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

Xujun Ye^{a,*}, Kenshi Sakai^b

^a *Faculty of Agriculture and Life Science, Hirosaki University, Aomori 036-8561, Japan*

^b *Environmental & Agricultural Engineering Department, Tokyo University of*

Agriculture and Technology, Tokyo 183-8509, Japan

ABSTRACT

Alternate bearing or masting is a general yield variability phenomenon in perennial tree crops. This paper first presents a theoretical modelling 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. (1997), 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

* Corresponding author.

E-mail address: yexujun@hirosaki-u.ac.jp (X. Ye)

models and help us to better understand the dynamics of vegetative-reproductive growth interactions in a real environment.

Keywords: alternate bearing; nonlinear dynamics; resource budget model; vegetative-reproductive growth interactions; modelling

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 *N. truncate* [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 favourable 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. (2013) 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 resource accumulation mechanism that triggers mast seeding in trees [5] exists. Further, radiocarbon (^{14}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 inter-relationships 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. (2012). By using a radiocarbon (^{14}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 and old leaves in the tree canopy change between different years, the energy accumulated by photosynthesis in the whole canopy is considered to be the same between years; 3). the environmental conditions are constant during the years, and the climate and weather conditions are favourable for the optimal growing activities of the tree.

In addition to the above assumptions, we further assume that the growth of new leaves in the early season constitutes a major part of energy consumption, and it is determined by the potential resource accumulation capacity that depends on the internal reproductive threshold (L_T), the amounts of energy reserve (I) and the new resources accumulated by photosynthesis (P_s) in the year:

$$C_l(t) = r(L_T + P_s - I(t)) \quad (4)$$

where C_l is the cost for new leaf growth; r is a parameter for new leaf growth of the plant.

In the model, we assume that there is a maximum limit of resource accumulation in the plant, which is the total amount of the reproductive threshold (L_T) and the new resources accumulated by photosynthesis (P_s) in the year (Fig. 3). The amount of energy used for new leaf growth (C_l) is determined by the empty portion ($L_T + P_s - I(t)$) of the resource tank at the beginning of the year, which is partially or fully filled by P_s during the growing cycle. The plant is assumed to be able to transmit a signal to regulate the amount of new leaves depending on the volume of the empty portion. Eq (4) describes a linearly decreasing cost for new leaf growth (C_l) with decreasing initial resource level (I) of the plant, as illustrated in Fig. 4. It can be further deduced from Eq. (4) that the maximal and minimal resources for new leaf growth in a growing cycle are $r(L_T + P_s)$ and rP_s , respectively.

The initial resource level of the plant body in a year is equal to the amount of resources remained after the fruiting event in the previous year, which is largely dependent on the amount of resources allocated to reproductive organs (flowers and fruits) in the previous year (Eq. (1)). In a year when the harvest is large, the accumulated amount of resources that is used as the initial resource level for the next year would be less. Hence, according to Eq. (4), the amount of resources allocated to new leaves would be larger in the next year. In contrast, the reduced harvest results in a larger accumulated amount of resources after the fruiting event, and consequently a less amount of resources allocated to new leaves in the next year. This relationship between the fruit yield and the number of new leaves grown in tree canopy has been

experimentally confirmed in our previous studies [24]. Eq. (4) reasonably explains this mechanism, and therefore it may have the potential to improve the resource budget model.

By incorporating the new leaf growth (C_l) defined in Eq. (4), the equations in resource budget model are rewritten as:

$$I(t+1) = I(t) + P_s - C_l(t) - C_f(t) - C_a(t) \quad (5)$$

$$C_f(t) = \begin{cases} I(t) + P_s - C_l(t) - L_T & \text{if } I(t) > L_T - P_s + C_l(t) \\ 0 & \text{if } I(t) \leq L_T - P_s + C_l(t) \end{cases} \quad (6)$$

$$C_a(t) = \begin{cases} R_c C_f(t) & \text{if } I(t) > L_T - P_s + C_l(t) \\ 0 & \text{if } I(t) \leq L_T - P_s + C_l(t) \end{cases} \quad (7)$$

The minimal I required for activating reproductive events in Eq. (6) and Eq. (7) becomes $L_T - P_s + C_l$ accordingly. This is a simple modified version of the resource budget model. Fig. 5 illustrates the diagrammatic representation of the new model. It is based on the same basic assumptions as Isagi's resource budget model: there is a constant amount of photosynthate (P_s) produced by each plant every year given that the environmental conditions are constant during the years; the photosynthate is consumed for the growths (vegetative and reproductive) and maintenance of the plant, and the rest of the photosynthate is stored in a pool in the plant body. In Fig. 5, the plant starts with a low deposit of reserve energy (I) after a heavy reproduction in the previous year. While maintaining the basic living activities, the plant uses part of the reserve energy for growing of new leaves in the early season, the amount of which is determined by the resource availability, as expressed in Eq. 4. In the year, the accumulated resources in plant body after the new leaf growth and the additional photosynthetic activities does not reach the reproductive threshold (L_T), therefore there is no flowering and fruiting

events on the plant, resulting in a non-fruiting year (completely off year). In the following year, the accumulated P_S after the new leaf growth exceeds the reproductive threshold (L_T), the surplus photosynthesis ($P_S - L_T$) is used for flowering as the cost of flowering (C_f). Then, the flowers are pollinated and bear fruits, whose cost (C_a) is defined as R_C times the cost for flowering (C_f). The R_C (ratio of C_a/C_f) represents the ability of how the plant can turn flowers into fruits and is assumed to be constant. After the reproductive event, the energy reserve will be depleted and it may take one year or several years before levels regain the reproductive threshold.

The resource budget model as well as the modified version described above can be graphically illustrated by return maps in terms of I (Fig. 6a) and C_a (Fig. 6b). Comparisons show that both models exhibit a line-shaped return map, but with different slopes of the line segment in the plane owing to the parameter r introduced into the new model. Models with the same parameter values and initial conditions predict that the yearly predictions as well as the overall patterns of C_a vary with different r values (Fig. 7a-c), and the new model becomes the resource budget model when r is set to 0 (Fig. 7a). Hence, the new model can be recognised as a generic model. Furthermore, with increasing r values, the range of predicted C_a values narrows and the number of years with little or no fruiting becomes larger (Fig. 7a-c). The phenomena of little or no fruiting during the initial and final stages of the life cycle of trees might be attributed to the large portion of resources that are consumed by vegetative growth [25]. This could be simulated by setting a variable, rather than fixed r value in our model (Fig. 7d). Moreover, the new model also demonstrates bifurcations and chaos in the dynamics of fruiting cost (C_a) as the ratio between costs for fruiting and flowering (R_c) increases (Fig. 8). However, the point at which fruiting cost (C_a) begins to bifurcate is shifted to a lower R_c , as compared to $R_c=1$ in the resource budget model.

2.2. Model with nonlinear relationship between flowering and fruiting

Both the resource budget model and our modified version predict that the dynamics of reproduction in individual plants show a line-shaped return map (Fig. 6). However, our experimental data demonstrate that for some trees a hump-shaped curve could better fit the data points in the phase plane [26]. To add nonlinearity to the model output, we therefore considered an alternative to Eq. (3) to describe the relationship between flowering and fruiting events in the model, using a Ricker-type equation [27]:

$$C_a(t) = \begin{cases} R_k C_f(t) e^{a(1 - \frac{C_f(t)}{K})} & \text{if } I(t) > L_T - P_s + C_l(t) \\ 0 & \text{if } I(t) \leq L_T - P_s + C_l(t) \end{cases} \quad (8)$$

where a represents the fruiting coefficient, which describes the characteristics of the fruiting ability of flowers; K represents the optimal cost of flowering; R_k equals the C_a/C_f ratio when C_f exactly equals the optimal cost of flowering (K).

Unlike the constant R_c which is used to describe the C_a/C_f ratio in Isagi's model, the C_a/C_f ratio in the new model exponentially decreases as C_f increases (Eq. (9)).

$$\frac{C_a}{C_f} = R_k e^{a(1 - \frac{C_f(t)}{K})} \quad (9)$$

Therefore, the resulting Ricker-type curve describes the relationship between the costs for flowering (C_f) and fruiting (C_a) more reasonably than the linear curve produced by Eq. (3): at low flowering level, the fruiting increases fast as the flowering increases because the resources are sufficient for fruiting in plant; at medium flowering level, the fruiting reaches its maximum when the flowering increases to a point at which the remaining resources after flowering are just suitable for maximal fruiting as well as the growth and maintenance of the plant; at high flowering level, the fruiting declines

and eventually approaches to zero as the resources are gradually depleted by the plant's effort to maximise the fruiting, which in turn leads to a decrease in the number of mature fruits because many flowers fail to normally fructify for lack of sufficient resources [28,29] (Fig. 9). The linear equation in the original resource budget model arbitrarily assumes that the C_a/C_f ratio (R_c) is constant and the fruiting will increase proportionally to the flowering, thereby leading to a rapid depletion of internal resources and subsequent frequent occurrence of fruiting failures (Fig. 1b,c). Hence, our proposed Ricker-type relationship between C_f and C_a is more relevant to the model under the limited resource budget.

The fruiting patterns generated by the model with the Ricker-type equation resemble the distributions of the observed data (Fig. 10). In model simulations with two different R_k (0.72 and 0.92), the fruiting behaviors show wide oscillations, with all fruiting years for $R_k=0.72$ (Fig. 10a,b), and the frequent occurrence of non-fruiting years for $R_k=0.92$ (Fig. 10c,d). These two models might be applied to two different types of perennial crops, i. e., fruit crops that seldom show a “completely off” year such as citrus, and forest trees that are characterised by more non-masting years such as acorn. A closer look at the simulated results indicates that the model will generate episodic mild fluctuations or even stable yields around a certain yield level (Fig. 10a,c). This explains the fact that despite wide inter-annual fluctuations the yield may also remain relatively constant over several years, as was observed in our field experiments [24]. Furthermore, we used the R_k as the bifurcation parameter to identify the different patterns of fruiting in the simulation. The R_k , defined as the C_a/C_f ratio when C_f equals the optimal cost of flowering (K) (Eq. (6)), can be recognized as an indicator of the plant's capability of fruiting. The model can simulate the dynamical behaviors of different plants with a different R_k . The model simulations predict that the fruiting

becomes stable when the plant has a low R_k . By a cascade of period doubling, increased R_k can generate chaos in the fruiting. Further increase in the R_k can even generate windows and self-similarity structures in the phase space, which are characteristic features of chaos (Fig. 11).

2.3. New model summary

The above proposed new model is summarized as follows:

$$I(t + 1) = I(t) + P_s - C_l(t) - C_f(t) - C_a(t) \quad (5)$$

$$C_l(t) = r(L_T + P_s - I(t)) \quad (4)$$

$$C_f(t) = \begin{cases} I(t) + P_s - C_l(t) - L_T & \text{if } I(t) > L_T - P_s + C_l(t) \\ 0 & \text{if } I(t) \leq L_T - P_s + C_l(t) \end{cases} \quad (6)$$

$$C_a(t) = \begin{cases} R_k C_f(t) e^{a(1 - \frac{C_f(t)}{K})} & \text{if } I(t) > L_T - P_s + C_l(t) \\ 0 & \text{if } I(t) \leq L_T - P_s + C_l(t) \end{cases} \quad (8)$$

When the parameters r in Eq. (4) and a in Eq. (8) are set to 0, the model will be the Isagi's resource budget model. By setting the parameter r in Eq. (4), the new model can regulate the proportion of plant resources that is allocated to new leaf growth in the plant. Proper settings for the parameters a , K and R_k can enable the model to simulate the nonlinear dynamics in crop production. Therefore, our new modified resource budget model could be recognized as a generic form of the resource budget model. Isagi's model can be viewed as a specific form of the generic model.

Previous simulation studies have demonstrated the possibility of controlling the yield oscillations in citrus by means of pruning in early season [10, 30]. In practice, early use of intervention measures, such as proper pruning and fruit thinning, has also proved effective in the suppression of yield fluctuations in various fruit trees [1].

Therefore, it is theoretically possible to use our models to predict the reproductive behaviors of individual trees, and then use the predicted yield information for individual tree management.

2.4. Model test

To evaluate our new resource allocation hypothesis as well as the new models for citrus fruit production, we tested the performance of the modified resource budget models using the yield data of two sample citrus trees (*Citrus unshiu* Marc.) in a citrus orchard of Japan. The yield data of these two trees were from a previous experiment from 1967 through 1982, which yielded an outstanding long-term 16-year fruiting record for each tree (Fig. 12) [30]. Previous analysis has revealed that these two trees showed a different pattern of the return map, one (tree A) with data points along a straight line (Fig. 12b), and the other (tree B) with data points producing a hump-shaped curve (Fig. 12d).

We employed a genetic algorithm [31] to fit the models. The optimization was carried out with a genetic algorithm toolbox under a Matlab R12 (The MathWorks, Inc., Natick, Massachusetts) environment. The minimization of the root mean squared error (RMSE) between the predicted and actual yields was set as the optimization target. Using default parameter settings, we obtained the optimized parameters for the two models as follows: Model I for tree A, $P_s=2900$, $L_T=4672$, $r=0.122$, $R_k=1.214$, $a=0$, $K=2403$, and initial conditions $I(0)=4102$. Model II for tree B, $P_s=2930$, $L_T=3625$, $r=0.113$, $R_k=0.957$, $a=1.915$, $K=2334$, and initial conditions $I(0)=2830$.

The predicted results of the optimized models in comparison with the actual yield data are shown in Fig. 13. The time series data (Fig. 13a,b) predicted by the two models show a similar fluctuating pattern with the actual yield obtained for the two citrus trees.

Both models demonstrate a higher level of accuracy in predicting the annual yield of the two citrus trees (Fig. 13c,d). Although the two trees showed a different pattern of the return map, the two models successfully produced the similar patterns of the return map for the two trees, respectively (Fig. 13e,f).

These results demonstrated that our new models could well explain the dynamics of alternating bearing in citrus crops. This generic model is superior to the original resource budget model, particularly in explaining the various patterns of the return map that are frequently observed in yield data of horticultural crops. However, the major input variables of the models such as the initial energy reserve and the amount of photosynthates are difficult to obtain, and this limits their application in practice. Although the radiocarbon (^{14}C) analysis has been recently used to measure the stored carbohydrate resources and photosynthates in several tree species [21], the application of the theoretical models will not be possible until these determination methods become available at an acceptable cost. Nevertheless, the findings from this study may enrich the mechanical dynamics in tree crop reproductive models, and help us to better understand the dynamics of interactions between vegetative and reproductive growths as well as the importance of early interventions for fruit management in practices.

3. Conclusion

This paper provides a new mechanical understanding of alternate bearing in citrus crops, and develops new models for the complex dynamics of alternate bearing. Based on our previous experimental evidence of the interdependency between new leaf growth and reproduction output of individual crops [24], we consider the mutual effects and trade-offs between vegetative and reproductive growths as a major contributing factor for the yield oscillations. Following the concept of the well-known resource budget

model [6,7], we first introduce the vegetative growth (mainly growing of new leaves) as an indispensable factor into the resource budget model. As the vegetative growth constitutes a major part of energy consumption in perennial crops, the incorporation of vegetative growth produces a more mechanically sound model for the dynamics of yield variability. Furthermore, we introduce a Ricker-type equation to describe the relationship between costs for flowering and fruiting, which proves superior to the resource budget model in simulating the nonlinear dynamics of annual variations in reproductive output. Models based on above modifications exhibit various dynamics caused by the mutual effects and resource trade-offs between vegetative and reproductive growths. Model tests demonstrate the power of our new models to simulate two different types of reproductive behaviors in citrus trees observed in our experiment. Our results may enrich the dynamical models for understanding the alternate bearing phenomenon in fruit crops.

Acknowledgements

The study was supported by the invitation fellowship program from the Japan Society for the Promotion of Science (L12560), Grants-in-Aid Scientific Research (B) 19380141, and the grants from the National Science Foundation of China (61273062).

References

- [1]Jonkers H. Biennial bearing in apple and pear: a literature survey. *Sci. Hortic.* 1979; 11: 303–317.
- [2]Norton DA, Kelly D. Masting seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (*Podocarpaceae*) in New Zealand: the importance of economics of scale. *Funct. Ecol.* 1988; 2: 399-408.

- [3]Sork VL, Bramble J, Sexton O. Ecology of mast fruiting in 3 species of North-America deciduous Oaks. Ecology 1993; 74: 528-541.
- [4]Koenig WD, Mumme RL, Carmen WJ, Stanback MT. Acorn production by oaks in central coastal California: variation within and among years. Ecology 1994; 75: 99-109.
- [5]Kelly D. The evolutionary ecology of mast seeding. Trends Ecol. Evol. 1994; 9: 465-470.
- [6]Isagi Y, Sugimura K, Sumida A, Ito H.. How does masting happen and synchronize? J. Theor. Biol. 1997; 187: 231-239.
- [7]Satake A, Iwasa Y. Pollen coupling of forest trees: Forming synchronised and periodic reproduction out of chaos. J. Theor. Biol. 2000; 203: 63-84.
- [8]Prasad, A., Sakai, K, Understanding the alternate bearing phenomenon: Resource budget model. Chaos 2015; 25, 123102.
- [9]Sakai K, Noguchi Y, Asada S. Detecting chaos in a citrus orchard: Reconstruction of nonlinear dynamics from very short ecological time series. Chaos Soliton Fract. 2008; 38: 1274-1282.
- [10]Sakai K, Noguchi Y. Controlling chaos (OGY) implemented on a reconstructed ecological two-dimensional map. Chaos Soliton Fract. 2009; 41: 630-641.
- [11]Monks A, Kelly D. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecology 2006; 31: 366-375.
- [12]Busgen M, Munch E. The structure and life of forest trees. Capman & Hall, London; 1929.
- [13]Kelly D, Sork VL. Mast seeding in perennial plants: why, how, where? Ann. Rev. Ecol. Syst. 2002; 33: 427-47.

- [14] Agren J. Between-year variation in flowering and fruit set in frost-prone and frostsheltered populations of dioecious *Rubus chamaemorus*. *Oecologia* 1988; 76: 175–183.
- [15] Allen RB, Platt KH. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* 1990; 57: 199–206.
- [16] Fenner M. Irregular seed crops in forest trees. *Q. J. For.* 1991; 85: 166–72.
- [17] Hoch G, Siegwolf RTW, Keel SG, Körner C, Han Q. Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia* 2013; 171:653-662.
- [18] Houle G. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *J. Ecol.* 1999; 87: 413–22.
- [19] Selas V. Seed production of a masting dwarf shrub, *Vaccinium myrtillus*, in relation to previous reproduction and weather. *Can. J. Bot.* 2000; 78: 423–29.
- [20] Inouye DW. The ecological and evolutionary significance of frost in the context of climate change. *Ecol. Lett.* 2000; 3: 457–63.
- [21] Ichie T, Igarashi S, Yoshida S, Tanaka K, Masaki T, Tayasu I. Are stored carbohydrates necessary for seed production in temperate deciduous trees? *Journal of Ecology* 2012; 101:525-531.
- [22] Ichie T, Nakagawa M. Dynamics of mineral nutrient storage for mast reproduction in the tropical emergent tree *Dryobalanops aromatica*. *Rcol. Res.* 2013; 28:151-158.
- [23] Sharp WM, Sprague VG. Flowering and fruiting in the white oaks: pistillate flowering, acorn development, weather, and yields. *Ecology* 1967; 48: 243-251.

408 [24] Ye X, Sakai K, Asada SI, Sasao A. Inter-relationships between canopy features and
409 fruit yield in citrus as detected by airborne multispectral imagery. *Trans. ASABE*.
410 2008; 51: 739-751.

411 [25] Forshey CG, Elfving DC. The relationship between vegetative growth and fruiting
412 in apple trees. *Horticultural Reviews* 1989; 11: 229–287.

413 [26] Ye X, Sakai K. Limited and time-delayed internal resource allocation generates
414 oscillations and chaos in the dynamics of citrus crops. *Chaos* 2013; 23: 043124-1-
415 10.

416 [27] Ricker WE. Stock and recruitment. *J. Fisheries Res. Board Can.* 1954; 11: 559–623.

417 [28] Ploschuk EL, Slafer GA, Ravetta DA. Reproductive allocation of biomass and
418 nitrogen in annual and perennial lesquerella crops. *Ann. Bot.* 2005; 96: 127–135.

419 [29] Primack RB. Relationships among flowers, fruits, and seeds. *Ann. Rev. Ecol. Syst.*
420 1987; 18: 409-430.

421 [30] Sakai K. *Nonlinear Dynamics and Chaos in Agricultural Systems*. Elsevier,
422 Amsterdam. 2001.

423 [31] Man KF, Tang KS, Kwong S. *Genetic Algorithms: Concepts and Applications*.
424 *IEEE Trans. Ind. Electron.* 1996; 43: 519-534.

Fig. 1. Simulation results of Isagi's resource budget model. (a) Bifurcation diagram shows the dynamics of fruiting cost (C_a) as a function of ratio between costs for fruiting and flowering (R_c). (b) Time series data of C_a . (c) Return map of C_a . Model parameters are $P_s=200$, $L_T=600$, and initial condition $I(0)=10$. For bifurcation map, R_c ranges from 0 to 3.0; Time series and return map of C_a are based on results obtained when R_c is 2.8.

Fig. 2. Model of an individual plant illustrates the interdependency between vegetative growth (new leaf growth (C_l)) and reproductive growth (fruiting cost (C_a)). In the model, new, young leaves and old, mature leaves in citrus canopy are represented by light green color and dark green color, respectively. The growing cycle starts from ①, passes through ②, ③ and ④, and returns to ①, then it starts over again with a new cycle.

Fig. 3. The concept of the resource tank and the different resource accumulation patterns for a tree in one year. The empty portion ($L_T + P_s - I(t)$) of the resource tank at the beginning of the year is partially or fully filled by P_s during the growing cycle.

Fig. 4. Relationship between the cost for new leaf growth (C_l) and the initial resource level (I) of the plant body in the modified resource budget model.

Fig. 5. Model of an individual plant constructed by incorporating new leaf growth into the resource budget model. The sum of the volumes for the resource tank and the dotted box represents the potential maximal capacity of resource accumulation ($L_T + P_s$) in a growing cycle.

Fig. 6. Comparisons between the return maps of a plant derived from the original Isagi's resource budget model (solid blue line) and the modified resource budget model (dashed red line). (a) In terms of resource reserve (I), (b) In terms of fruiting cost (C_a).

Fig. 7. Model simulations with different new leaf growth coefficients (r). (a) Same pattern as the original Isagi's resource budget model ($r=0$); (b)-(c) Yield bounds become narrower and occurrences of no fruiting increase as r increases from (b) 0.10 to (c) 0.20; (d) Simulation of a life cycle with variable r values ($r=0.20$ for $0 < t \leq 5$, 0.05 for $5 < t \leq 50$, 0.35 for $50 < t \leq 80$, and 0.59 for $80 < t \leq 100$). In (a)-(d), model parameters are $P_s=200$, $L_T=600$, $R_c=2.5$, and initial condition $I(0)=10$.

Fig. 8. Bifurcation diagram shows the dynamics of fruiting cost (C_a) as a function of the ratio between costs for fruiting and flowering (R_c). The point at which fruiting cost (C_a) begins to bifurcate is shifted to a lower R_c (dotted red line), as compared to $R_c=1$ in the resource budget model. Model parameters are $P_s=200$, $L_T=600$, $r=0.2$, and initial condition $I(0)=10$.

Fig. 9. Two curves represent the linear (solid blue line), and Ricker-type (dashed red line) relationships between costs for flowering (C_f) and fruiting (C_a).

Fig. 10. Model simulations with two different R_k (the C_a/C_f ratio when $C_f=K$). (a) Time series and (b) return map of fruiting cost (C_a) for $R_k=0.72$, showing a fluctuating dynamics with continuous fruiting. (c) Time series and (d) return map of fruiting cost (C_a) for $R_k=0.92$, showing a fluctuating dynamics with intermittent occurrences of no fruiting. The solid red square data points indicate the relatively stable yields that occurs during short periods (2~4 years). In (a)-(d), Ricker-type equation is integrated into the model; model parameters are $P_s=200$, $L_T=600$, $r=0.1$, $a=2.0$, $K=160$, and initial condition $I(0)=10$.

Fig. 11. Bifurcation diagram shows the dynamics of fruiting cost (C_a) as a function of R_k (the C_a/C_f ratio when $C_f=K$). Ricker-type equation is integrated into the model; model parameters are $P_s=200$, $L_T=600$, $r=0.1$, $a=2.0$, $K=160$, and initial condition $I(0)=10$.

Fig. 12. Time series ((a) and (c)) of fruit yield for two tree samples over a 16 year period, both showing a significant pattern of yield oscillations. Return maps ((c) and (d)) of fruit yield for these two trees, showing a different shape of data distribution in return map. The solid red square data points represent the relatively stable yields (in transient episodes) observed in the experiments.

Fig. 13. Simulations for two citrus trees with the new models. Left column (Model I) is the results for the new model with a simple line in the return map, which is obtained with model parameters $P_s=2900$, $L_T=4672$, $r=0.122$, $R_k=1.214$, $a=0$, $K=2403$, and initial conditions $I(0)=4102$. Right column (Model II) is the results for the new model with a hump-shaped curve in the return map, which is obtained with model parameters $P_s=2930$, $L_T=3625$, $r=0.113$, $R_k=0.957$, $a=1.915$, $K=2334$, and initial conditions $I(0)=2830$. (a)-(b) illustrate the fluctuating patterns of the real yields (blue diamond points) and the predicted yields (pink square points) by the two models. (c)-(d) Linear regressions between the real yields and the predicted yields of the trees, showing the degree of predictive accuracy of the two models. The solid black lines are the fitted regression lines. (e)-(f) The return maps for the real yields (blue diamond points) and the predicted yields (pink square points). The fitted lines (purple solid line) illustrate two different types of return maps generated by the models. $y(t)$ and $y(t+1)$ are yields (number of fruit) in two sequential years.