

GROWTH OF VEGETATIVE PLANT ORGANS; THE RESULT OF INTERACTING ONTOGENETIC PATTERNS

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Abstract

In indeterminate growing crops (e.g. tomato, cucumber) the dynamic allocation of assimilates to fruits and vegetative organs has been successfully described on the basis of the Relative Sink Strength (RSS) concept. The essence of this concept is that each organ has a potential to attract assimilates (sink strength) that can be expressed by its potential growth rate, that is the growth rate at non-limiting assimilate supply. This characteristic sink strength is not a constant, but changes with development of the organ under consideration. The share each organ receives from the total daily amount of assimilates available is the Relative Sink Strength, defined as the ratio of Sink Strength of the organ over Total Plant Sink Strength. This simple, but useful concept dealing with dry matter distribution at the level of the whole plant, could have a wider application in plant morphogenesis. Potential applications to the growth of individual organs of vegetative plant parts are discussed and consequences for studies of organ growth in relation to radiation and temperature considered.

1. Introduction

When dealing with the environmental regulation of plant morphogenesis, the usual approach, as demonstrated also in this workshop, is to compare the growth of organs, such as internodes, or leaves, over a certain time interval, under different environmental conditions. The interpretation of such experiments, however, may be difficult, because quite often manipulation of a factor may affect several processes at the same time. As a consequence results are often difficult to interpret and hence to generalise.

A common way to generalise knowledge of complex systems is to design a model, preferably at the level of, at least some of, the major processes involved (explanatory models) and often supplemented with empirical knowledge on the behaviour of the system. Explanatory plant growth models are generally photosynthesis driven, that means that they describe growth under source limitation. As a consequence the process of light harvesting and utilisation for dry matter production is elaborated considerably, but the distribution of assimilates represents a weak point (Evans, 1990). A more or less separate line of descriptive models deals with plant morphogenesis on the basis of empirical relations and without any explicit reference to photosynthesis at all (e.g. Larsen & Gertsson, 1993).

In recent years considerable progress has been made with the extension of photosynthesis driven crop growth models with modules dealing with partitioning of assimilates among fruits in indeterminate growing crops, such as cucumber and tomato (Marcelis, 1993a). The concept of development related sink strength of individual organs that was used in these studies to handle competition among different plant organs at different developmental stages, proved to be very effective to describe these complex systems (Marcelis, 1994a; Heuvelink, 1996a). In addition, they represent a bridge between the dry weight oriented growth models and the more empirical models dealing with plant architecture. Although fruit growth may represent a simple case, the linkage that has been made between organ dimensions and photosynthesis may offer further opportunities to bring both approaches together.

The objective of the present contribution is to explain briefly the concept of sink strength based dynamic dry matter allocation in indeterminate growing fruit vegetables and to discuss its potential to describe and understand the growth of vegetative plant organs.

2. Modelling growth of dynamically competing fruits

In indeterminately growing crops, such as tomato, cucumber, pepper, etc., the allocation of assimilates is complex. As a result of the continuous formation and harvesting of organs (fruits, leaves), ageing of the crop and the yearly and weekly dynamics in the crop environment (radiation, temperature) the competitive balance between different plant parts changes dynamically. The resulting assimilate allocation patterns are therefore hard to understand and hence to control. A considerable body of research of the last decade (Dayan et al., 1993a,b; De Koning, 1994; Marcelis, 1994b; Heuvelink, 1996b), has contributed to a better understanding of this complex system, the essence of which can be summarised as follows.

The carbohydrate reserves within a plant, in spite of their spatial distribution, chemical diversity and compartmentalisation, may be considered as belonging to one common assimilate pool, that is equally available to any plant part. Variations in assimilate availability to different plant parts are the consequence of fluctuations in supply through photosynthesis and consumption by the competing sinks. Assimilate availability is an abstraction that, I believe, could be represented by the apparent sugar concentration (ASC) of the common assimilate pool. The distribution of assimilates, in this view is not controlled by local levels, but exclusively by the power of organs to attract assimilates, their sink strength (SS). Sink strength of an organ is an abstraction, which theoretically could be interpreted as a conductivity term, because at the same ASC the rate of assimilate import will be proportional to SS of an organ. It is assumed that SS of an organ is proportional to (and hence characterised by) its potential growth rate, that is its growth rate at non limiting ASC. The cumulative growth curve of fruits may be represented by a Richards equation. SS of individual fruits therefore may be represented by the derivative of a Richards equation as a function of developmental stage (DVS) of the fruit (Fig. 1). In other words, at a given DVS all fruits have the same growth potential, irrespective of their origin (it should be noticed that this is an approximation, there are some factors that do affect the growing potential of fruits, but they are ignored here).

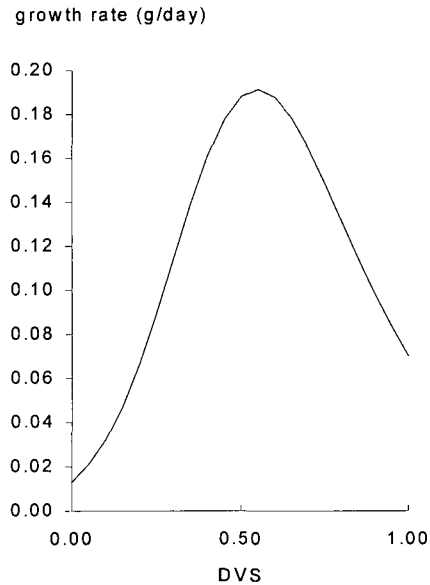


Figure 1. Potential growth rate of a tomato fruit as a function of developmental stage (DVS), after Heuvelink (1996a). The developmental stage is 0 at anthesis and is 1 when the harvestable stage is reached.

The actual daily growth of a given fruit (i) at time t is determined by the daily amount of assimilates formed (ignoring variations in the amount of assimilates stored in the common assimilate pool) and its relative competitive power, or relative sink strength (RSS): $RSS_i(t) = SS_i(t)/SS(t)$.

In this approach the vegetative sink is represented by one value for all vegetative plant parts (leaves, stem and roots), with a fixed ratio for the distribution among these categories. Because non limiting assimilate conditions disturb normal leaf growth (Ho et al., 1983), sink strength of the vegetative plant parts is derived indirectly from growth experiments with known SS of fruits.

The concept works well (Fig. 2), the major limitations are the phenomenon of dominance, observed with e.g. cucumber (Marcelis, 1993b), where older fruits suppress the growth of younger fruits, and the phenomena of flower and fruit abortion, which play an essential role in long-term feed back in fruit vegetables. Attempts to model these phenomena on the basis of ASC (e.g. Dayan et al., 1993a) are still speculative (Heuvelink, 1996: p.269).

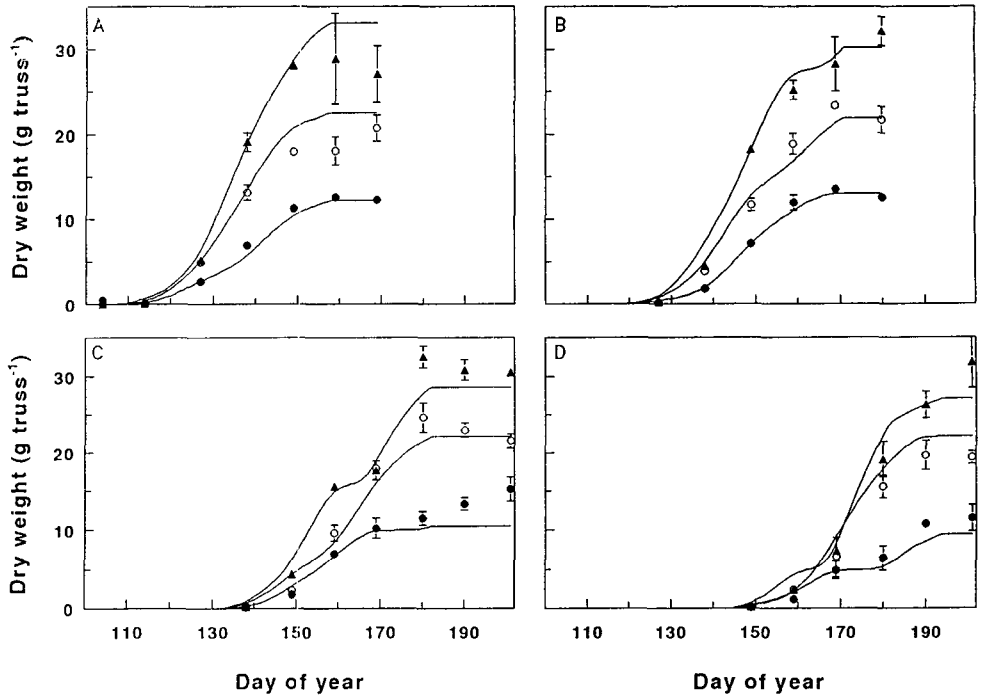


Fig. 2. Measured (points) and simulated (solid lines) growth rates of trusses of tomato fruits in the case of 3 ●, 5 ○ and 7 fruits ▲ per truss, for truss 1 (A), truss 3 (B), truss 5 (C) and truss 7 (D). Vertical bars indicate standard error of mean, when larger than symbols. After Heuvelink (1996a).

3. Applicability of this concept to vegetative growth patterns

When it is realised that competition for assimilates, together with the ontogenetic sink patterns of individual organs, play a key role in the growth of generative organs of indeterminate growing fruit vegetables, it seems logical to believe that the same principle could hold in other crops and other organs, in particular leaves and internodes. I will elaborate on the case of leaf growth, because of the availability of information, but the approach should be equally applicable to the growth of internodes. Whether the concept may be valid for leaves can be investigated by considering critically the applicability of the underlying principles in relation to leaf growth and by a preliminary comparison of some resulting growth patterns with patterns observed in the literature.

The first question to consider is the assumption of the common assimilate pool. A fundamental difference between leaves and fruits is the autotrophic character of leaf growth during most of its life span. The kinetics of leaf growth, however, provide little evidence for a dominant role of locally formed versus imported assimilates in the control of this process (Dale, 1992), suggesting that this aspect does not play an important role. I will therefore assume that the common assimilate pool for the whole plant is equally available to all plant organs, including leaves (Heuvelink, 1995a).

The second question is whether a generic (Richards) equation could be used to describe sink strength of any leaf. Indeed, the Richards equation that was used to describe growth of fruits, proved to be also suitable in the case of leaves (Causton and Venus, 1981), which supports the idea that growth of fruits and leaves is similar. However, whether all leaves exhibit identical sink strength patterns is questionable. As was pointed out before, it is not feasible to assess the sink strength of leaves directly at non-limiting assimilate supply, because under these conditions leaf growth is disturbed, so conclusions have to be derived from indirect evidence.

Pieters (1983) observed that the mature size of successive leaves of poplar increased with leaf position until a certain equilibrium size was obtained that depended on irradiance. Before reaching this equilibrium size, however, the mature size of leaves of plants grown at low (7.5 W m^{-2}) and at high (30 W m^{-2}) irradiance was equal. This observation indicates that the increase in mature leaf size with leaf position should primarily be attributed to an increase in SS with leaf position (at comparable leaf developmental stage). In this and another study with sunflower (Pieters, 1985) the increase in SS with increasing leaf position was correlated with the development of the vascular system. These (slow) adaptations of the plant to the growing conditions will be further referred to as "plant status". Leaves formed on a plant with a favourable plant status will have a strong competitive power. Also with tomato fruits, there is an effect of position within the truss and of truss position (De Koning, 1994, Heuvelink, 1995b), which may have a similar background.

Beef steak and round tomato could be approached with an identical growth function adapted only by a proportionality factor (Heuvelink, 1996). Such a parameter could also be used to accommodate variations in leaf growth potential associated with the status of the plant (Pieters, 1983). In this way growth of successive leaves could be described by:

1. a Richards equation with fixed parameters describing the SS of a reference leaf as a function of leaf developmental stage (LDVS)
2. a function relating leaf development rate to temperature (the heat sum approach could be a first approximation)
3. a proportionality factor to accommodate variations in plant status at the moment a leaf is formed, which adapts slowly to ASC
4. a function describing the rate of leaf initiation as a function of temperature and eventually (depending on the species) radiation
5. the leaf's competitive power for assimilates (RSS)
6. supply with assimilates and related ASC over time.

On the basis of these elements leaf growth of successive leaves can be generated. A preliminary test was carried out with a normalised Richards curve (parameters resp. $a = 1$, $b = 9$, $c = .3$ and $d = 1.3$) for leaf growth where LDVS (by definition) varied between 0 and 1 and maximum relative leaf size was 1 (Fig. 3A), with the derivative of the Richards growth function according to Heuvelink (1996a):

$$SS_t = \frac{1}{a b (1 + e^{-b (LDVS_t - c)})^{1-d}}$$

$$(d-1) (e^{b (LDVS_t - c)} + 1)$$

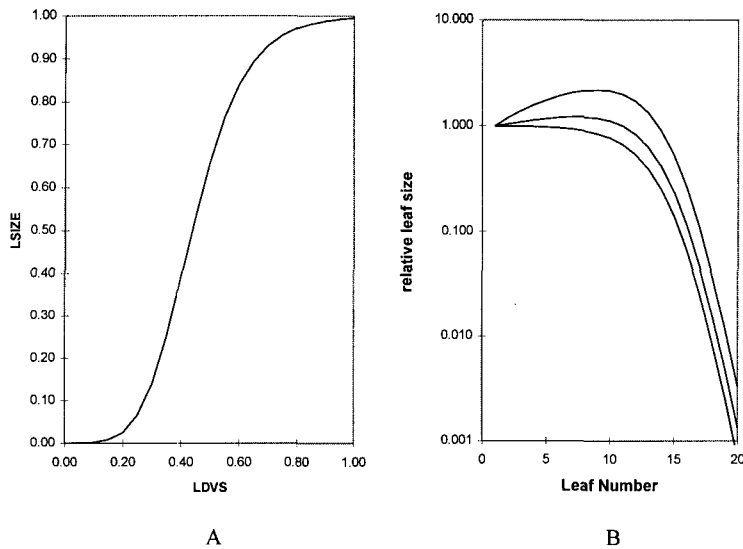


Figure 3. Calculated potential growth curve of the reference leaf as a function of its developmental stage (LDVS) (A) and a logarithmic plot of leaf size of growing leaves as a function of leaf number (B), with from bottom to top: reference leaves and leaves with SS increasing linearly with leaf number until resp. 2 and 5 times the reference value. Leaf 1 is the only mature leaf.

The relationship between leaf number and size of successive leaves growing under steady state conditions (identical growth curves) was approximately linear (Fig. 3B), in accordance with the literature (Horie et al., 1979). Moreover, such a linear relationship was maintained under non-steady-state conditions (assuming a SS increasing linearly with leaf number until a value of 2 or 5 times for leaf 20 compared to the reference SS at the same LDVS) (Fig. 3B). This result suggests that the approach based on the growth of

individual leaves could account for this relation that has intrigued researchers for long. If the approach is correct it would suggest that the strong co-ordination between growth of leaves should be considered as the result of the fixed patterns of leaf growth and formation and not the other way around, as in the approach of Horie et al. (1979). It should be noted that the bi-phasic character in the linear response, observed by these authors, did not occur in the present results. Obviously this matter needs further investigation and may be attributed to the particular choice of the function and its parameters. It should be noted that a large part of this so called linear phase is below 10% of the potential leaf size, where it is difficult to perform accurate measurements and where, moreover, the share in intra-plant competition for assimilates and in plant photosynthesis are negligible.

Until now I have only considered leaf size, but the relation between leaf size and leaf (dry) weight is an additional complication that needs further investigation. Within the framework of the present preliminary investigation it is not possible to deal with this aspect, which is obviously of vital importance to link dry matter production and morphogenesis properly with each other. I would anticipate that ASC should play a role in a model covering this aspect adequately, to accommodate feed-back for variations in source activity.

4. An interpretation of the role of radiation and temperature

If we accept the concept described before, it enables us to consider possible responses of leaf growth to temperature and radiation from this point of view as a basic pattern over which other morphogenetic responses may be superposed. It is essential to be aware of these basic patterns, because they may interfere with or mask the responses that are to be investigated and interpreted in morphogenetic studies.

Analogously to the response of fruit growth to radiation and temperature it may be anticipated that different processes with different response times that may interact will simultaneously play a role. Although the basic principles may be the same, it is likely that the response to these factors cannot be described adequately in general terms, and that the species or cultivar, but also the status of the plant (that is the previous history) may play an essential role.

The best way to analyse the response of leaf growth to radiation and temperature is to consider again Fig. 3A, where potential leaf size is related to LDVS. The rate of leaf development (LDVR) will be affected by temperature (over a certain range it will stimulate this process). With the same assimilate supply and RSS, the actual growth rate at any LDVS will remain the same, but since the whole life cycle is faster the final size will be reduced. An increase in radiation will primarily affect the supply of assimilates and as a consequence, the actual growth rate will increase at any LDVS. If the rate of leaf development is not affected the final size will increase. This concerns the straightforward relations.

Complications arise when (in some crops) the rate of leaf formation is also affected by radiation (e.g. cucumber; Horie et al., 1979). Furthermore, temperature may affect

RSS by a differential effect on SS of various competing sinks (Heuvelink, 1995b). In addition, we have already seen that plant status has an important effect on SS of an organ. Plant status is a characteristic that evolves gradually with plant development, depending on the assimilate balance, which itself is influenced by the plant status (feed-back). Finally, it should be realised that the distribution of age and sink characteristics that are influenced by plant status exhibit a dynamically changing pattern. Although perhaps discouraging, it is important to be aware of these complication in the set-up and interpretation of experiments on organ and plant morphogenesis.

5. Conclusion

The concept of dynamic sink strengths has features that reflect known plant responses and it creates a link between photosynthesis based and morphogenetic models. The concept could be promising to describe the basic growth patterns and how they would be modified by "special" treatments like diurnal temperature patterns and spectral factors. Close co-operation between modellers and researchers on plant morphogenesis would be required to handle the complexity of the system that arises from the present analysis. Especially in ornamentals such a joint effort is indispensable for the further development of useful crop growth models: plant form is an essential quality attribute in ornamentals.

For a correct set-up and interpretation of growth experiments, designed to analyse effects of temperature and radiation on morphogenesis in plants, it is of utmost importance to be aware of the complex relations that exist among the competing organs and the possibilities of direct or indirect disturbance of these relations by radiation and temperature treatments and to eliminate such effects.

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