0.76 nmol \( \text{s}^{-1} \) per culm, using a 500 mM sucrose concentration; if \( K_s=3000 \text{mM} \), \( V_f \) is thus 5.3 nmol \( \text{s}^{-1} \) per culm.

The parametrization of resistance is by far the most speculative component of the model, but it is probably unavoidable if the aim is to find a single parameter to represent the complete pathway between organs. According to Fisher and Gifford (1987), the bundle cross-sectional area is constant over the length of organs, this parameter was therefore measured at a single point to estimate the corresponding organ resistance. However, because there was not a single leaf but several leaves, the estimate of \( R_0 \) resistance of the leaves needed prior consideration. The flag leaf contained about 40% of total leaf nitrogen, so it was assumed that it provided 40% of photosynthate (Sinclair and Horie, 1989). It was further hypothesized that the conductance of phloem bundles was proportional to the flow rate they transported, meaning that the inverse of flag leaf resistance was 40% of \( 1/R_0 \). To estimate resistances, three plants were sampled from the field, and the stems and flag leaves were hand-cut into thin slices. The slices were then digested in hypochlorite and stained. Each slice exhibited about 50–60 vascular bundles, which were individually micro-photographed, and the pictures digitized. The cross-sectional area for every phloem cell was automatically recorded using image analysis procedures. However, the phloem bundles varied considerably in size and location. In stems, as reported in Fisher and Gifford (1987), large vascular bundles were interior whereas small bundles were adjacent to chlorenchyma tissue. A wide range of bundle sizes was observed in leaves, with some of the smallest directed transversally rather than longitudinally. If this variation in bundle size is related to differences between the organs they irrigate, then not all of them should be involved in \( R_0 \) and \( R_f \) calculation. When only the biggest bundles are considered, the resistances increase. Only these last values were used in this paper, and the Poiseuille law was then applied to each selected phloem cell according to equation (4) and using \( L=0.2 \text{m} \) for the leaves and \( L=0.4 \text{m} \) for the stems. The temperature was 20 °C and the viscosity 3 mPa s, as indicated in Minchin et al. (1993), leading to \( R_0=3.9 \text{Tmol s}^{-6} \text{m} \) and \( R_f=7.5 \text{Tmol s}^{-6} \text{m} \), respectively. However, the estimates for \( R_0 \) and \( R_f \) were obtained from the cross-sectional area of phloem cells when the hydraulic resistance is greatly enhanced at the end of sieve tubes. It is clearly not possible to measure the number, diameter separation and direction of all the sieve pores in a plant. Instead, the preceding resistances were increased by 50% to take into account the greater resistance at pores at the end of sieve tubes (Sheehy et al., 1995), so that \( R_0 \) and \( R_f \) are 5.7 and 10.9 Tmol s \( \text{m}^{-6} \), respectively. As indicated earlier, the resistance \( R_f \) is that from one part of the stem to another part of the stem. Of course, specific phloem strands can run towards particular tissues. Nevertheless, \( R_0 \) is set at zero in this paper. This statement suggests that the sinks are serially connected to the source, which is clearly a simplification. Thus the simulation demonstrates that it has paradoxically little effect on the partition between sinks.

### Results

#### Correction for variable resistance

In this section, an investigation was made of the partitioning of assimilates exported from one source to two unequal sinks. In Fig. 3 the sink parameters \( \{R;K;V\} \) are arbitrarily chosen \( \{10;100;50\} \) and \( \{200;100;50\} \) so that the sinks only differ by a very large difference in resistance. The resistance of the common pathway \( R_0 \) is set to 0.4 m as indicated in Minchin et al. (1993), leading to 0.4 m as indicated in Minchin et al. (1993), leading to
at zero (otherwise in this example \( R_0 \) will just dampen the observed effects). In Fig. 3A, \( U_1 \), the activity of the sink 1, is plotted against the concentration \( S_0 \) at the source compartment, using three different calculation hypotheses. If resistance is not taken into account, then the concentrations will not change from source to sink compartments, and the curve (dotted line) will be hyperbolic, like any Michaelis kinetic. If constant resistances are involved, their effect is to decrease the concentration in the sink compartment relative to that in the source compartment: \( S_1 < S_0 \). However, for high \( S_0 \), the resulting \( S_1 \) is high enough to saturate the sink activity anyway. Consequently, the effect of the resistances on sink activity is important when concentrations are low, but it is essentially overcome when they increase: the resulting curve (dotted line) shifts from an hyperbola to a sigmoid. Now if the resistances are corrected for viscosity as indicated in this paper, the resulting curve (solid line) is situated between the other two. The correction indeed leads to a decrease in the resulting curve (solid line) is situated between the other two. The correction indeed leads to a decrease in the resistances at low concentrations, where they affect the sink activities. In this example the way resistances are taken into account only has an effect for low \( S_0 \) (see insert in Fig. 3A): beyond 0.5 M the curves overlap. However, as previously observed, concentration is an inadequate way of characterizing a source, which is better achieved using source activity.

**Characterizing the source by activity rather than compartment concentration**

Using the corrected model, it is not possible to calculate \( S_0 \) from \( U_0 \); however, numeric resolutions for \( U_1 \) and \( U_2 \) can be obtained, starting from \( S_0 \). The relationship between \( S_0 \) and \( U_0 \) is then easily deduced according to the mass conservation law, since the flux exported by the source \( U_0 \) cannot differ from the flux imported by the sinks \( U_1 + U_2 \), so

\[
U_0 = U_1 + U_2 \quad (7)
\]

Consequently, \( U_0 \) is obtained numerically from \( S_0 \), and it is not difficult to deduce \( S_0 \) from \( U_0 \) using a computer program, but it should be noted that although the concentration in the source compartment can be increased virtually to infinity, this is not possible for source activity. From equations (2) and (7), \( U_0 < V_1 + V_2 \). When \( U_0 = V_1 + V_2 \), the concentrations are infinite, so a source activity \( U_0 \) higher than \( V_1 + V_2 \) falls outside the model. This will be discussed later. Note that in the example shown in Fig. 3, \( V_1 + V_2 = 100 \text{ nmol s}^{-1} \), which is thus the maximum possible \( U_0 \) source activity. The relationship between source activity \( U_0 \) and concentration \( S_0 \) of the source compartment (Fig. 3B) is clearly not linear, but rather hyperbolic with an asymptote for \( U_0 = V_1 + V_2 \). For low and medium activity, up to 75 nmol s\(^{-1} \), the way resistances are taken into account for the calculation of sink activities strongly affects this relationship, \( S_0 \) increases more rapidly with \( U_0 \) using constant resistances (dotted line) than using variable resistance (solid line), the smaller increase being obtained when resistance is not taken into account (dashed line). However, the resulting concentrations for these low and medium activities are low: less than 0.5 M. For activity greater than 75 nmol s\(^{-1} \), the importance of the calculation hypothesis on the resulting concentrations declines progressively, and the lines overlap. The 1.5 M concentration, which can be regarded as a physiological maximum, is obtained for 93 nmol s\(^{-1} \).

Consequently, despite the fact that the way resistances are taken into account may appear quite unimportant when \( U_1 \) is related to \( S_0 \) (Fig. 3A), it clearly is meaningful in the relationship between \( U_0 \) and \( U_1 \) (Fig. 3C). If the resistances are not taken in to account (dashed line), then both sinks are equivalent and, consequently, \( U_1 \) is just half of \( U_0 \). On the other hand, constant resistances clearly advantage sink 1, whose activity \( U_1 \) is more than half of \( U_0 \) (solid line). This advantage increases up to approximately \( U_0 = 40 \text{ nmol s}^{-1} \), it rapidly declines thereafter and becomes negligible only when beyond approximately \( U_0 = 80 \text{ nmol s}^{-1} \). The effect of variable resistances (dotted line), while of less importance, is essentially the same as that of constant resistances. It is thus visible over almost the whole source activity range. In the preceding example, the importance of the resistances for the calculation of sink activities appears more clearly using \( U_0 \) rather than \( S_0 \) to characterize the source, but the converse could also be observed using other \([R;K;V]\) parameters (data not shown).

**Sensitivity of the corrected model to its parameters \([R;K;V]\)**

For Fig. 4, as for Fig. 3, the resistance \( R_0 \) of the common pathway is arbitrarily set at zero, and \( V_1 + V_2 = 100 \text{ nmol s}^{-1} \). The sinks differ by one parameter only, i.e. either \( R \) \( ([10;100;50] \text{ for sink 1 and } [200;100;50] \text{ for sink 2}), or \( K \) \( ([10;30;50] \text{ sink 1 and } [10;600;50] \text{ sink 2}) or \( V \) \( ([10;100;95] \text{ sink 1 and } [10;100;5] \text{ sink 2}). The partitioning coefficient for sink 1 (\( U_1 / U_0 \) ratio) is plotted against the source activity \( U_0 \). The lines obtained for \( S_0 \) concentrations in the 0.1–1.5 M range are drawn in bold; note that the corresponding \( U_0 \) source activity range is not the same for the three curves. This range is thought to correspond to physiologically relevant situations (see Discussion). The left part of the figure, drawn in thin lines, corresponds to very low \( S_0 \) source concentrations, covering a very large range of \( U_0 \) source activity in the example shown, due to the choice of parameters. This is not always true, and will be discussed later. The parameters were chosen largely to advantage sink 1, therefore its partitioning coefficient is always higher than the 50% (which would be partitioned if the sinks were equivalent).
The three parameters do not determine the partition in the same activity range. The effect of resistance, while maximum at medium source activity for absolute sink activity (Fig. 3C; dotted line), is maximum at low source activities for the partitioning coefficient (Fig. 4; solid line). The resistance effect progressively declines with greater source activity. By contrast, the $K$ parameter, which mainly determines the partition at medium source activities (Fig. 4; dashed line), has no influence on partitioning, either at low or at high source activity. Once more the resistance effect dominates at low source activity, in this case leading to a 50% partitioning coefficient because the resistances are equal. At medium source activity, the $K$ parameter affects the partition, here favouring sink 1 until concentrations exceed $K_2$. Higher activities lead to a saturation trend for both sinks, in this case at the same $V$ activity, and the partitioning coefficients therefore return to 50%. Lastly, a difference in the $V$ parameter (Fig. 4; dotted line) affects the partitioning at high, but not at low activities. This is not surprising: when concentrations are high, the sinks saturate anyway, and their activities approach their $V$ parameter, which logically determines competition. On the other hand, $V$ has very little influence at low concentrations and, consequently, at low source activities, leading to a 50% partition because the $R$ and $K$ parameters are equal here.

**Model adaptation for a specific purpose**

In the preceding examples, some particular properties of the model were emphasized using arbitrarily chosen parameters. In the following section, the model is worked using parameters from partitioning in wheat. This section does not set out to provide a complete description of wheat carbon metabolism, but just uses wheat to illustrate how the model of carbon partitioning may be used: because the parameter effects vary over the range of source activity, the model can usefully be modified for such specific purposes. Figure 5 indicates the result of simulating either grain-filling rate $U_1$ (Fig. 5A) or partition to grain-filling $U_1/U_0$ (Fig. 5B) when the $U_0$ source activity varies. Lines drawn in bold correspond to the $S_0$ concentrations in the range 0.1–1.5 M.

The solid lines indicate the simulation produced by the complete $\{R;K;V\}$ model. Physiologically relevant $S_0$ were obtained in the 2.0–5.5 nmol s$^{-1}$ $U_0$ activity range, i.e. 20–60% of $V_1+V_2$. The grain-filling rate $U_1$ increases linearly with $U_0$ until this latter reaches approximately 3 nmol s$^{-1}$, then $U_1$ progressively saturates. The partition to grain-filling is very small at very low source activities, corresponding to $S_0$ concentrations less than 0.1 M. But the partition then increases rapidly, up to 90% with $U_0$ from 1 to 3 nmol s$^{-1}$, progressively declining thereafter to 70% at 5.5 nmol s$^{-1}$ $U_0$ activity. This decline continues thereafter, yet is meaningless since the corresponding $S_0$ concentration is physiologically too high.

Such results can be compared with data from plants. For instance, $U_0$ activity in control plants ranged within 3.5–
5.0 nmol s\(^{-1}\) which, according to the model, is approximately 0.25–0.80 M for the \(S_0\) concentration. Such comparisons, however, are not the topic of this paper. Rather, the complete \(\{R;K;V\}\) model will now be compared with other simple models designed for this specific purpose. For instance, several classic partition models calculate, according to the overall plant status, a potential activity for each sink, for instance \(U_1'\) and \(U_2'\) for sinks 1 and 2, respectively. The models then compare the sum of potential sink activities to the source activity to obtain the actual sink activity. For sink 1, it will be

\[
U_1 = U_1' + U_0 = \alpha_1 U_0
\]

where \(\alpha_1 = U_1'/(U_1' + U_2')\), independent of \(U_0\) activity, is actually a partitioning coefficient to sink 1. Sinks eventually become completely saturated, so that \(U_1\) activity calculates as

\[
U_1 = \min [\alpha_1 U_0; U_1']
\]

Simulations by such a partition model, using \(\alpha_1 = 90\%\) and \(U_1' = V_1\) defined from the \(\{R;K;V\}\) model, are drawn in Fig. 5 (dotted lines). The resulting curves are similar to that of the \(\{R;K;V\}\) model in the 1–3.5 nmol s\(^{-1}\) range of \(U_0\) activity. For greater activities, however, the progressive saturation of sink 1 is not taken into account. Consequently, both sink 1 activity and partition are overestimated. Unfortunately, this occurs within the natural range of variation for \(U_0\) activity. Some partitioning models also involve transport and resistance from source to sinks. Such models would produce curves that are closer to the \(\{R;K;V\}\) model than that shown, especially in the left part of the Fig. 5B. In the case of wheat however, this part of the curve is of little interest.

In wheat, the resistance mostly affects partition in the range of \(U_0\) activity where the \(S_0\) concentration is lower than 0.1 M, considered as physiologically too low, so a model using Michaelis-type sinks connected without resistance was also tested (dashed lines). The \(\{K;V\}\) parameters are the same as those of the complete \(\{R;K;V\}\) model (solid lines). However, as previously indicated, the concentration does not change from source to sinks \(S_0 = S_1 = S_2 = S\). Consequently, from equation (7):

\[
U_0 = \frac{V_1 S (K_1 + S)}{V_2 S (K_2 + S)} + \frac{V_2 S (K_2 + S)}{V_2 S (K_2 + S)}
\]

So \(S\) (and thus \(U_1\)) can easily be calculated from \(U_0\). Even though this last model does not describe the transport from source to sinks, it is much more readily usable than the former model. In Fig. 5B, the simulated partitions are very close except at low, unrealistic \(U_0\) source activities. The simulated activities of sink 1 (Fig. 5A) differ so little that this could not have been detected using experimental, noisy, data.

Because it is difficult to assign a precise value to the resistances (see Materials and methods), Fig. 6 further explores the resistance effect in the specific function of grain-filling in wheat for three \(S_0\) concentrations, 0.1, 0.5 and 1.5 M. In Fig. 6A, the resistance to sink 2, \(R_2\), is varied from 0 to 100 Tmol s m\(^{-6}\) in order to study the partitioning coefficient to sink 1 in both the complete \(\{R;K;V\}\) model and its simplified version in which no account is taken of resistance. In the latter (dashed lines) of course, the \(R_2\) value does not alter the partition, which is only affected by the \(\{K;V\}\) parameters and the \(S_0\) concentration. The partition coefficient to sink 1 is thus constant at 94\%, 83\% and 70\% for \(S_0 = 0.1, 0.5\) and 1.5 M, respectively. This coefficient is very similar to that of the complete \(\{R;K;V\}\) model (solid lines) when \(R_2 = 0\) Tmol s m\(^{-6}\) reaching 91\%, 84\% and 71\% for \(S_0 = 0.1, 0.5\) and 1.5 M, respectively. For the lower \(S_0\) concentration, however, the models differ more rapidly.
With the actual value measured for $R_1$ (10.9 Tmol s m$^{-6}$), the partitioning to sink 1 is already 3% underestimated and the error rapidly increased with increasing $R_1$. An error less than 10% (obtained for any $R_1<26.9$ Tmol s m$^{-6}$) is of course negligible in the estimation of sink 1 nutrition, but it could be important when focusing on sink 2 nutrition. However, apart from the case of continuous very low source activity, the simplified version provides an easy and useful way to model the partition from source activity. Even in such a case, the results of the complete $\{R;K;V\}$ model do not require high precision in the resistance measurement.

**Discussion**

As far back as 1967, Warren-Wilson tried to define the sink strength as the product of a size and a specific activity, i.e. by two distinct parameters, which would be local properties of a plant organ (Warren-Wilson, 1967). However, over the years, the sink strength became defined by a single parameter that various authors widely discussed. Thus a debate entitled ‘Sink strength, what is it and how do we measure it?’ was edited by Farrar (Farrar, 1993). It is clear, however, that it is very difficult, by using a single parameter, to describe the switches in partition that can frequently be noted when source activity varies.

The Münch theory applied to model phloem translocation (Christy and Ferrier, 1973) introduced a new variable into the source/sink world. According to this theory, sources and sinks are defined by compartment concentrations. Logically, Magnuson et al. (1979) therefore describe the activities of sink as enzyme kinetics, because such activities are easily obtained from a concentration using the Michaelis equation. A considerable advance in the understanding of source/sink relationships was thus obtained. Minchin et al. (1993) indeed combined the Münch and Michaelis equations to obtain a model in which the partition is explained by plant architecture and local properties of the sink compartments. Models published before their paper referred, to a greater or lesser extent, to the functional balance hypothesis of Thornley (1972) to explain the shoot/root ratios. According to such models, what is in one respect a sink (e.g. for carbon metabolism) is a source in other respects (e.g. for nitrogen metabolism). Close links between these metabolic pathways explained the partition. Such models were therefore unable to explain the partition to a sink that provides nothing to the rest of the plant, such as the two examples used in this paper, grain-filling and temporary reserves.

In addition, the Michaelis parameters $\{K;V\}$ also appear to be useful for the proper characterization of the sinks. The $V$ parameter is both a sink size (linked to quantitative properties of an organ, as emphasized by Warren-Wilson, 1967), and a sink potential (a mathematical limit for an activity which would be obtained under infinite nutrient provision, as suggested by Wareing and Patrick, 1976). Being a sink potential, $V$ could be measured by fitting the actual sink activity to a Michaelis model using a range of source activities. Being a sink size, $V$ can be obtained by every existing growth model. The best way of obtaining it is likely to be through the quantitative properties built by the previous growth of the corresponding organ (Munier-Jolain and Ney, 1998). So the partition will be included in growth models. The $K$ parameter on the other hand explains the sink hierarchy observed in response to source variation (Wardlaw, 1990). Being linked to the overall metabolism of the sink organ, $K$ will change along with ontological evolution in metabolism. On the other hand, since it roughly reflects enzyme affinities, $K$ will be little affected by the actual physiological conditions, such as temperature, water status or nitrogen nutrition. Thus, this parameter could be obtained either from the bibliography or from specifically designed experiments, unrelated to even the model application.

These useful attributes of the $\{K;V\}$ parameters have meant that the Minchin et al. (1993) paper has been referred to by several other authors, such as Sheehy et al. (1996) or Lemaire and Millard (1999). However, they are theoretical descriptions rather than usable models. The characterization of the source as a compartment may contribute to this misuse. Calculations can, in fact, only be made by using the concentration of the source compartment as a variable and not by using the source activity. However, characterizing the source as an activity is much more convenient than characterizing it as a compartment concentration. Firstly, while activities are easily obtained, concentrations are difficult both to measure accurately in vivo as well as to model independently. Secondly, the concentration in the source compartment is itself a result of source/sink interactions, even in those cases where the activity of a source is regulated through the concentration in their compartment. It is proposed here to link the source and sink activities according to the mass conservation law: the flux formed by the sources is the flux imported by the sinks. In other models, these two fluxes can differ by variation in the content of so-called labile compounds. However, temporary storage, such as that of starch in the leaves, is a sink in our definition, thus the labile compounds are only those located within the phloem bundles. According to Schnyder (1993) such ‘en-route’ compounds would sustain sink activities for less than 1 h; they can thus be left out of the partition model at the day or week scale.

Now equalizing source and sink activities leads to some quite surprising observations. It is no longer possible to tell whether a source is in excess relative to the sinks (or vice versa) because the fluxes are equal. Neither source nor sink limitation, nor limiting or non-limiting conditions can be emphasized. According to the Michaelis equation, any sink activity is always limited both through sink parameters and
through source concentration, i.e. there is always co-limitation between source and sink (Kacser and Burns, 1973). Another paradoxical observation is that the source activity becomes limited by the $V$-sum, and thus by sink parameters! In fact, the $V$-parameters reflect the sink sizes, which are built up by sink growth (Black, 1993), that is, through source activity during the previous weeks. Relationships between sources and sinks thus appear not only through nutrition, but also through ontogeny. However, this balance can be broken: if a sink-bearing organ suddenly disappears, do the source activities become excessive? Many papers report such pruning experiments, and they always show that the plant adapts rapidly to the new situation. Models already exist which can take such accidents into account. Thornley (1995) for instance, inhibited the source when solute concentrations increase; Sheehy et al. (1996) instead turned their attention to excretion sinks with low affinity. Both these mathematical solutions, agreeing with physiological observations, avoid any accidental excessive accumulation of assimilates, but are essentially turned off in normal cases.

Although easily compatible with computer procedures, the calculation of sink activities is more complicated starting from source activity rather than source concentration, which comes mathematically from the use of resistance. Resistance is needed to explain the transport from source to sinks physically. However, in the Materials and methods, the difficulties in obtaining a fair value were indicated: Which bundles are involved in the pathway from a source to a sink? Is the resistance constant along a bundle (clearly not if variations in viscosity are taken into account)? How precisely is the effect of pores quantified? Moreover, the assumptions made in order to apply the Poiseuille law are far from realistic: the phloem cells are not impermeable cylindrical tubes. Clearly only a crude estimate of resistance can be obtained in such a manner. These difficulties led Maillard et al. (2000) to regard the description of resistance as too difficult to be used at crop level. On the other hand, the Münch theory is itself criticized as being too simple (Tyree and Dainty, 1975; Milburn and Kallarackal, 1989; Kargol et al., 2001). Alternative models need still more parameters, which are no easier to obtain. A correction of resistance for the variations in viscosity is now proposed. Many of the previous reports, using a single constant viscosity (generally that of pure water!), should at least be re-examined. If they somehow agree with data, it may be because the transport simulation is not always a critical part of the model.

In fact, resistances only affect the partition at low source activities; correcting them for viscosity variation further reduces the range over which they have an effect. However, source activities that are too low should not be taken into consideration because they would correspond to unacceptably low concentrations. As far as is known, phloem concentrations lower than 0.1 M have never been reported; and it is thought that they could only be considered for non-photosynthesizing, reserve-less, i.e. dying plants. In the case of wheat-grain filling, it is demonstrated that, since the resistance effect is limited to this non-physiological range of source activity, it can be left out of the simulation. This conclusion is in good agreement with experiments suggesting that transport capacity is not a limiting factor. Wardlaw and Moncur (1976) showed that cutting one half of the stem phloem does not affect grain filling. According to Wang et al. (1993) an excess transport capacity may actually be built, under the control of the sink itself.

Without resistance, the calculations become much simpler and intuitive. But while resistance is not a required factor in the case of wheat grain-filling, this is not always the case, as indicated in Figs 3–4. So two tests should be done using the complete $\{R; K; V\}$ model before simplifying it. First, the strength of the resistance effect should be tested throughout the range of source activity. This, of course, depends on the $R$ parameters themselves: resistances greater than 10 Tmol s m$^{-6}$ will likely modify the partitioning for low, but still possible, source activities. The $K$ parameters are also involved: the resistance effect is more important when sinks are far from being saturated. Hence sinks half-saturate only when their concentration reaches $K$. The lower the $K$ value, the wider the source activity range in which sink activities can be decreased by resistance. The second test is to verify the left part of the curves, which sometimes includes a very large range of source activity, but corresponds to phloem concentrations, that are too low to have any physiological meaning. The extent of this excluded range will be sensitive to the same parameters $R$ and $K$: the lower the $K$ value, the wider the range of source activities in which concentration will be lower than $K$, and possibly less than 0.1 M.

Resistances are likely to remain key factors where numerous similar sinks interact with numerous similar sources such as fruits on a tree, which can explain the preferential pathways used by assimilates. Other examples of resistance involvement can be found where source activity is low and/or resistances are increased, such as bud nutrition in early spring or pest attacks. Even when resistances cannot be avoided, however, the partitioning will respect the law of mass conservation, and the consequent relationships between source activity and sink parameters will still apply.

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