

# Sink strength as a determinant of dry matter partitioning in the whole plant

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## Abstract

Dry matter partitioning is the end result of the flow of assimilates from source organs via a transport path to the sink organs. The dry matter partitioning among the sinks of a plant is primarily regulated by the sinks themselves. The effect of source strength on dry matter partitioning is often not a direct one, but indirect via the formation of sink organs. Although the translocation rate of assimilates may depend on the transport path, the transport path is only of minor importance for the regulation of dry matter partitioning at the whole plant level.

To understand the regulation of dry matter partitioning by the sinks, a parameter like sink strength is needed that describes a sink's ability to influence assimilate import and is independent of the rest of the plant. The term sink strength can be defined as the competitive ability of an organ to attract assimilates. However, there is much debate and confusion about the term sink strength because this term is often not clearly defined. Sink strength has been proposed to be the product of sink size and sink activity. Although cell number is often considered as a suitable measure of sink size, it appears not always to be an important determinant of sink size. Moreover, sink strength may depend on sink age rather than sink size.

A model for dry matter partitioning into generative plant parts, which is based on sink strengths of the organs, is described. The potential growth rate (potential capacity to accumulate assimilates) has been shown to be an important parameter that quantitatively reflects the sink strength of an organ. The potential growth rates of the plant's organs are not static but change dynamically. The potential growth rate of a fruit is a function of both its age and temperature. For

several crops it has been shown that the dry matter partitioning into an organ can be quantitatively described as a function of its potential growth rate relative to that of the other plant organs.

Key words: Dry matter distribution, potential growth rate, sink, source, translocation.

## Introduction

The term dry matter partitioning is used in various meanings. It may be defined as, for instance, the distribution of dry matter between the organs of a plant, or as the distribution between different processes (e.g. synthesis and hydrolysis of sugars, export, respiration, etc.) or as all the processes acting on dry matter in the plant. In this paper, the first definition will be used, where partitioning is, in fact, the end result of the processes acting on dry matter. Moreover, in this paper the term partitioning will be used in a relative sense, i.e. it refers to fractions of the dry matter of the whole plant: Hence, the flux of dry matter into an organ may increase while dry matter partitioning into that organ does not necessarily increase.

Although there is considerable information on the operation of individual processes in plants such as photosynthesis, sugar metabolism, translocation, and cell expansion, the controls which actually regulate the partitioning of dry matter at the whole plant level are still only poorly understood (Wardlaw, 1990). Several theories have been put forward to explain the mechanism by which dry matter is distributed among plant organs, but no unequivocal theory is available at present (Gifford and Evans, 1981; Wolswinkel, 1985; Farrar, 1988, 1992; Patrick, 1988; Wardlaw, 1990). Moreover, quantitative data on dry matter partitioning within whole plants—in

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particular, during the generative stage of crops—are scarce (Wareing and Patrick, 1975; Marcelis, 1993a).

In crop growth models, the dry matter partitioning among plant organs is often described as only a function of the developmental stage of the crop (Penning de Vries and van Laar, 1982). However, this description is entirely empirical and usually only valid under a limited range of growing conditions (Fick *et al.*, 1975; Loomis *et al.*, 1979; Wilson, 1988).

The dry matter partitioning between root and shoot has been described as a functional equilibrium between root activity (water or nutrient uptake) and shoot activity (photosynthesis); i.e. the ratio of root-to-shoot weight is proportional to the ratio of shoot-to-root specific activity (Brouwer, 1963). Although in this way the ratio between shoot and root dry weight can often be estimated fairly well in vegetative plants, the mechanism underlying this equilibrium is quite complicated and not well understood (Brouwer, 1983; Lambers, 1983; Farrar, 1992). Furthermore, this equilibrium can only be applied to shoot:root ratios and not easily to ratios between other plant organs, because of the absence of functional interdependence.

Dry matter partitioning is the end result of a co-ordinated set of transport and metabolic processes governing the flow of assimilates from source organs via a transport path to the sink organs. The activities of these processes are not static, but may change both diurnally and during plant development (Patrick, 1988). Assimilates are produced by photosynthesis in the source organs (mainly leaves). The assimilates can be stored or transported from the source to the different sink organs via vascular connections (phloem). The translocation rate of assimilates in the phloem is often considered to be driven by gradients in solute concentration or in water or turgor potential between the source and the sink ends of the phloem (Ho, 1979; Wolswinkel, 1985; Lang and Thorpe, 1986; Patrick, 1988; Lang and Düring, 1991). Utilization and compartmentation of the assimilates in the sink are important to maintain these gradients. The control of dry matter partitioning may be at the source, at the sink and/or at the transport path. However, several authors have found indications that dry matter partitioning among sink organs is primarily regulated by the sinks themselves (Evans, 1975; Gifford and Evans, 1981; Farrar, 1988; Ho, 1988; Verkleij and Challa, 1988),

In this paper, partitioning is studied at the whole plant level because regulation that may occur in one region of the plant is not isolated from the other parts of the plant (Daie, 1985). Furthermore, it is more likely that a series of events rather than a single limiting event controls partitioning (Wardlaw, 1990). Emphasis is put on the partitioning into generative plant parts. The importance of the source, the transport path and the sinks in the regulation of dry matter partitioning at the whole plant

level is discussed and the concept of sink strength is evaluated—what is sink strength? what is its importance and how can it be measured? Finally, a model for dry matter partitioning based on sink strengths of the organs is described.

### Effect of source on dry matter partitioning

A source can be crudely defined as an organ that is a net exporter of carbon assimilates. Source strength refers to the rate at which carbon assimilates are produced. A high source strength due, for example, to high irradiance strongly enhances the total plant growth, but information on the effect of source strength on the partitioning of the assimilates among the plant organs is limited.

Ho (1988, 1992) concluded that assimilate supply affects only the degree of competition among sinks, but not the partitioning among sinks. Daie (1985) also concluded that the source seems not to control partitioning. However, Wardlaw (1990) discussed that there is often an hierarchy among sinks. That is, some organs (e.g. fruits, seeds or underground storage organs) have priority and suffer less from a reduction in assimilate supply than other organs (e.g. flowers). Minchin *et al.* (1993) showed that this behaviour could be predicted by a simple model based on mass flow according to the Münch hypothesis through the phloem and Michaelis-Menten kinetics of unloading in the sinks and they (Minchin *et al.*, 1994) applied this model to root:shoot partitioning in barley seedlings. However, the reported hierarchy among organs for assimilates is often an apparent one. A change in weight ratio between organs with changing source strength does not always indicate a true change in dry matter partitioning, for instance, the allometric relationship of the organs (a constant relation between the relative growth rates) might still be unchanged as discussed by Farrar and Williams (1991). Equally, the effects of source strength might primarily be on ontogeny which may indirectly lead to a change in weight ratios (Terry, 1968). Organ initiation often decreases and organ abortion increases with decreasing source strength (Wardlaw, 1990). As a consequence in the long term the number of sink organs may change considerably and hence the dry matter partitioning.

In cucumber no noticeable relationship between the partitioning of dry matter into the fruits and solar radiation of the same day or week was observed during a growing season (Liebig, 1978; Marcelis, 1992a). However, a large change in solar radiation seemed to induce a change in dry matter partitioning to the fruits, but the time lag between the change in radiation and the change in partitioning was variable (Marcelis, 1992a). That the direct effect of irradiance on dry matter partitioning is limited, is substantiated by an experiment where cucumber plants of identical size and with a fixed number of fruits

were shaded for 4 d (Marcelis, 1993*d*). Total plant growth rate decreased by 60%, but the partitioning between generative and vegetative growth was not significantly affected. Heuvelink (1995*b*) also concluded for tomato that source strength had no direct effect on dry matter partitioning between generative and vegetative parts. However, Yoshioka and Takahashi (1979, 1981) found that the distribution of  $^{14}\text{C}$  and dry matter to the fruits decreased at increasing irradiance in tomato plants with a fixed number of fruits per plant.

Although effects of source strength in the short term may be limited, in the long term increased source strength may increase dry matter partitioning into the fruits, as shown for cucumber (Marcelis, 1993*d*). This effect of source strength on dry matter partitioning was an indirect effect via an increase in number of fruits on the plant rather than a direct effect on dry matter partitioning (Marcelis, 1993*d*). Accordingly, an enhancement of source strength by  $\text{CO}_2$  enrichment during an extended period increased dry matter partitioning into the fruits for cucumber and sweet pepper (Nederhoff, 1994) and tomato (Tripp *et al.*, 1991). However, in some experiments no effects of source strength on the dry matter partitioning between fruits and vegetative parts were observed in tomato and soybean (Egli, 1988; Cockshull *et al.*, 1992; Nederhoff, 1994).

In conclusion, source strength *per se* seems to have no direct effect on dry matter partitioning. However, in the long term (weeks) dry matter partitioning may change because of a change in number of sinks and thus in amount of machinery. According to Farrar (1992) this can be interpreted as source strength exerting coarse control but not fine control over dry matter partitioning.

### Effect of transport path on dry matter partitioning

As the assimilates move from source to sink organs via the phloem, this transport system may control dry matter partitioning. According to the Hagen-Poisseeuille relationship the cross-sectional area of the phloem and the length of the phloem pathway from source to sink are important determinants of the resistance of the transport path (Farrar, 1992). Hence, proximity of sink and source could be important in regulating dry matter partitioning. Moreover, differentiation of the phloem determining the vascular link and phyllotaxis may affect dry matter partitioning. Experiments with labelled carbon have shown that assimilates may be transported according to the phyllotaxic link between sources and sinks (Wardlaw, 1968; Russell and Morris, 1983). However, when the source:sink balance is modified these apparent phyllotaxic limitations on assimilate partitioning are readily overcome (Wardlaw, 1968; Oparka and Davies, 1985). Hocking and Steer (1994) also concluded that, in general, phyllo-

taxis is not an important factor regulating dry matter partitioning.

Generally, the phloem does not limit translocatory flux, as it appears to have considerable spare transport capacity (Milthorpe and Moorby, 1969; Kallarackal and Milburn, 1984; Wardlaw, 1990; Passioura and Ashford, 1974). However, in apical meristems and young primordia the phloem may not yet be differentiated to ensure enough transport capacity (Williams, 1960; Milthorpe and Moorby, 1969; Patrick, 1972). Despite the fact that, in some cases, partitioning is related to the relative distance between sinks and sources (Cook and Evans, 1983), distance is generally not an important factor in dry matter partitioning. It has been shown that increasing the distance between source leaves and fruits had no effect on fruit growth in apple (Hansen, 1977) and cucumber (Schapendonk and Brouwer, 1984). Further evidence that transport distance is not important in regulating dry matter partitioning in the whole plant was found by Gent (1982) for soybean plants with two branches. Pod growth was similar for all branches whether 2 leaflets and 2 pods per node were retained on each branch or whether on one branch 1 leaflet and 3 pods and on the other branch 3 leaflets and 1 pod per node were retained (Gent, 1982). Similarly, Heuvelink (1995*a*) showed that in tomato plants with two shoots and a shoot length of more than 2 m dry matter partitioning between vegetative and generative parts was not affected whether the fruits were located on only one shoot or whether the same number of fruits were divided over the two shoots. Part of these results can be explained by the fact that sometimes sinks were functioning close to assimilate saturation (sink limitation). The model on phloem transport proposed by Minchin *et al.* (1993) showed that the transport resistance does not affect partitioning when sinks are functioning at saturation. In many situations plant organs may function close to saturation (Lambers, 1983; Hocking and Steer, 1994), which further substantiates that the transport path is normally not a dominating factor in dry matter partitioning.

### Effect of sink on dry matter partitioning

The partitioning of assimilates among sinks has often been suggested to be regulated primarily by the sinks themselves (Evans, 1975; Gifford and Evans, 1981; Farrar, 1988; Ho, 1988; Verkleij and Challa, 1988). Effects of sinks on dry matter partitioning have been clearly demonstrated by experiments on several fruit crops (Heim *et al.*, 1979; Lenz, 1979; Nielsen and Veierskov, 1988; Richardson and McAneny, 1990; Marcelis, 1993*c*; Heuvelink and Buiskool, 1995): An increase in number of generative sinks increased the generative:vegetative ratio, but decreased the partitioning into the individual generative sinks. In cucumber the daily dry matter parti-

tioning to the fruits showed a closer relationship to the total weight than to the total number of fruits growing at the same time on a cucumber plant (Fig. 1). Hence the sink strength (competitive ability to attract assimilates) is not only correlated with the number of sinks, but also with the weight of the individual sink organs. As will be discussed later the correlation with weight of individual sink organs seems not to be a causal one.

To understand the regulation of dry matter partitioning by the sinks, there has been substantial interest in a property of a sink, called sink strength, that determines this regulation. The term sink strength can be defined as the competitive ability of an organ to receive or attract assimilates (Wareing and Patrick, 1975; Wolswinkel, 1985; Farrar, 1993b). At present many discussions focus on the question whether the concept of sink strength is a useful one, or a vague and confusing concept (Farrar, 1993a). Much confusion is due to lack of a clear definition of sink strength. The actual rate of assimilate import or of growth has often been used as a measure of sink strength (Warren Wilson, 1972). When defined in this way, sink strength in fact represents the net result of assimilate flow which may depend on the competitive ability of all sinks on a plant and the assimilate supply (source strength). This is not a useful measure of sink strength and it is the prime cause why some authors reject the use of the concept of sink strength. Minchin and Thorpe (1993), dismissing sink strength (as measured by the actual import rate) as a misnomer, and other authors (e.g. Patrick, 1993) stated that it should be possible to identify a set of parameters to describe a sink's ability to influence assimilate import which are independent of the rest of the plant.

#### *Gross versus net sink strength*

The carbon assimilates an organ receives are used for dry weight accretion and respiration. To estimate the net gain of carbon from the dry weight, the carbon concentration of the dry matter should be taken into account. This concentration differs between types of plant organs (Vertregt and Penning de Vries, 1987), but it may be fairly constant for one type of organ, as observed for cucumber fruits (Marcelis and Baan Hofman-Eijer, 1995). However, Ho (1976) observed a distinct change in carbon concentration of tomato leaves during ontogeny. Due to respiratory losses of assimilates in the sink organ, the absolute growth rate or the net accumulation rate of dry matter in a sink organ underestimates the total amount of assimilates a sink receives. According to Ho *et al.* (1989) the net accumulation rate of dry matter is a measure of 'net sink strength', while the net gain of dry matter plus respiratory loss of dry matter is a measure of 'gross sink strength'.

When carbon partitioning among fruits in cucumber is measured in terms of dry weight distribution on average

85–87% of all the carbon is considered, because 13–15% is respired (Marcelis and Baan Hofman-Eijer, 1995). For fruits of other species 8–22% is respired (Blanke and Lenz, 1989; Walton and DeJong, 1990; Pavel and DeJong, 1993; DeJong and Walton, 1989). However, over the course of a growing season up to one-half of the gross carbon produced by photosynthesis may be lost by respiration (Amthor, 1984). Respiration can be separated conceptually into two functional components: maintenance respiration and growth respiration (Thornley, 1970). Maintenance respiration is primarily a function of organ weight, organ composition, temperature, and metabolic activity (Amthor, 1984; Lambers, 1985). Growth respiration is, in general, linearly related to the growth rate (Penning de Vries *et al.*, 1974; Marcelis and Baan Hofman-Eijer, 1995). This relationship may depend on the type of organ due to differences in chemical composition (Penning de Vries *et al.*, 1974; Vertregt and Penning de Vries, 1987). Due to linearity between dry weight increase and growth respiration, net sink strength can be a good indicator for the total flux for dry weight growth plus growth respiration. In those cases where the fractional loss by maintenance respiration is low, for example, when the relative growth rate is high, net sink strength can also be an indicator for gross sink strength.

#### *Potential growth rate as a measure of sink strength*

Wareing and Patrick (1975) and Wolswinkel (1985) suggested the potential capacity of a sink to accumulate assimilates as a measure of sink strength. This potential capacity reflects the intrinsic ability of the sink to receive or attract assimilates, which has also been stressed by Ho (1988) as a critical determinant of organ growth. More precisely, the sink strength can be measured as the potential capacity to import assimilates into the phloem of the sink region and to transport the imported substances from the phloem into the cells of the sink organ (Wolswinkel, 1985). The potential capacity for assimilate accumulation of a sink can be quantified by the potential growth rate of a sink, i.e. the growth rate under conditions of non-limiting assimilate supply. Conditions for potential growth can be created by growing plants at a high irradiance and/or reducing the number of sinks on a plant. Sometimes problems may arise in measuring the potential growth rate, as reported by Lieth and Pasion (1991) for rose leaves and Marcelis (1994) for vegetative growth in cucumber, while in sweet pepper potential growth rate of the fruits is hardly measurable as in many fruits blossom-end rot occurs when assimilate supply is high (Marcelis, unpublished data). Potential growth rate is not a static parameter, but may change with, for example, developmental stage or temperature, but not with factors such as light intensity or CO<sub>2</sub> concentration which are assumed to affect only the availability of

assimilates. During development of an organ the potential growth often shows a sigmoid growth pattern (Bollard, 1970; Dennett *et al.*, 1978; Marcelis, 1992*b*). Effects of temperature on growth rate are often confounded with effects of the developmental stage. Marcelis and Baan Hofman-Eijer (1993) showed that the development of a cucumber fruit was closely related to the temperature sum and that the effect of temperature on the growth rate of a fruit could be separated from developmental effects by considering growth as a function of the temperature sum. As development is related to temperature sum, the growing period (in days) decreases with increasing temperature. The growth rate of organs usually increases with increasing temperature (Wardlaw, 1970; Auld *et al.*, 1978; Egli and Wardlaw, 1980; Dekhuijzen and Verkerke, 1986; Marcelis and Baan Hofman-Eijer, 1993), although Heuvelink and Marcelis (1989) and De Koning (1994) did not observe a significant effect of temperature on potential growth rate of tomato fruits. For cucumber fruits it was concluded that the potential growth rate is a function of both its temperature sum after anthesis and the actual temperature (Marcelis and Baan Hofman-Eijer, 1993).

When organ growth was not limited by assimilate supply, the increase in growth rate with increasing temperature was much higher than at a lower level of assimilate supply (Wardlaw, 1970; Egli and Wardlaw, 1980; Marcelis and Baan Hofman-Eijer, 1993); a non-limiting assimilate supply was achieved in cucumber by removing competing fruits (Marcelis and Baan Hofman-Eijer, 1993), in wheat by growing grains at high irradiance (Wardlaw, 1970) or in soybean by growing cotyledons *in vitro* (Egli and Wardlaw, 1980). As the level of assimilate supply hardly affects the growing period of an organ (Dennett *et al.*, 1979; Cockshull *et al.*, 1992; De Koning, 1994; Marcelis, 1993*b*), while it affects the magnitude of the response of the growth rate to temperature, at a non-limiting assimilate supply the final organ size (potential size) may increase whereas at a low assimilate supply the final size may decrease with increasing temperature.

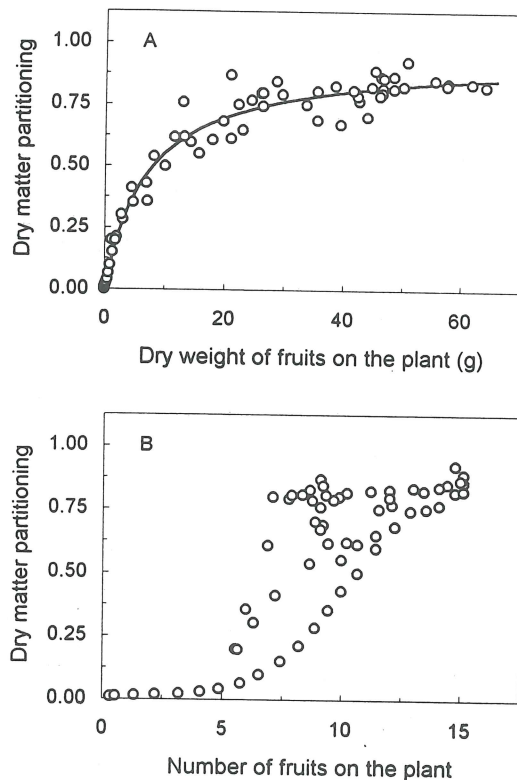
Several authors (Coombe, 1976; Ho, 1984; Jenner, 1985; Patten *et al.*, 1986) have argued that growth potential of sink organs is largely determined during the early development of the sink organ. However, these conclusions may partly be the result of effects of environmental factors during early sink development on the future source capacity of the plant rather than on the future sink strength. Marcelis (1993*b*) showed that assimilate supply during ovary development in cucumber had no subsequent effects on fruit growth, except for effects mediated through the source capacity of the plants. However, increasing the temperature of the ovary (from 17.5 to 27.5 °C), while plant temperature was kept constant (17.5 °C), showed that environmental factors during early development can also have a positive effect on the poten-

tial growth rate of the cucumber fruit when source capacity is not affected (Marcelis and Baan Hofman-Eijer, 1993).

*Sink strength = sink size × sink activity?*

Warren Wilson (1972) proposed that sink strength is the product of sink size and sink activity, which can also be stated as the product of sink weight and relative growth rate (*RGR*). Ho (1988, 1992) suggested that sink size reflects the physical constraint while sink activity reflects the physiological constraint upon a sink organ's assimilate import. Ho (1988, 1992) considered cell number as a suitable measure of sink size, and the physiological processes for the uptake and accumulation of imported assimilate in the sink cells as a meaningful measure of sink activity. However, in cucumber fruits grown at non-limiting assimilate supply, a small number of cells, due to a low assimilate supply during early fruit development, was to a great extent compensated by an increased expansion rate of individual cells (Marcelis, 1993*b*). Therefore, cell number seems not to be an important determinant of fruit size, although fruit size often correlates positively with cell number (Marcelis, 1993*b*). In potato, Sattelmacher and Laidig (1991) also observed a positive correlation between tuber size and cell number, but the growth rate seemed not to be causally related to cell number. In addition, Büniger-Kibler and Bangerth (1982) and Bohner and Bangerth (1988) observed an inverse relationship between cell number and cell size in tomato fruits when parthenocarpy was induced by exogenously applied hormones or when distal and proximal fruits were pollinated simultaneously. These results indicate that cell number is not a suitable measure of sink size.

According to Wardlaw (1990) sink strength may increase with increasing sink size, because of an associated increase in the size of the surface (membrane) area across which metabolites are transferred from the vascular system to the zone of utilization (unloading area). As shown in Fig. 1A, dry matter partitioning into cucumber fruits correlates with the total fruit weight (sink size), which might indicate a correlation between sink size and sink strength. However, the size often correlates with the age of an organ, which might have led to an apparent relationship between sink size and sink strength. The actual growth rate of a cucumber fruit depended on its age rather than its size (Marcelis, 1993*b*). Different weights of cucumber fruits were achieved by retaining 6 or no competing fruits during 6, 12 or 18 d (Table 1). Despite strong differences (>300%) in fruit weight, a few days after removal of the competing fruits the small fruits grew almost at the potential rate, i.e. the growth rate of fruits which were grown without competing fruits throughout. A small size was fully compensated by an increased sink activity (*RGR*). Comparable results were



**Fig. 1.** The daily fraction of dry matter partitioned into the fruits of cucumber as a function of total dry weight (A) or number (B) of actively growing fruits on a cucumber plant. The partitioning was measured non-destructively on three replicate plants each day during a growing season (redrawn from Marcelis, 1993c).

**Table 1.** The growth rate and relative growth rate (RGR) of cucumber fruits at day 19 after anthesis when different fresh weights were achieved by retaining six or no competing fruits on a plant during 6, 12 or 18 d from anthesis

Assimilate supply was assumed not to constrain fruit growth, except when the six competing fruits were present on the plant (data are based on results of Marcelis, 1993b).

Duration of competition (d)	Weight <sup>a</sup> (g)	Growth rate <sup>a</sup> (g d <sup>-1</sup> )	RGR <sup>a</sup> (g g <sup>-1</sup> d <sup>-1</sup> )
0	1393 a	52 a	0.038 a
6	1209 b	49 ab	0.040 a
12	670 c	49 ab	0.072 b
18	395 d	40 b	0.102 c
Continuous (19 d)	356 d	12 c	0.034 a

<sup>a</sup> Means followed by the same letter were not significantly different ( $P \leq 0.05$ ).

observed for tomato fruits (De Koning, 1994). However, in peach, fruit growth generally did not fully reach the potential growth rate after removal of competing fruits (Grossman and DeJong, 1995). Moorby (1968) also found indications that sink size is not an important determinant of sink strength, as he observed a poor correlation between the size of individual potato tubers and the amount of photosynthate transported into them.

Starck and Ubysz (1974) concluded that dry matter partitioning into an organ was determined by its growth rate rather than its size. When the sink strength of an organ is high, its growth rate will be high and, consequently, its size will increase. Therefore, sink strength and sink size are often intercorrelated, but sink strength is probably not causally related to sink size.

### Model for dry matter partitioning based on sink strengths

As discussed before, dry matter partitioning is primarily regulated by the sink strengths of the sink organs, while neither the source nor the transport path are dominating factors in regulating dry matter partitioning. Moreover, it has been discussed that the potential growth rate may quantitatively reflect the sink strength of an organ. Based on these conclusions, dry matter partitioning in several crops has been modelled as a function of the potential growth rates of the plant organs (Jones *et al.*, 1980, 1989; Lieth and Pasian, 1991; De Koning, 1994; Grossman and DeJong, 1994; Heuvelink and Bertin, 1994; Marcelis, 1994; Wermelinger *et al.*, 1991).

In most of these models the plant is considered to consist of a set of sink organs which derive their assimilates for growth from one common assimilate pool. The pool with the assimilates is replenished by photosynthesis in the source organs. Part of the assimilates from the assimilate pool are used for maintenance respiration and the remaining assimilates are available for growth. Thus, maintenance respiration is assumed to have priority above growth. Growth respiration of an organ is linearly related to its growth rate. The growth rates of the organs are determined by the amount of assimilates in the assimilate pool and sink strengths of the sink organs. Differences in growth rates between sink organs depend on differences in sink strengths. Hence, dry matter partitioning depends on the sink strengths. Using potential growth rate as a measure of sink strength, the fraction of dry matter partitioned into each sink is proportional to its potential growth rate relative to the total potential growth rate of all sinks together.

The utilization of assimilates in the sink can be related to the level of assimilates by a curvilinear relationship, obeying Michaelis-Menten kinetics (Patrick, 1988).

$$Y_i = Y_{\text{pot},i}A/(K_{m,i} + A) \quad (1)$$

where  $Y_i$  is the flux for dry weight growth of organ  $i$  (including growth respiration);  $Y_{\text{pot},i}$  is the flux for potential growth of organ  $i$  (including growth respiration), the maximum rate under the prevailing conditions for  $A \rightarrow \infty$ ;  $K_{m,i}$  is the Michaelis-Menten constant, which determines the affinity for assimilates (low  $K_m$  value means high affinity);  $A$  is the level of assimilates available for growth.

As the dry matter partitioning into an organ can be

characterized by the ratio between its growth and that of all organs together, in a plant with  $n$  organs the fraction of dry matter partitioned into organ  $i$  ( $f_i$ ) can be calculated as

$$f_i = \frac{Y_{\text{pot},i}/(K_{m,i} + A)}{\sum_{j=1}^n (Y_{\text{pot},j}/(K_{m,j} + A))} \quad (2)$$

From eqn. 2 it can be deduced that when all organs have the same affinity for assimilates ( $K_m$ -value), the fraction of dry matter distributed to an organ equals the ratio of its potential growth rate to that of all organs together (eqn. 3). In this case dry matter partitioning is not affected by source strength (Fig. 2A). As discussed before, source strength indeed has generally no direct effect on dry matter partitioning.

$$f_i = \frac{Y_{\text{pot},i}}{\sum_{j=1}^n Y_{\text{pot},j}} \quad (3)$$

In those cases where source strength has a direct effect on partitioning the fraction of dry matter partitioned into an organ can be calculated according to eqn. 2. In this

situation two properties of the sink (potential growth rate and affinity for assimilates) determine its sink strength. When the affinity differs between two organs the dry matter partitioning changes with source strength, such that the organ with the lowest  $K_m$ -value gets an increasing fraction of dry matter when assimilate supply decreases (Fig. 2B). Hence, an hierarchy or priority in dry matter partitioning between organs may be explained by two properties of the sink organs. In fact, this calculation procedure is a simplified version of that of Minchin *et al.* (1993). It ignores the transport resistance (resistance is set to zero) and assimilate concentration in the sink region is not simulated. As discussed before, transport resistance is generally not a dominating factor in dry matter partitioning. Moreover, proper estimates of transport resistance and photosynthate concentrations at the source (loading) and sink (unloading) regions are difficult to obtain (Cooper and Thornley, 1976; Brouwer, 1983; Mäkelä and Sievänen, 1987), which may limit the possibilities for application and validation of models with transport resistances and photosynthate concentrations. The level of assimilate availability that an organ experiences increases with source strength, but decreases with sink

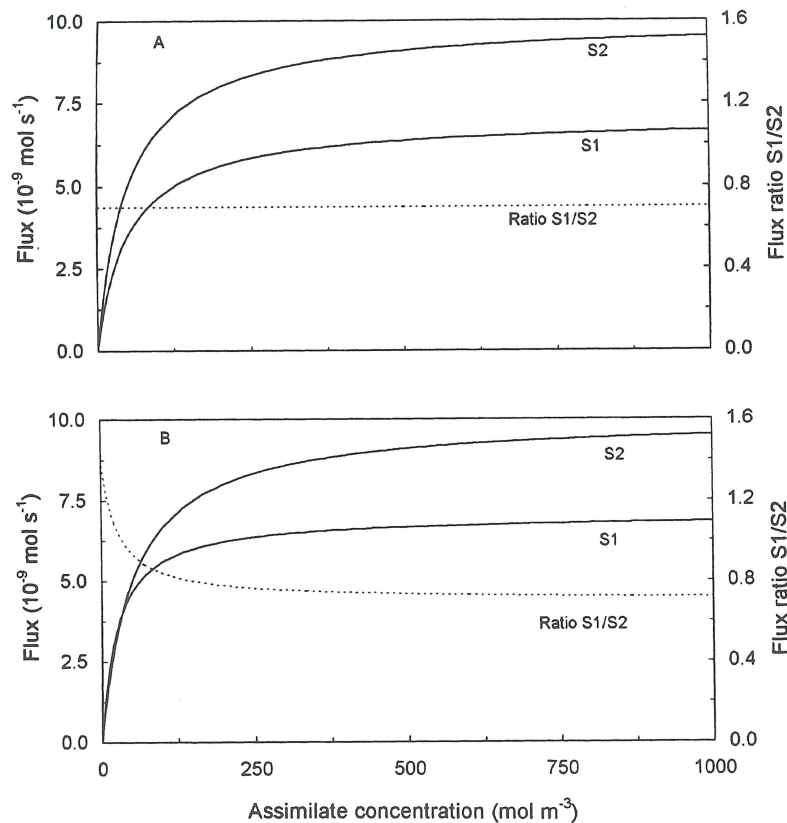


Fig. 2. Assimilate fluxes into two hypothetical sink organs (S1 and S2) and the ratio of these fluxes as a function of the level of assimilate supply (assimilate concentration in the assimilate pool of the plant). Fluxes are described by Michaelis-Menten kinetics (eqn. 1). The two sinks have different potential growth rates: 7 and  $10 \times 10^{-9}$  mol s<sup>-1</sup> for sinks 1 and 2, respectively. The  $K_m$ -values of sinks 1 and 2 are both 50 mol m<sup>-3</sup> (A) or 25 and 50 mol m<sup>-3</sup>, respectively (B).

strengths of the plant's organs. Therefore, several authors (Hansen, 1989; Marcelis, 1994; Bertin, 1995) used the source:sink ratio, expressed as the ratio of total plant growth rate to total potential growth rate, as a measure for the level of assimilates available for growth.

In a model for dry matter partitioning in cucumber (Marcelis, 1994), the potential growth rate of each fruit was described as a function of both its temperature sum after anthesis and the actual temperature. The potential growth rate of the vegetative parts was described as a function of the temperature. During a growing season the potential growth rate of the fruits changed considerably due to changes in number and age of the fruits on the plant (Fig. 3A). During most of the time the actual growth rate was far less than the potential growth rate (the average ratio between actual and potential rate was 0.35). Thus, sink demand exceeded assimilate supply. The

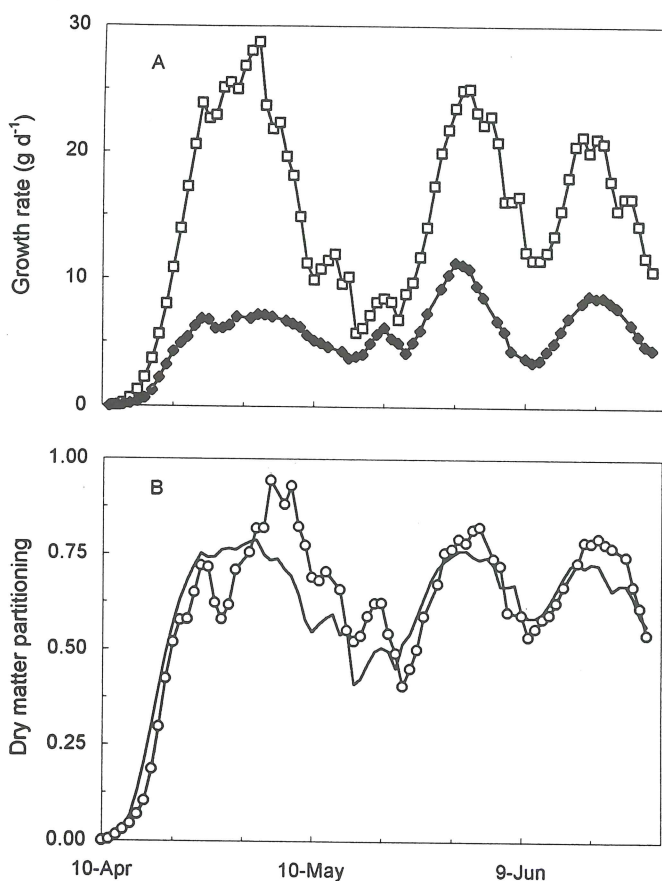


Fig. 3. Time-course of the actual (A,  $\blacklozenge$ ) and potential growth rate of fruits (A,  $\square$ ) and the measured (B,  $-\circ-$ ) and simulated (B,  $—$ ) fraction of dry matter partitioned into the fruits of cucumber. According to eqn. 3, dry matter partitioning into the fruits was simulated as the potential growth of the fruits divided by that of the total plant (fruits and vegetative parts). Potential growth rate of the vegetative parts was  $9.1 \text{ g d}^{-1}$ . Calculation of fruit potential growth rate was based on measurements of temperature and dates of anthesis and harvest of the non-aborting fruits. (A) Measured actual rates from Marcelis (1992a) and calculated potential rates were based on a model described by Marcelis (1994). (B) From Marcelis (1994).

fraction of dry matter partitioned into the generative parts was well predicted by the ratio between their potential growth rate and that of the total plant (fruits+vegetative parts) (Fig. 3B). Marcelis (1994) showed that the partitioning among the individual fruits could also be reasonably simulated by a model based on potential growth rates. However, the growth rate of young fruits was often somewhat overestimated and that of old fruits underestimated, because of dominance among fruits. Taking the  $K_m$ -values of the fruits into account, the simulation of the competition between young and old fruits improved.

The number and timing of the fruits on the plant was shown to have a strong impact on model results (Marcelis, 1994). The formation rate of non-aborting fruits was calculated as a function of the source:sink ratio and the temperature. However, there were some deviations between the simulated and measured formation rate of non-aborting fruits. As our knowledge on fruit abortion is limited, while abortion has a large effect on dry matter partitioning, more research is needed on the regulation of fruit abortion.

Wareing and Patrick (1975) and Patrick (1988) emphasized the importance of identifying whether organ growth is either limited by assimilate supply (source limited) or saturated by assimilate supply (sink limited), because this might have implications for the regulation of organ growth. Under sink limitation, organ growth solely depends on its potential capacity to accumulate assimilates (potential growth). Under source limitation, organ growth depends on the source strength and may also depend on the organ's potential capacity and affinity to accumulate assimilates and on the hydraulic resistance. However, often the term source-limitation is interpreted as organ growth being determined only by the source, while sink-limitation is interpreted as organ growth only determined by the sinks. Farrar (1993c) suggested abandoning the traditional attempts to speak of sink- or source-limitation, because control of fluxes (growth) will be shared by both source and sink rather than centred on any single one. The results on cucumber indicate that although growth may be source limited, the fraction of dry matter partitioned into an organ can, to a great extent, be related to its potential growth rate relative to that of other organs. Thus, although source limited, the fraction of dry matter partitioned into each organ is still primarily regulated by the sinks. However, the absolute growth rates of the organs also depend strongly on the source strength.

The study on cucumber has shown that most of the data on dry matter partitioning can be described by the variation among organs in their potential capacity to accumulate assimilates (potential growth rate). For other crops there are also indications that dry matter partitioning into an organ is proportional to the potential



growth rate of that organ (Jones *et al.*, 1980, 1989; Lieth and Pasion, 1991; De Koning, 1994; Grossman and DeJong, 1994; Heuvelink and Bertin, 1994; Wermelinger *et al.*, 1991). This corroborates that the hydraulic resistance of the transport path is negligible in most cases. Although these studies have identified the potential capacity to accumulate assimilates as an important determinant of sink strength, the mechanism determining this potential capacity is not elucidated yet. At least for cucumber fruits, neither cell number nor the initial assimilate supply are essential in determining this capacity. It could be worthwhile studying whether the maximum rate of unloading or utilization and compartmentation in the sink organ are important determinants of the potential growth rate, and how these processes are controlled by hormones or, as suggested by Farrar (1992), by sucrose. In addition, the use of molecular tools may help in a better mechanistic understanding of the control of sink strength and dry matter partitioning (Frommer and Sonnewald, 1995).

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### References

- Amthor JS.** 1984. The role of maintenance respiration in plant growth. *Plant, Cell and Environment* **7**, 561–9.
- Auld BA, Dennett MD, Elston J.** 1978. The effect of temperature changes on the expansion of individual leaves of *Vicia faba* L. *Annals of Botany* **42**, 877–88.
- Bertin N.** 1995. Competition for assimilates and fruit position affect fruit size in indeterminate greenhouse tomato. *Annals of Botany* **75**, 55–65.
- Blanke MM, Lenz F.** 1989. Fruit photosynthesis. *Plant, Cell and Environment* **12**, 31–46.
- Bohner J, Bangerth F.** 1988. Effects of fruit set sequence and defoliation on cell number, cell size and hormone levels of tomato fruits (*Lycopersicon esculentum* Mill.) within a truss. *Plant Growth Regulation* **7**, 141–55.
- Bollard EG.** 1970. The physiology and nutrition of developing fruits. In: Hulme AC, ed. *The biochemistry of fruits and their products*. London: Academic Press, 387–425.
- Brouwer R.** 1963. Some aspects of the equilibrium between overground and underground plant parts. *Mededelingen IBS* **213**, 31–9.
- Brouwer R.** 1983. Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science* **31**, 335–48.
- Bünger-Kibler S, Bangerth F.** 1982. Relationship between cell number, cell size and fruit size of seeded fruits of tomato (*Lycopersicon esculentum* Mill.), and those induced parthenocarpically by the application of plant growth regulators. *Plant Growth Regulation* **1**, 143–54.
- Cockshull KE, Graves CJ, Cave CRJ.** 1992. The influence of shading on yield of glasshouse tomatoes. *Journal of Horticultural Science* **67**, 11–24.
- Cook MG, Evans LT.** 1983. The roles of sink size and location in the partitioning of assimilates in wheat ears. *Australian Journal of Plant Physiology* **10**, 313–27.
- Coombe BG.** 1976. The development of fleshy fruits. *Annual Review of Plant Physiology* **27**, 507–28.
- Cooper AJ, Thornley JHM.** 1976. Response of dry matter partitioning, growth and carbon and nitrogen levels in the tomato plant to changes in root temperature: experiment and theory. *Annals of Botany* **40**, 1139–52.
- Daie J.** 1985. Carbohydrate partitioning and metabolism in crops. *Horticultural Reviews* **7**, 69–108.
- De Koning ANM.** 1994. Development and dry matter distribution in tomato: a quantitative approach. Dissertation, Agricultural University, Wageningen.
- DeJong TM, Walton EF.** 1989. Carbohydrate requirements of peach fruit growth and respiration. *Tree Physiology* **5**, 329–35.
- Dekhuijzen HM, Verkerke DR.** 1986. The effect of temperature on development and dry-matter accumulation of *Vicia faba* seeds. *Annals of Botany* **58**, 869–85.
- Dennett MD, Auld BA, Elston J.** 1978. A description of leaf growth in *Vicia faba* L. *Annals of Botany* **42**, 223–32.
- Dennett MD, Elston J, Milford JR.** 1979. The effect of temperature on the growth of individual leaves of *Vicia faba* L. in the field. *Annals of Botany* **43**, 197–208.
- Egli DB.** 1988. Alterations in plant growth and dry matter distribution in soybean. *Agronomy Journal* **80**, 86–90.
- Egli DB, Wardlaw IF.** 1980. Temperature response of seed growth characteristics of soybeans. *Agronomy Journal* **72**, 560–4.
- Evans LT.** 1975. Beyond photosynthesis—the role of respiration, translocation and growth potential in determining productivity. In: Cooper JP, ed. *Photosynthesis and productivity in different environments*. Cambridge University Press, 501–7.
- Farrar JF.** 1988. Temperature and the partitioning and translocation of carbon. In: Long SP, Woodward FI, eds. *Plants and temperature*. Symposium of the Society of Experimental Biology **42**. Cambridge: Company of Biologists, 203–35.
- Farrar JF.** 1992. The whole plant: carbon partitioning during development. In: Pollock CJ, Farrar JF, Gordon AJ, eds. *Carbon partitioning within and between organisms*. Oxford: BIOS Scientific Publishers, 163–79.
- Farrar JF.** (ed.) 1993a. Forum on sink strength: What is it and how do we measure it? *Plant, Cell and Environment* **16**, 1013–46.
- Farrar JF.** 1993b. Sink strength: What is it and how do we measure it? Introduction. *Plant, Cell and Environment* **16**, 1015.
- Farrar JF.** 1993c. Sink strength: What is it and how do we measure it? Summary. *Plant, Cell and Environment* **16**, 1045–6.
- Farrar JF, Williams ML.** 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment* **14**, 819–30.
- Fick GW, Loomis RS, Williams WA.** 1975. Sugar beet. In: Evans LT, ed. *Crop physiology*. Cambridge University Press, 259–95.
- Frommer WB, Sonnewald U.** 1995. Molecular analysis of carbon partitioning in solanaceous species. *Journal of Experimental Botany* **46**, 587–607.
- Gent MPN.** 1982. Effect of defoliation and depodding on long distance translocation and yield in Y-shaped soybean plants. *Crop Science* **22**, 245–50.
- Gifford RM, Evans LT.** 1981. Photosynthesis, carbon partitioning and yield. *Annual Review of Plant Physiology* **32**, 485–509.
- Grossman YL, DeJong TM.** 1994. PEACH: A simulation model

- of reproductive and vegetative growth in peach trees. *Tree Physiology* **14**, 329–45.
- Grossman YL, DeJong TM.** 1995. Maximum fruit growth potential following resource limitation during peach growth. *Annals of Botany* **75**, 561–7.
- Hansen P.** 1977. Carbohydrate allocation. In: Landsberg JJ, Cutting CV, eds. *Environmental effects on crop physiology*. London: Academic Press, 247–58.
- Hansen P.** 1989. Source/sink effects in fruits: an evaluation of various elements. In: Wright CJ, ed. *Manipulation of fruiting*. London: Butterworths, 29–37.
- Heim G, Landsberg JJ, Watson RL, Brain P.** 1979. Eco-physiology of apple trees: dry matter production and partitioning by young golden delicious trees in France and England. *Journal of Applied Ecology* **16**, 179–94.
- Heuvelink E.** 1995a. Dry matter partitioning in a tomato plant: one common assimilate pool? *Journal of Experimental Botany* **46**, 1025–33.
- Heuvelink E.** 1995b. Effect of plant density on biomass allocation to the fruits in tomato (*Lycopersicon esculentum* Mill.). *Scientia Horticulturae* **64**, 193–201.
- Heuvelink E, Buiskool RPM.** 1995. Influence of sink–source interaction on dry matter production in tomato. *Annals of Botany* **75**, 381–9.
- Heuvelink E, Bertin N.** 1994. Dry-matter partitioning in a tomato crop: comparison of two simulation models. *Journal of Horticultural Science* **69**, 885–903.
- Heuvelink E, Marcelis LFM.** 1989. Dry matter distribution in tomato and cucumber. *Acta Horticulturae* **260**, 149–57.
- Ho LC.** 1976. Variation in the carbon/dry matter ratio in plants. *Annals of Botany* **40**, 163–5.
- Ho LC.** 1979. Regulation of assimilate translocation between leaves and fruits in the tomato. *Annals of Botany* **43**, 437–48.
- Ho LC.** 1984. Partitioning of assimilates in fruiting tomato plants. *Plant Growth Regulation* **2**, 277–85.
- Ho LC.** 1988. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**, 355–78.
- Ho LC.** 1992. Fruit growth and sink strength. In: Marshall C, Grace J, eds. *Fruit and seed production: aspects of development, environmental physiology and ecology*. Society of Experimental Biology, Seminar series **47**. Cambridge University Press, 101–24.
- Ho LC, Grange RI, Shaw AF.** 1989. Source/sink regulation. In: Baker DA, Milburn JA, eds. *Transport of photoassimilates*. Harlow, Essex: Longman, 306–43.
- Hocking PJ, Steer BT.** 1994. The distribution of assimilates in tomato with special reference to stem reserves. *Annals of Botany* **73**, 315–25.
- Jenner CF.** 1985. Control of the accumulation of starch and protein in cereal grains. In: Jeffcoat B, Hawkins AF, Stead AD, eds. *Regulation of sources and sinks in crop plants*. Monograph **12**. Long Ashton: British Plant Growth Regulator Group, 195–209.
- Jones JW, Brown LG, Hesketh JD.** 1980. COTCROP: a computer model for cotton growth and yield. In: Hesketh JD, Jones JW, eds. *Predicting photosynthesis for ecosystem models II*. Boca Raton: CRC Press, 209–41.
- Jones JW, Dayan E, van Keulen H, Challa H.** 1989. Modelling tomato growth for optimizing greenhouse temperatures and carbon dioxide concentrations. *Acta Horticulturae* **248**, 285–94.
- Kallarackal J, Milburn JA.** 1984. Specific mass transfer and sink-controlled phloem translocation in castor bean. *Australian Journal of Plant Physiology* **11**, 483–90.
- Lambers H.** 1983. The functional equilibrium, nibbling on the edges of a paradigm. *Netherlands Journal of Agricultural Science* **31**, 305–11.
- Lambers H.** 1985. Respiration in intact plants and tissues: its regulation and dependence on environmental factors, metabolism and invaded organisms. In: Douce DA, Day DA, eds. *Encyclopedia of plant physiology*. New series, Vol. 18. Berlin: Springer Verlag, 418–73.
- Lang A, Düring H.** 1991. Partitioning control by water potential gradient: evidence for compartmentation breakdown in grape berries. *Journal of Experimental Botany* **42**, 1117–22.
- Lang A, Thorpe MR.** 1986. Water potential, translocation and assimilate partitioning. *Journal of Experimental Botany* **37**, 495–503.
- Lenz F.** 1979. Fruit effects on photosynthesis: light- and dark-respiration. In: Marcelle R, Clijsters H, van Poucke M, eds. *Photosynthesis and plant development*. The Hague: Dr W Junk Publishers, 271–81.
- Liebig HP.** 1978. Einflüsse endogener und exogener Faktoren auf die Ertragsbildung von Salatgurken (*Cucumis sativus* L.) unter besonderer Berücksichtigung von Ertragsrhythmik, Bestandesdichte und Schnittmassnahmen. Dissertation, Technischen Universität, Hannover.
- Lieth JH, Pasian CC.** 1991. A simulation model for the growth and development of flowering rose shoots. *Scientia Horticulturae* **46**, 109–28.
- Loomis RS, Rabbinge R, Ng E.** 1979. Explanatory models in crop physiology. *Plant Physiology* **30**, 339–67.
- Mäkelä AA, Sievänen RP.** 1987. Comparison of two shoot-root partitioning models with respect to substrate utilization and functional balance. *Annals of Botany* **59**, 129–40.
- Marcelis LFM.** 1992a. The dynamics of growth and dry matter distribution in cucumber. *Annals of Botany* **69**, 487–92.
- Marcelis LFM.** 1992b. Non-destructive measurements and growth analysis of the cucumber fruit. *Journal of Horticultural Science* **67**, 457–64.
- Marcelis LFM.** 1993a. Simulation of biomass allocation in greenhouse crops—a review. *Acta Horticulturae* **328**, 49–67.
- Marcelis LFM.** 1993b. Effect of assimilate supply on the growth of individual cucumber fruits. *Physiologia Plantarum* **87**, 321–8.
- Marcelis LFM.** 1993c. Fruit growth and biomass allocation to the fruits in cucumber. 1. Effect of fruit load and temperature. *Scientia Horticulturae* **54**, 107–21.
- Marcelis LFM.** 1993d. Fruit growth and biomass allocation to the fruits in cucumber. 2. Effect of irradiance. *Scientia Horticulturae* **54**, 123–30.
- Marcelis LFM.** 1994. A simulation model for dry matter partitioning in cucumber. *Annals of Botany* **74**, 43–52.
- Marcelis LFM, Baan Hofman-Eijer LR.** 1993. Effect of temperature on the growth of individual cucumber fruits. *Physiologia Plantarum* **87**, 313–20.
- Marcelis LFM, Baan Hofman-Eijer LR.** 1995. Growth and maintenance respiratory costs of cucumber fruits as affected by temperature, and ontogeny and size of the fruits. *Physiologia Plantarum* **93**, 484–92.
- Milthorpe FL, Moorby J.** 1969. Vascular transport and its significance in plant growth. *Annual Review of Plant Physiology* **20**, 117–38.
- Minchin PEH, Thorpe MR.** 1993. Sink strength: a misnomer, and best forgotten. *Plant, Cell and Environment* **16**, 1039–40.
- Minchin PEH, Thorpe MR, Farrar JF.** 1993. A simple mechanistic model of phloem transport which explains sink priority. *Journal of Experimental Botany* **44**, 947–55.
- Minchin PEH, Thorpe MR, Farrar JF.** 1994. Short term control

- of root:shoot partitioning. *Journal of Experimental Botany* **45**, 615–22.
- Moorby J.** 1968. The influence of carbohydrate and mineral nutrient supply on the growth of potato tubers. *Annals of Botany* **32**, 57–68.
- Nederhoff EM.** 1994. Effects of CO<sub>2</sub> concentration on photosynthesis, transpiration and production of greenhouse fruit vegetable crops. Dissertation, Agricultural University, Wageningen.
- Nielsen TH, Veierskov B.** 1988. Distribution of dry matter in sweet pepper plants (*Capsicum annum* L.) during the juvenile and generative growth phases. *Scientia Horticulturae* **35**, 179–87.
- Oparka KJ, Davies HV.** 1985. Translocation of assimilates within and between potato stems. *Annals of Botany* **56**, 45–54.
- Passioura JB, Ashford AE.** 1974. Rapid translocation in the phloem of wheat roots. *Australian Journal of Plant Physiology* **1**, 521–7.
- Patrick JW.** 1988. Assimilate partitioning in relation to crop productivity. *HortScience* **23**, 33–40.
- Patrick JW.** 1972. Vascular system of the stem of the wheat plant. II. Development. *Australian Journal of Botany* **20**, 65–78.
- Patrick JW.** 1993. Sink strength: whole plant considerations. *Plant, Cell and Environment* **16**, 1019–20.
- Patten KD, Patterson ME, Proebsting EL.** 1986. Factors accounting for the within-tree variation of fruit quality in sweet cherries. *Journal of the American Society for Horticultural Science* **111**, 356–60.
- Pavel EW, DeJong TM.** 1993. Estimating the photosynthetic contribution of developing peach (*Prunus persica*) fruits to their growth and maintenance carbohydrate requirements. *Physiologia Plantarum* **88**, 331–8.
- Penning de Vries FWT, van Laar HH.** 1982. Simulation of growth processes and the model BACROS. In: Penning de Vries FWT, van Laar HH, eds. *Simulation of plant growth and crop production*. Wageningen: Pudoc, 114–35.
- Penning de Vries FWT, Brunsting AHM, van Laar HH.** 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology* **45**, 339–77.
- Richardson PT, McAneny KJ.** 1990. Influence of fruit number on fruit weight and yield of kiwifruit. *Scientia Horticulturae* **42**, 233–41.
- Russell CR, Morris DA.** 1983. Patterns of assimilate distribution and source–sink relationships in the young reproductive tomato plant (*Lycopersicon esculentum* Mill.). *Annals of Botany* **52**, 357–63.
- Sattelmacher B, Laidig R.** 1991. Interrelation between growth rate of individual potato (*Solanum tuberosum* L.) tubers and their cell number. *Annals of Botany* **68**, 41–5.
- Schapendonk AHCM, Brouwer P.** 1984. Fruit growth of cucumber in relation to assimilate supply and sink activity. *Scientia Horticulturae* **23**, 21–33.
- Starck Z, Ubysz L.** 1974. Effect of limited supply of assimilates on the relationships between their sources and acceptors. *Acta Societas Botanicorum Poloniae* **43**, 427–45.
- Terry N.** 1968. Developmental physiology of sugar beet. I. The influence of light and temperature on growth. *Journal of Experimental Botany* **19**, 795–811.
- Thornley JHM.** 1970. Respiration, growth and maintenance in plants. *Nature* **227**, 304–5.
- Tripp KE, Peet MM, Pharr DM, Willits DH, Nelson PV.** 1991. CO<sub>2</sub>-enhanced yield and foliar deformation among tomato genotypes in elevated CO<sub>2</sub> environments. *Plant Physiology* **96**, 713–19.
- Verkleij FN, Challa H.** 1988. Diurnal export and carbon economy in an expanding source leaf of cucumber at contrasting source and sink temperature. *Physiologia Plantarum* **74**, 284–93.
- Vertregt N, Penning de Vries FWT.** 1987. A rapid method for determining the efficiency of biosynthesis of plant biomass. *Journal of Theoretical Biology* **128**, 109–19.
- Walton EF, DeJong TM.** 1990. Estimating the bioenergetic cost of a developing kiwifruit berry and its growth and maintenance respiration components. *Annals of Botany* **66**, 417–24.
- Wardlaw IF.** 1968. The control and pattern of movement of carbohydrates in plants. *The Botanical Review* **34**, 79–105.
- Wardlaw IF.** 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Australian Journal of Biological Sciences* **23**, 765–74.
- Wardlaw IF.** 1990. The control of carbon partitioning in plants. *New Phytologist* **116**, 341–81.
- Wareing PF, Patrick J.** 1975. Source-sink relations and the partition of assimilates in the plant. In: Cooper JP, ed. *Photosynthesis and productivity in different environments*. Cambridge University Press, 481–99.
- Warren Wilson J.** 1972. Control of crop processes In: Rees AR, Cockshull KE, Hand DW, Hurd RG, eds. *Crop processes in controlled environments*. London: Academic Press, 7–30.
- Wermelinger B, Baumgärtner J, Gutierrez AP.** 1991. A demographic model of assimilation and allocation of carbon and nitrogen in grapevines. *Ecological Modelling* **53**, 1–26.
- Williams RF.** 1960. The physiology of growth in the wheat plant. I. Seedling growth and the pattern of growth at the shoot apex. *Australian Journal of Biological Sciences* **13**, 401–28.
- Wilson JB.** 1988. A review of evidence on the control of shoot:root ratio, in relation to models. *Annals of Botany* **61**, 433–49.
- Wolswinkel P.** 1985. Phloem unloading and turgor-sensitive transport: factors involved in sink control of assimilate partitioning. *Physiologia Plantarum* **65**, 331–9.
- Yoshioka H, Takahashi K.** 1979. Studies on the translocation and accumulation of photosynthates in fruit vegetables. II. The translocation and distribution of <sup>14</sup>C-photosynthates in tomato plants during reproductive development and effects of topping and shading. *Bulletin of the Vegetable and Ornamental Crops Research Station Japan* **A6**, 71–84.
- Yoshioka H, Takahashi K.** 1981. Studies on the translocation and accumulation of photosynthates in fruit and vegetables. V. Translocation of photosynthates in a day, and effects of light conditions and night temperature on translocation and distribution of <sup>14</sup>C-photosynthates in tomato plants. *Bulletin of the Vegetable and Ornamental Crops Research Station Japan* **A9**, 63–81.