CHAPTER 9

CONCEPTS OF MODELLING CARBON ALLOCATION AMONG PLANT ORGANS

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Abstract. The simulation of carbon allocation among plant organs is one of the weakest features of crop growth models. This paper briefly discusses five concepts of modelling carbon partitioning: 1. Descriptive allometry, proposing a predetermined ratio between the (relative) growth rates of plant organs; 2. Functional equilibrium, proposing an equilibrium between root and shoot activity; 3. Canonical modelling, a mathematical approach based on only a qualitative understanding of the allocation process; 4. Sink regulation, proposing allocation to be determined by sink strengths of the different organs; and 5. Transport resistance, calculating carbon transport from source to sink through a resistance and its utilization in the sink organs. These five concepts are ordered in increasing complexity. Pros and cons of the different concepts are discussed. The most appropriate concept will depend on the species studied and the aim of the research.

INTRODUCTION

Carbon allocation to the different organs of a plant is clearly of great importance in crop growth, development and yield. However, the regulation of carbon allocation at the whole-plant level is still poorly understood. There is a great diversity in the way crops partition assimilates. Consequently, simulation models developed so far are rather species-specific. Within species, genotype, developmental stage of the plant, many growth conditions and internal regulation by the plant may also affect dry-matter allocation (e.g. Marcelis 1996).

Many theories have been put forward to explain the mechanism by which assimilates are partitioned among plant organs. However, still no unequivocal theory is available at present. Therefore, it is not surprising that explanatory models often give way to empirical ones when they deal with allocation of assimilates (Marcelis 1993b; Marcelis et al. 1998). The simulation of carbon allocation is one of the weakest features of current crop growth models. The different approaches of modelling carbon allocation have been reviewed by several authors, e.g., Marcelis

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(1993b), Cannell and Dewar (1994), Marcelis et al. (1998) and Lacointe (2000). In this paper, which is partly based upon an earlier review (Marcelis et al. 1998), we will briefly discuss five concepts of modelling carbon allocation among plant organs. These five concepts are ordered in increasing complexity: 1. Descriptive allometry; 2. Functional equilibrium; 3. Canonical modelling; 4. Sink regulation; and 5. Transport-resistance. Canonical modelling is described in more detail by Renton et al. (this volume, Chapter 13). Drouet and Pagès (this volume, Chapter 14), and Kang and De Reffye (this volume, Chapter 6) use in their models the sink-regulation concept, whereas the transport-resistance concept is used by Minchin (this volume, Chapter 10), Prusinkiewicz et al. (this volume, Chapter 11) and Allen et al. (this volume, Chapter 12).

FIVE CONCEPTS OF MODELLING CARBON ALLOCATION

Descriptive allometry models

Most crop growth models simulate dry-matter allocation using descriptive allometry models assuming a predetermined ratio between the (relative) growth rates of the plant organs (Wilson 1988). Such ratios are empirically derived and usually change with phenological development (time, temperature sum or plant size), as shown in Figure 1. Although the allometric relations are affected by environmental conditions (e.g. Niklas and Enquist 2002), in many models these effects are not taken into account.

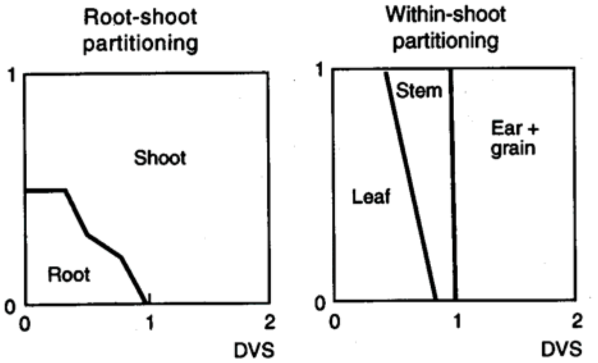

Figure 1*. Diagram of allocation of assimilates in wheat as a function of development stage (DVS): an example of descriptive allometry (from Goudriaan and Van Laar 1994)*

This simulation approach provides a simple description of the dry-matter allocation and has a high level of empiricism (Marcelis 1993b). In many situations both quantitative and mechanistic information on dry-matter allocation are limited. Therefore, a more detailed simulation approach is often not feasible. The model results may agree rather well with experimental results. However, these models describe dry-matter distribution often only under a limited range of growth conditions (Wilson 1988) and cannot deal with dynamic fluctuations in dry-matter allocation.

Functional equilibrium models

The ratio of shoot to root growth varies widely between species, it changes during plant development and can be modified by external conditions. The shoot fixes CO_2 from the air, and the root extracts mineral nutrients and water from the soil. There is a balance between these functions of shoot and root. After defoliation or root pruning, the plant acts so as to restore the balance of root and shoot functions. The functional equilibrium approach (e.g. Brouwer and De Wit 1969; De Willigen and Van Noordwijk 1987) is based on these observations and proposes that the dry-matter distribution between root and shoot is regulated by an equilibrium between root activity and shoot activity. This approach can be formulated as:

$$W_r / W_s \propto A_s / A_r \tag{1}$$

where W_r is root mass; W_s is shoot mass; A_s is specific photosynthesis rate of the shoot and A_r is specific absorption rate of the root. According to this approach environmental conditions that reduce the specific activity of the roots such as a decrease in water or nutrients availability, a decrease in water potential, and temperature above or below the optimum temperature for root functioning, increase the dry-matter allocation towards the roots. Similarly, conditions that decrease the specific activity of the shoot, such as a reduction in light intensity or CO_2 concentration, increase the dry-matter allocation toward the shoots (Wilson 1988; Enoch 1990).

In some models root and shoot activity affect dry-matter allocation indirectly as the dry-matter distribution is related to the ratio of the C and N concentrations of the plant (Reynolds and Thornley 1982; Mäkelä 1986) or to the N concentration of the plant (Ågren and Ingestad 1987; Van der Werf et al. 1993).

The functional equilibrium models can be considered teleonomic models (Thornley and Johnson 1990). Teleonomic models are applicable to goal-directed behaviour and are formulated explicitly in terms of goals. For instance, the proportionality between W_r/W_s and A_s/A_r in Eq. 1 can be considered to be a goal or it can be interpreted as that the plant ‘seeks’ more carbon by allocating more growth to the shoot when the supply of carbon is reduced; similarly it ‘seeks’ more nitrogen by allocating more growth to the root when the supply of nitrogen is reduced (Thornley and Johnson 1990). Many teleonomic models assume that dry-matter allocation between shoot and root is regulated in such a way that the relative growth rate of the plant is maximized (Hilbert 1990; Kastner-Maresch and Mooney 1994).

Although the functional equilibrium approach is often rather successful in simulating the ratio between shoot and root dry weight in vegetative plants, it is not easily applicable to ratios between other plant organs, and the underlying mechanism is quite complicated and not well understood (see special issue of Plant and Soil, 185, 1996).

Canonical models

The canonical concept is an intermediate approach. Canonical modelling is a mathematical modelling approach which uses nonlinear ordinary differential equations with products of power-law functions. It can be used to describe rather complex biological systems and provides guidelines for model design, (numerical) analysis and interpretation of results. Its complexity is in between a purely empirical model (descriptive allometry model) and a detailed mechanistic model (transport-resistance model). The approach requires no detailed quantitative assumptions about underlying mechanistic processes. Rather it is based on a qualitative understanding of these processes, e.g., what variables influence the process and whether they enhance or repress it, and on experimental data in the form of carbon budgets (Voit and Sands 1996). Carbon allocation is represented by a number of fluxes between compartments, and these fluxes are in turn represented using flux functions of a standard mathematical form. So-called influences can be used from compartments on fluxes to model, for example, feedback. So far only a few authors have used this approach in plant modelling. Renton et al. (this volume, Chapter 13) discuss the usefulness of this approach in functional-structural plant modelling. It offers a useful, flexible and relatively simple way of simulating plant function at an intermediate level of complexity. It could also be used to test different hypotheses of carbon allocation models.

Sink regulation models

In many crops dry-matter allocation among plant organs is primarily determined by the sink strengths of the organs, whereas neither the source strength nor the transport path are dominating factors in regulating dry-matter allocation at the whole-plant level (Marcelis 1996). Furthermore, it seems a reasonable assumption that there is one common assimilate pool in the plant (Heuvelink 1995). Based on this knowledge, the fraction of dry matter partitioned into an organ (f_i) can be calculated as the ratio between its organ sink strength (S_i) and the total sink strength of all organs together (ΣS):

$$f_i = S_i / \Sigma S \qquad (2)$$

Sink strength can be defined as the potential demand or potential capacity of an organ to accumulate assimilates. It has been considered a product of sink size and sink activity. However, attempts to quantify sink strength by defining organ weights as sink size and relative growth rates as sink activity did not improve our understanding of the mechanism regulating sink strength (Ho 1988). Evaluating sink strength as growth rate (e.g. Balibrea et al. 2003) is also not improving our understanding, as growth rate is usually determined by both organ sink strength and available assimilates (source strength). More successfully, sink strength has been quantified by the potential growth rate of the organ, i.e., the growth rate under conditions of non-limiting assimilate supply (Marcelis 1996). Potential growth of an organ can be measured when plants are grown at high irradiance and/or low number of sinks on the plant. For example, Heuvelink and Marcelis (1989) reported the same growth rate for tomato fruits grown with one or two fruits per truss. Hence this growth rate is the potential growth rate, as it is no longer limited by assimilate supply. The potential growth rate of an organ may change with, for example, its developmental stage or temperature. For cucumber fruits, the simulation of the allocation among individual fruits was improved when the sink strength of each fruit was not only dependent on its potential demand for assimilates but also on its affinity or priority for assimilates (Marcelis 1994).

In some models potential growth rates are used in combination with a priority sequence for (groups of) organs: First Eq. 2 is used to distribute dry matter among a group of organs, and only if supply exceeds demand of these organs (e.g., fruits, leaves and stems) assimilates are distributed to other organs (e.g., roots) (Wermelinger et al. 1991; Grossman and DeJong 1994). These models, which are often used for trees, are also called hierarchical models (Lacointe 2000). Sometimes organ relative growth rate instead of absolute growth rate is used as a measure for sink strength. However, Marcelis (1993a) showed for cucumber that it is the absolute growth rate rather than the relative growth rate that reflects organ sink strength.

In models based on sink strengths the number of organs and the timing of their presence on the plant have a strong impact on simulation results. The number and timing of organs depends on the rates of initiation, abortion, harvest and/or senescence of the organs. The fraction or number of non-aborting fruits is often simulated as a function of the source–sink ratio (e.g. Marcelis 1994). However, a better understanding of the abortion process is necessary because simulation results of organ abortion are usually not very accurate, while they have a strong impact on the simulation of dry-matter allocation. Developing a truly predictive submodel of organ abortion is a great challenge.

Most of the applications of the modelling approach based on sink strengths or potential demands are found in reproductive crops, like cucumber (Figure 2), sweet pepper, tomato, peach, grapevine, kiwifruit, citrus, rose and bean (Marcelis et al. 1998). In general, model results seem to agree rather well with measured data. Kang and De Reffye (this volume, Chapter 6) and Drouet and Pagès (this volume, Chapter 14) successfully applied this approach in functional-structural plant models. This approach has some mechanistic aspects and can be used to model dry-matter allocation between all different plant organs. Effects of environmental conditions, pruning strategies and plant densities can be simulated through their effects on the sink strengths of individual organs and the number of organs on the plant. Even at constant growth conditions, cyclic fluctuations in dry-matter allocation occur as a result of internal regulation, and these fluctuations can be simulated by the sink regulation concept (Marcelis 1994).

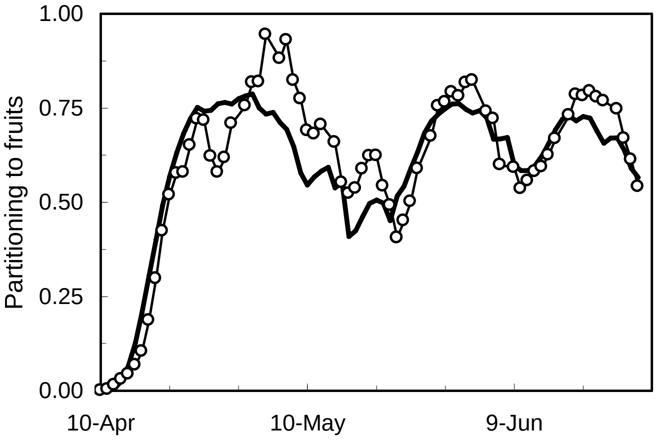

***Figure 2**. Measured (-o-) and simulated (—) time course of the daily fraction of dry matter distributed to the fruits in cucumber. Dry-matter distribution was simulated by a sink-regulation model with temperature and dates of anthesis and harvest of non-aborting fruits as input to the model (from Marcelis 1994)*

Transport-resistance models

Transport-resistance models provide the most mechanistic description of carbon allocation among plant organs. In these models the formation of assimilates in source organs, its subsequent transport to sink organs and the utilization in the sink organs are simulated.

Several authors (Thornley 1976; Dewar 1993; Minchin et al. 1993; Minchin and Lacointe 2005) have developed mechanistic models, in which the transport of assimilates from source to sink organs is simulated to be proportional to an osmotically generated pressure gradient or to differences in concentration of labile carbon divided by a transport resistance. The simulated labile carbon in the sink organs is used for growth according to Michaelis-Menten kinetics. As in many crops neither the source strength nor the transport path is a dominating factor in regulating dry-matter allocation at the whole-plant level (Marcelis 1996), transport-resistance models are in many cases unnecessarily complex.

Minchin (this volume, Chapter 10) describes a transport-resistance model including current relevant knowledge of phloem physiology. Related to this concept Prusinkiewicz et al. (this volume, Chapter 11) gives a detailed description of an analogy to an electric network for calculating the flow and allocation of assimilates. This approach is applied by Allen et al. (this volume, Chapter 12) to model carbon allocation in peach.

This mechanistic approach has been used with some success to simulate the distribution between shoot and root of young tomato (Cooper and Thornley 1976) and barley plants (Minchin et al. 1994). Its main disadvantages are its complexity and the difficulties to measure the relevant parameters, like transport resistance and labile carbon concentrations or potentials (Reynolds and Thornley 1982; Lacointe 2000), although the transport resistance might be estimated numerically from anatomical data (e.g. Sheehy et al. 1995). In addition, Bancal and Soltani (2002) stated that the use of resistances in modelling is just a mathematical burden. They suggested a simplification where resistances were left out and sink activities were directly calculated from the source activities. However, Minchin (this volume, Chapter 10) discusses some flaws of that model. In a number of cases transport resistance does not seem that important (e.g. Marcelis 1996), but in large plants (e.g., trees) it may become important. In conclusion, the transport resistance-modelling approach includes most of the physiological knowledge available, but due to the complexity a wide application of this approach in crop production models is in many cases not likely and not necessary.

DISCUSSION AND CONCLUSIONS

Due to their simplicity and lack of understanding of the allocation among plant organs, descriptive allometry models that are entirely empirical, are the most widely used models. For simulating allocation between shoot and root in vegetative plants the functional equilibrium approach often appears to be suitable. The canonical modelling concept offers more flexibility to cope with higher levels of complexity and it can be useful to model processes such as allocation, where detailed knowledge of underlying physiology is limited but where a reasonable idea of the involved processes exists. However, this approach has hardly been applied and tested yet. Sink regulation models based on the demand (sink strength) of the organs have some mechanistic aspects and have been applied successfully in many situations. Estimation of the potential demand for all organs can, however, be tedious. Transport-resistance models deal with the most mechanistic approach. This may be particularly interesting in functional-structural modelling, when the architecture of plants is considered and plants are represented as a large number of interconnected components (such as internodes, leaves, flowers and fruits). However, in many cases transport resistance does not play a dominant role and the complexity and difficulties in parameter estimation will probably hamper a wide application of transport-resistance models. Each of the different modelling approaches has its pros and cons. The choice for an approach depends on the aim of the study. For example, for a simple practical application, descriptive allometry might be a good choice, and when the aim is only to simulate root:shoot allocation the functional equilibrium can be very useful. Furthermore, there is a great diversity in the way a crop partitions its assimilates. Consequently, the most suitable simulation approach depends on the type of crop studied and on the aim of the simulation study.

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