# Self-organized resource allocation and growth partitioning at the whole plant level: a modeling study

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## Introduction

The development of different parts of a plant is highly coordinated, which enables them to capture and use resources efficiently in spatially and temporally heterogeneous environments (Sachs, 2006). The underlying physiological mechanisms that coordinate the growth of distantly located plant tissues/organs are still not fully understood. It is well known that the phytohormone auxin plays a pivotal role in integrating development throughout a plant (Leyser, 2003). But how auxin acts to integrate activities at the whole plant level remains to be elucidated.

Recent advances in complexity science have suggested that, based on distributed-control mechanisms, complicated structures and functions can emerge from the collective behavior of aggregates of smaller-scale subunits (Camazine et al., 2003). Because of their distributed-control character, self-organized systems tend to be robust and flexible in the face of varying environmental conditions. Plants are modular organisms. They consist of morphological and physiological subunits that act semi-autonomously (Orians et al., 2005). The morphological development of a plant largely relies on distributed-control mechanisms. The concept of self-organization based on distributed-control mechanisms holds great promise for an in-depth understanding of the organizational laws that generate overall plant structure and functions (Colasanti and Hunt, 1997; Sachs, 2004).

Based on a self-organization mechanism for resource allocation mediated by auxin, a mathematical model is proposed in this study to explain the origin of coordination among shoot branches.

## The model

According to the hypothesis of pipe model and the theory of branch autonomy, the shoot canopy of an individual plant is represented as an assemblage of relatively independent modular subunits (branches) competing for root-derived resources (water, nutrients and/or hormonal factors). The allocation of root-derived resources to different parts of the shoot canopy is determined by their relative vascular contacts with the root system. For simplicity, in this study, the shoot canopy of an individual plant is divided into *n* macro-branches arranged in parallel. These macro-branches can be divided into more detailed subunits in a nested hierarchical way and included in the model following the same rules. Subunits of a macro-branch compete for resources allocated to this macro-branch, but they join force to compete with other macro-branches.

It is well known that the basipetal flow of auxin plays a pivotal role in the regulation of primary and secondary growth of vascular tissues. Auxin moves in a basipetal polar manner in defined pathways, which leads to oriented vascular differentiation (Aloni, 2004; Berleth et al., 2000). In the model, development of vascular network is specified by the polar transport of auxin produced by various parts of the shoot canopy in response to their immediate internal and external environments. Conductivity of vascular elements is modeled as a power function of their cross-sectional area.

The site and mechanism of auxin synthesis and activation are still not well known. High levels of IAA are found in regions of active cell division. Young leaves, especially the fast growing regions, are generally considered to be the primary locations of auxin biosynthesis. In the model presented here, rates of bioactive auxin production are determined by rates of branch growth and are modified by local light conditions.

## Simulation results

Model behaviors were studied by running the model under various light conditions. In response to within canopy light heterogeneity, proportionally more root-derived resources were allocated to branches growing under better light conditions so the growth of this branch was enhanced. The performance of shaded branches declined gradually and, when the maintenance requirement exceeded their nitrogen capture rate, senescence occurred (Fig. 1). These simulation results are consistent with general observations in realistic plants that, in response to light heterogeneity within a single canopy, plant tends to partition proportionally more growth to branches in more favorable positions whereas shaded branches gradually cease growing and are eventually shed.

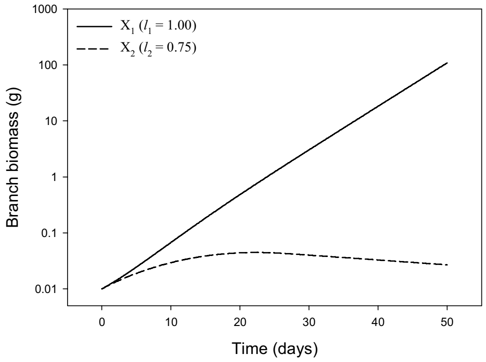

**Figure 1**. Simulated branch growth in response to a spatially heterogeneous light environment within the shoot canopy. Branch $X_1$ was growing under saturating light while $X_2$ on the same plant was shaded.

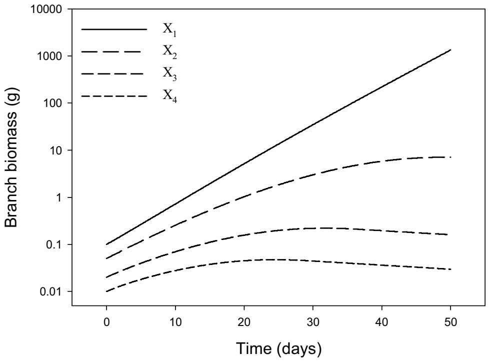

**Figure 2**. Simulations including four branches with different initial sizes. Showing the inhibition effects of $X_1$, the largest dominant branch, on the development of smaller branches ($X_2$, $X_3$ and $X_4$).

It has generally been assumed that morphological adjustment in response to light heterogeneity within a shoot canopy will lead to an advantage to the plant in terms of resource acquisition and whole plant performance. In order to assess the cost and benefit of the optimal partitioning function, the performance of the whole plant was simulated under heterogeneous light conditions. This simulation result was compared with the performance of the plant under the same light profile but without morphological adjustment ability. The simulation results suggest that, in a spatially heterogeneous light environment, the performance of the whole plant can be greatly improved by selective placement of shoot canopy under better light conditions.

Asymmetric competition also occurs when changing the relative initial size of competing branches. Fig. 2 shows the simulated correlative interactions among four branches with different initial sizes. In the presence of the largest branch ($X_1$), the development of other smaller branches ($X_2$, $X_3$ and $X_4$) was greatly inhibited (Fig. 2). If $X_1$ was removed or shaded, the second largest branch ($X_2$) was released from inhibitory control and became the dominant branch which exerted inhibitory effects over the growth of other two smaller branches ($X_3$ and $X_4$). This inhibitory effect might be able to explain the origin of apical dominance and apical control in which the primary shoot apex exerts inhibitory control over the growth of smaller lateral buds and branches.

## Discussion

The model was constructed on the basis of minimal requirement, but it displays rich and realistic behaviors with respect to light foraging and correlative control. In the model, subunits of a plant follow only simple local rules regarding growth and auxin production. By altering the amount of auxin they release individually in response to the local environment and modifying their relative vascular contact with the root system, subunits of a shoot canopy are able to coordinate without a central controller and self-organize into functional and structural patterns. The results of this modeling study indicate that morphological dynamics at the whole plant level can be understood as the sum of all modular responses to their local environments.

Oriented vascular differentiation specified by polar auxin transport plays a central role in the model. The auxin production by growing branches creates a self-reinforcing feedback loop. Branches with greater sizes and/or developing under better light conditions release more auxin, which enhances their vascular contact with the root system and further increases their competitive ability. This self-reinforcing mechanism might have adaptive significance, as it enables the plant to invest proportionally more and more biomass in the most promising branches with greater developmental potential and higher photosynthetic activity (Sachs, 2006). Nutrient diversion hypotheses have long been proposed to explain the phenomena of light foraging and correlative dominance, but how allocation of resource to different parts of a plant is controlled remains unclear. The success of this simple abstract model in reproducing realistic correlative effects suggests that oriented-vascular-differentiation specified by polar auxin transport could be the invisible ‘guiding hand’ that controls the proportion of resource going to each sink. Growing shoot parts, including vegetative and reproductive organs, continuously release auxin to maintain adequate vascular links for resource supply.

Similar to the architecture of shoot canopies, root systems are modular and plastic. Different parts of the root system of an individual plant compete for auxin and photoassimilates from the shoot canopy. An extension of the model including root development and function may well be able to account for the root morphological response to the patchy distribution of nutrient resources in the soil. This model does not consider reproductive growth. Similar to the competition between vegetative modules, reproductive organs compete with one another. Early-formed fruits and seeds inhibit later-established fruits and seeds. It is possible that the self-organizing control for resource allocation is a basic mechanism for all developing sinks including both vegetative and reproductive organs.

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