



# A new modified resource budget model for nonlinear dynamics in citrus production



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## ABSTRACT

Alternate bearing or masting is a general yield variability phenomenon in perennial tree crops. This paper first presents a theoretical modeling and simulation study of the mechanism for this dynamics in citrus, and then provides a test of the proposed models using data from a previous 16-year experiment in a citrus orchard. Our previous studies suggest that the mutual effects between vegetative and reproductive growths caused by resource allocation and budgeting in plant body might be considered as a major factor responsible for the yield oscillations in citrus. Based on the resource budget model proposed by Isagi et al. (J Theor Biol. 1997;187:231-9), we first introduce the new leaf growth as a major energy consumption component into the model. Further, we introduce a nonlinear Ricker-type equation to replace the linear relationship between costs for flowering and fruiting used in Isagi's model. Model simulations demonstrate that the proposed new models can successfully simulate the reproductive behaviors of citrus trees with different fruiting dynamics. These results may enrich the mechanical dynamics in tree crop reproductive models and help us to better understand the dynamics of vegetative-reproductive growth interactions in a real environment.

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## 1. Introduction

Alternate or biennial bearing (also known as masting in forest production), a phenomenon where fruit production alternates between large crops and little or no crops, is commonly found in fruit tree crops [1–10]. Such yield variability phenomena are permanent features in almost all perennial crops [1]. The large yield variance between years commonly appears, yet perfect periodicity in reproduction is rarely observed for both individual trees and the whole orchard [3,4]. This implies that the reproductive output of individual trees may undergo an irregular fluctuation that is governed by a specific reproduction mechanism, and the resulting individually different reproductive dynamics for different trees might eventually lead to more complexity in the yield behavior of the whole orchard. Ecologists have investigated the yield fluctuations in various perennial crops and developed empirical models to predict the dynamics [2–4,9,10], however very few studies are able to reveal the mechanism responsible for these dynamics [6,7].

It is generally thought by ecologists that weather conditions and field management are associated with this phenomenon [6].

The resource matching (or weather tracking) hypothesis is the oldest hypothesis for mast seeding [7]. It has been recently evaluated for variation in seed production in *Nothofagus truncata* [11]. The hypothesis postulated that plants could simply be matching their reproductive output each year to the variable resources available to them, and that each plant's available resources vary each year, being higher during favorable conditions, and reproductive effort mirrors this variation [2–5,12,13]. This hypothesis is supported by the evidence that adverse weather (e.g., frost or drought) sometimes prevents reproduction, causing synchronization of low years [5,6,12–20]. However, it was argued that the large variance between years in reproductive output is too large to be explained by the environmental fluctuation in annual productivity [7]. Furthermore, the large fluctuation of reproductive activity has been suggested to be an adaptive strategy of individual forest trees [7].

Recent research has attempted to unfold the mechanism of masting for several tree species by analyzing the contribution of resources or nutrients from different storage parts of the plants. Hoch et al. [17] found that stored carbon reserves were not directly tapped by fruit production in three mature tree species (*Carpinus betulus*, *Fagus sylvatica*, *Quercus petraea*), and the fruit production was supplied entirely by current photo-assimilates [17]. Therefore, they suggest that other non-C-based resources (e.g., nitrogen or phosphorus) might be responsible for the masting patterns if the

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resource accumulation mechanism that triggers mast seeding in trees [5] exists. Further, radiocarbon ( $^{14}\text{C}$ ) analyses of three tree species (*Quercus serrata*, *Fagus crenata* and *F. japonica*) revealed that temperate canopy trees used photosynthates produced in the current and/or the previous year for seed production, regardless of reproductive intervals, suggesting the necessity to reconsider the importance of stored carbohydrate resources for masting [21]. Moreover, a recent study of the dynamics of mineral nutrient storage for mast reproduction in *Dryobalanops aromatica* revealed that the species supplies the majority of phosphorus (67.7%) needed for reproduction mainly from stored resources in the tree. Therefore, it is concluded that the accumulation of phosphorus could be the decisive factor in the occurrence and frequency of mast reproduction in the relatively poor soil conditions [22].

Besides the intuitive understanding that external conditions influence the variability of yield, several hypotheses have been proposed for the phenomenon from the perspective of internal resource accumulation and consumption in individual plants [5–7,23]. Among them, the resource budget model was first proposed and tested with experimental data for *F. crenata* [6]. It was later expanded for pollen coupling analysis of forest trees [7], and was recently investigated for a better understanding of the model behaviors by varying a range of the parameters [8]. The model generates intermittent reproduction by each plant, driven by resource thresholds for reproduction coupled with large expenditure when reproduction occurs [6,7]. The model describes a deterministic process of energy storage due to photosynthesis, and energy depletion due to flower and fruit production in the plant. It is hypothesized that each crop accumulates photosynthate every year, producing flowers when energy reserves exceed a threshold level, and sets fruits at a rate limited by the ratio between costs for flowering and fruiting in individual plants. The model is generally written as follows:

$$I(t+1) = I(t) + P_s - C_f(t) - C_a(t) \quad (1)$$

$$C_f(t) = \begin{cases} I(t) + P_s - L_T & \text{if } I(t) > L_T - P_s \\ 0 & \text{if } I(t) \leq L_T - P_s \end{cases} \quad (2)$$

$$C_a(t) = \begin{cases} R_c C_f(t) & \text{if } I(t) > L_T - P_s \\ 0 & \text{if } I(t) \leq L_T - P_s \end{cases} \quad (3)$$

where  $t$  indicates the year in time-series simulation;  $I$  is the energy reserve of an individual plant;  $C_f$  is the cost for flowering;  $C_a$  is the cost for fruiting;  $L_T$  is the reproductive threshold of energy in plant body;  $P_s$  is the accumulated photosynthates in the year; and  $R_c$  is the ratio of the cost for fruiting to the cost for flowering ( $C_a/C_f$ ).

Typical simulation results obtained from this model are illustrated in Fig. 1. Fig. 1a shows the bifurcation diagram of yield ( $C_a$ ) with  $R_c$  as the control parameter. A clear route from a stabilized level to oscillations and chaos in yield is observed with increasing  $R_c$ . For instance, when  $R_c$  is set to 2.8, the crop demonstrates a chaotic yield pattern over time (Fig. 1b). From the return map of yield (Fig. 1c), it is found that the fruit yield falls to zero in a large portion of the years in the simulation. The data points on the abscissa and ordinate represent the data of a fruiting year followed or preceded by a non-fruiting year, and the data points on the origin indicate the data of two consecutive non-fruiting years. By excluding these non-fruiting data points, the remaining scattered data points which indicate the data of two consecutive fruiting years can be fitted by a straight line. The above resource budget model suggests that after a major reproductive event, energy reserves will be depleted and it may take one year or several years before levels regain the reproductive threshold.

Motivated by our previous findings that the vegetative growth (mainly growing of new leaves) may inhibit the reproduction output on individual crops [24], in this paper we first introduce the

new leaf growth factor into the resource budget model to study the dynamics of citrus crops. The addition of vegetative growth in the model extends the model's capability, and leads to a generalized linear model for the resource budget model. Further, in addition to the line-shaped return map as demonstrated in the resource budget model, we also found that the yield fluctuations in some citrus trees showed a hump-shaped curve in the return map [24]. Therefore, we introduce a nonlinear Ricker-type equation to describe the relationship between costs for flowering and fruiting in the new resource budget model. Further, we used the real data for two citrus trees to test the new models. Model simulation results demonstrate that our new model, as a generalized form of the resource budget model, could be potentially used to simulate the chaotic dynamics with various patterns of the return map in citrus production, showing its superiority over the original resource budget model.

## 2. Methodology and results

### 2.1. Model incorporating new leaf growth factor

Our previous studies have revealed the significant interrelationships between the vegetative and reproductive growths in citrus crops [24]. The number of new, young leaves grown in the early season was found to be negatively correlated with the reproduction output on an individual tree basis, indicating a direct inhibiting effect on the subsequent fruiting event in the same growing season. On the other hand, this amount of new, young leaves on individual canopies showed a significant positive correlation with the reproduction output in the previous year, suggesting the enhancing effect of increased reproduction output on subsequent vegetative growth in the next growing season. Furthermore, we found that the old, mature leaves were highly correlated with the fruit yield of the current growing season, whereas the new, young leaves were more significantly correlated with those in the next growing season. These findings suggest that the old, mature leaves in the early season may contribute their energy reserves (including the new energy accumulated by photosynthesis along the later growing season) directly to the fruiting of the same year, while the new, young leaves grown in the early season may contribute their energy, in a time-delayed manner, to the fruiting in the next year. The above mechanism has been diagrammatically illustrated in Fig. 2. This mechanism might explain the annual yield fluctuations as well as the canopy structural variations on individual trees, as were observed in field experiments. These findings suggest that the interdependency between the vegetative and reproductive growths exists not only within a particular growing season, but it also appears across consecutive growing seasons. This result is supported by a recent study of three tree species (*Quercus serrata*, *Fagus crenata* and *F. japonica*) by Ichie et al. [21]. By using a radiocarbon ( $^{14}\text{C}$ ) analysis method, they proved that the above temperate canopy trees used photosynthates produced in the current and/or the previous year for seed production regardless of reproductive intervals [21]. Therefore, the vegetative growth that significantly affects the resource consumption and accumulation in the current and the adjacent (previous and/or next) years should be taken into account in the models.

Based on above findings, we introduce the vegetative growth as an indispensable factor into the resource budget model to develop the new models. To simplify the models, the following assumptions are made: 1) the energy used for the maintenance activities such as respiration remains constant (same as the original model); 2) the energy accumulated by photosynthesis during a growing season is assumed to be constant for a tree. It is used not only for the reproductive growth (flowering and fruiting) but also for the vegetative (new leaf) growth. Although the proportions of new leaves

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