Competition-based Model of Pruning: Applications to Apple Trees

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Introduction

Pruning is widely used in horticulture to control tree shape and balance between vegetative and reproductive growth. Several pruning models have been developed. They are based upon competition mechanisms and transport network to distribute resources to different sinks using either a source-sink allocation function (Borchert and Honda, 1984; de Reffye *et al.*, 1999; Balandier *et al.*, 2000) or an electrical analogy (Lopez *et al.*, 2008). In pruning models, reaction to pruning originates from competition between organs (de Reffye *et al.*, 1999), or reassignment of bud fates depending on apical dominance (Borchert and Honda, 1984; Lopez *et al.*, 2008), or from new bud-break occurrences (Balandier *et al.*, 2000). The output of these models were compared in a qualitative way to small samples of real observations. In this paper, we present a new model based upon resource partitioning between competing sites (with no explicit transport) and growing processes so as to study and simulate the development and pruning reactions of fruit trees. It is supported by recent studies carried out on a large data set from two apple cultivars (880 trees) that show both local and distant reactions to pruning (Fumey *et al.*, submitted). Although apple tree model like MappleT (Costes *et al.*, 2008) that combines stochastic (branching pattern) and mechanistic (bending) modules already exists, it does not include resource allocation mechanism nor pruning reactions. The present model uses an abstract resource allocation with a notion of *context* for each meristem, which is used in a botanical sense, taking into account the meristem position in the plant architecture as well as its environment. First results show that realistic pruning reactions can be obtained as an emerging property of the model.

Pruning Model Design

The proposed competition-based approach utilizes a hierarchical allocation model (Lacointe *et al.*, 2000; Génard *et al.*, 2008). Each tree component has a demand and possibly provides resource at each time step to a global pool of resources. Each component, v, has an initial demand $d_{0;v}$ that depends on its *context;* this abstract notion encapsulates the organ position in the tree and may be generalized to other variables. The context function, $C_v(t)$, normalizes the initial demand so that each initial demand becomes $d_v = d_{0;v}C_v(t)$. In the following, we use an instance of context that is defined by $C(t) = O_v(t)A_v(t)S_v(t)$, where $O_v(t)$ is inversely proportional to the order, $A_v(t)$ is function of the component's age, and $S_v(t)$ is a *satisfaction* function that increases or decreases when demand is satisfied or not, respectively. Consequently, organs will have different demand and diverse branching patterns will emerge, as shown hereafter.

The simulation loops over three different steps: (i) *Resource and demand computation* -- each element has an initial demand to fulfill its needs for growth and maintenance. Leaves produce resources stored into a common pool. Root system is abstracted as a single compartment. Initial demand of each meristem is normalized by its relative context. (ii) *Resource Distribution* -- total resource is computed and distributed among processes and components. A fraction of the resource is used to maintain components alive and the remaining resource is used for primary growth (distributed among meristems based on a hierarchical allocation and their respective demands). (iii) S*tructure Update* -- production rules are applied if the allocated resource in a meristem exceeds a predefined threshold, which prevent bud break everywhere.

Main physiological processes are taken into account (e.g., leaf and internode production, and extension rate). The model is implemented as an L-system (Prusinkiewicz and Lindenmayer, 1990) within the OpenAlea framework (Pradal *et al.*, 2008) to capitalize on packages dedicated to plant modeling.

Results

The model is used to simulate apple trees over one growing season so as to reproduce the main branching patterns observed on one-year-old apple trees and to study their reactions to pruning. First, we fixed parameters such as the initial resource in the root system and used a hierarchical model for resource allocation. Then, we performed a sensitivity analysis on the leaf production parameter, which led to different branching systems (Fig. 1). Finally, the leaf production parameter was set so that the branching system mimicked those of one-year real trees. Simulated and measured trunks showed similar heights and dynamic elongations (internode length).

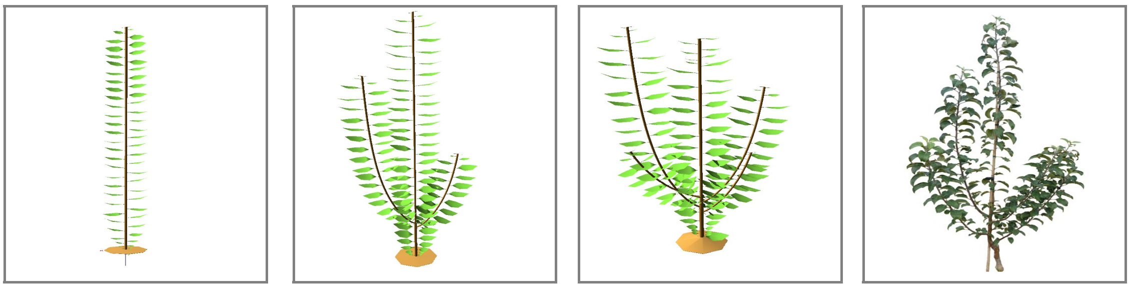

Fig. 1: Sensitivity analysis on the leaf resource production: the branching pattern, which can vary from a single trunk to several branches, depends on the available resource (right-side picture shows a control tree).

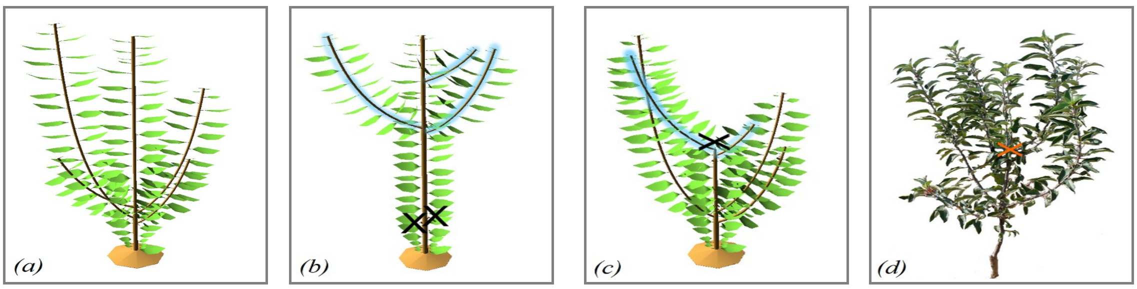

Fig. 2: Comparison between a control tree (a) and pruned trees (b,c,d). Pruning (crosses) (b) on the sylleptic branches show emergence of new branches on the main trunk while (c) pruning on the trunk shows emergence of new branches below the cut like in (d) a real tree pruned on the main axes.

As expected, heading cut (shortening) of axes, either trunk or laterals induced local emergence of released axes, just below the cut. Several distant reactions were highlighted, in particular the emergence of new axes along the trunks after the heading cut of laterals, which are emerging properties of the model. Indeed, pruning provokes a simultaneous decrease in resources and competing sites, which creates a new hierarchy between growing axes and new axes. The context function as defined earlier prioritizes youngest organs and lowest order therefore organs below the apex tend to be first in the hierarchy. Already growing branches are also favored because of the satisfaction variable. This mechanism reproduces pruning reactions observed in field experiments: if sylleptic branches are removed then new axes emerge on the main trunk in a second sylleptic zone (Fig. 2-b); if pruning is done on the main trunk then new axes emerge below the cut (Fig. 2-c).

Conclusions

The model presented is a competition-based model for resources that takes into account the *context* of each organ. The model includes interactive pruning capabilities that makes it possible to study pruning reactions. Although only basic physiological processes are included, it is already possible to estimate parameters to fit the growth of control trees and to reproduce realistic reactions to pruning. We qualitatively compared unpruned and pruned simulated trees with real trees and could reproduce observed phenomena such as local and distant reactions. Finally, we plan to perform quantitative comparative studies with the large database of field measurements available.

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