A First Order Piece-Wise Linear Differential Equation Explains Alternate Bearing In Perennial Plants

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Abstract

The phenomenon of Alternate Bearing observed in polycarpic plants has long been a problem of interest for ecologists and biologists due to its cascading ecological and socio-economical effects. The discrete Resource Budget Model (RBM) with tent-map equations was the first mathematical attempt to model the underlying physical mechanism behind the phenomenon. In this work, the presence of resource budgeting of photosynthate in plants confirmed by past experimental studies was modeled as a continuous process and an ordinary, first-order, and piece-wise linear differential equation was derived in compliance with the discrete model. This led to the emergence of additional parameters that introduced an evolutionary window to understand the onset of flowering and fruiting phenophases of different plant species. The new parameters were dependent on the plant's internal reproductive clock evolutionarily set by the regional duration of favorable weather conditions and defined the duration of flowering and fruiting phenophases of the species. This could not be explained by the discrete model. The continuous model also allowed for different annual onset times of flowering phenophase for different species.

Modifications to RBM have been made in the literature to address problems related to alternate-bearing in individual trees and masting in a coupled population of trees but those models do not address the storage of photosynthate as a continuous process as done in this work. The continuous model is a more realistic approach to understand resource budgeting and alternate bearing in perennial plants and can lead to a better understanding of other related ecological phenomena and can be extended to perform more accurate ecological modelling that captures the real world in a better way.

Keywords

Alternate Bearing, Biophysical Modelling, Chaotic Solutions, First Order Differential Equation, Mathematical Modelling, Piece-Wise Linear Differential Equation, Resource Budget Model

1. Introduction

Alternate bearing is the phenomenon of excess fruit/seed production followed by much lesser or negligible yield which is commonly known to be exhibited by perennial polycarpic plants. The years of high and low yields are called the On-years and Off-years of the plant, respectively. The phenomenon of synchronized alternate bearing exhibited by a plant population is called masting. Different species of fruit crops have their characteristic number of Off-years following an On-year, and the corresponding pattern is called a cycle. Forest trees commonly show cycles of more than two years, and also exhibit masting. The seed production in sweet chestnuts, hazelnuts, elms, and apples is found to exhibit cycles of 2-3 years, in pines and oaks the cycles are of 3-5 years, and in spruces and beaches, they are of 5-7 years and 10-15 years respectively. The phenomenon is exhibited by both deciduous and evergreen trees, and by a wide variety of polycarpic species irrespective of their temporal differences in flowering and fruiting patterns. This widespread behavior was argued to be suggesting the presence of a common resource budgeting mechanism in polycarpic plants in Monselise & Goldschmidt (1982).

Additionally, the experimental results of a study conducted by Davis & Sparks showed the usage of the previous year's photosynthetic resource production in the plant's current year development and reproductive phenophases [Davis & Sparks (1974)]. Considering these observed characteristics of the alternation phenomenon, a Resource Budget Model (RBM) was proposed by Isagi to explain alternation and masting (Isagi et al., 1997). The presence of resource budget in plants was later experimentally confirmed (Crone et al., 2009).

RBM consists of a set of tent-map equations that describe the annual usage and storage of photosynthate (P) in the plant by using time as a discrete variable [Isagi et al. (1997)]. In this work, we have tried to understand the resource budgeting present in plants as a continuous process by incorporating time as a continuous variable in the new model equations. It was found that the extended model explained additional features related to the varied durations of flowering and fruiting for different species apart from reproducing the results of the discrete model. It also provided an avenue for considering varied onset flowering-times for different species and simulating the effect of short-term weather fluctuations that can have a significant impact on the plant's annual yield, though we have not done so in this study.

Modifications to RBM have involved the removal of the threshold, putting a limit on the maximum amount of photosynthate a plant can store, assuming a non-linear relationship between flowering and fruiting, and introducing different kinds of couplings (Ye & Sakai, 2016; Esmaeili et al., 2021). These modifications explored mechanisms outside the plant that could contribute to a plant population exhibiting synchronous yield behavior. However, these attempts were not aimed at gaining more insight into the inner working of an alternate bearing plant. In this study, we have tried to understand resource budgeting by formulating it as a continuous process which led to the necessary incorporation of two new parameters R_{f_o} and R_{a_o} in the new model. On further investigation, the parameters were found to be related to the duration of flowering and fruiting phenophases of the plant, respectively, and were understood as being determined by the biological clock of the plant which is set by the regional climatic conditions. Modeling alternate bearing as a continuous process can open new avenues of understanding the internal physical and biological mechanisms present inside the plant and how they affect its interaction with the environment. This, in turn, helps in understanding the process of masting comprehensively which is also one of the objectives of trying to understand the alternate-bearing pattern of an individual plant.

2. Materials & Methods

2.1 The Discrete Resource Budget Model

Isagi proposed that a plant stores a fixed amount of photosynthate every year, apart from the amount used in its development and maintenance. If during a year the stored amount of photosynthate surpasses a threshold value (L_T), the excess amount of it is used up in flowering during that year and is called the cost of flowering (C_f). Another amount proportional to C_f is used up in fruiting during the same year and is called the cost of fruiting (C_a). The ratio of C_a and C_f is the model's species-specific parameter (R) whose value determines the period of the plant's On-Off alternation cycle and whether the fruit-production time-series behavior is periodic or not (Isagi et al., 1997).

2.2 Formulation of the Continuous Model

A plant produces photosynthate continuously as long as it is exposed to photosynthesis-sustaining factors. The process undergoes a variable rate that changes throughout the day. The rate of change of the amount of the net photosynthate accumulated in the plant (P_{Net}) is directly related to the processes undergoing in the plant. The main processes that use the photosynthetic resource of a plant are the development, repair, and reproductive phenophases (flowering and fruiting) of the plant. The growth and repair of a plant is an ongoing process whereas the production of flowers and fruits occurs during its annual season. This would suggest that the resource being used up in the process is derived from both the current and the already stored resource production. P_{Net} is therefore dependent on the rate of storage of photosynthate (A) and the rates of usage of photosynthate in flowering and fruiting ($\dot{P}_{fl}$ and $\dot{P}_{fr}$ respectively). A is assumed to be an annually averaged constant to account for the daily variations in photosynthetic rate and the non-storage of P during nights due to the absence of photosynthesis. $\dot{P}_{net}$ is positive when the plant is only storing photosynthate, whereas it decreases in the presence of flowering/fruiting. The rates are therefore related by the following equation:

$\dot{P}_{net} = A - \dot{P}_{fl} - \dot{P}_{fr}$. $\dot{P}_{fl}$ and $\dot{P}_{fr}$ share a negative direct proportionality with $\dot{P}_{net}$ that can be given by the proportionality equations: $\dot{P}_{fl} = -R_f\,\dot{P}_{net}$ and $\dot{P}_{fr} = -R_a\,\dot{P}_{net}$, respectively. R_f and R_a are step functions that assume non-zero values during flowering and fruiting respectively. It is known that different species of plants flower within a respective favorable seasonal time of the year specific to the region. It is assumed in the model solely for the sake of simplicity that flowering is initiated in the plant at the same annual time each time the plant flowers instead of a seasonal time-period. If at the annual flowering-time, the amount of photosynthate accumulated in the plant is above the threshold, flowering onsets and proceeds at a rate defined by the parameter $R_{f_o} = \dot{P}_{fl}/\dot{P}_{net}$. The excess amount of stored photosynthate present above the threshold at the time (t_f) of onset of flowering is used up as the cost of flowering. For the sake of simplicity in numerical simulation, it is assumed that fruiting onsets after the completion of the flowering phenophase. $C_a = RC_f$ amount of photosynthate is used in fruit development at a rate defined by the parameter $R_{a_o} = \dot{P}_{fr}/\dot{P}_{net}$. R determines the kind—periodic or chaotic—and the time-period of the plant's On-Off alternation cycle. Fruit development completes and stops at the time t_{a_f}. The plant continues accumulating photosynthate at the constant rate A until the next annual flowering-time at which, if the accumulated photosynthate is greater than L_T, the above process repeats or continues storing photosynthate otherwise until the next annual flowering-time resulting in a year of no fruit yield. The year of completion of fruiting is considered as the plant's On/Off year for the convenience of plotting yearly time-series. A schematic diagram of the continuous RBM is shown next in Fig. 1.

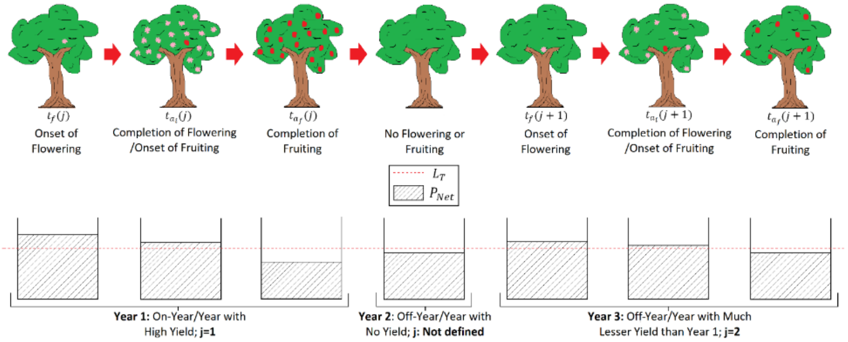


Fig. 1: Schematic diagram of the continuous model.

Figure 1 shows P_{Net} to be greater than L_T at the time of completion of flowering or the onset of fruiting in years 1 and 3. This is because of the continuous storage of photosynthate in the plant while a part of it is being used in the development of flowers. The model assumes the time at which flowering ends to be the time (t_{a_i}) of onset of fruiting though plants are often seen to have both flowers and fruits simultaneously. This assumption is made mainly to simplify model calculations, and also to account for flowering and fruiting being consecutive developmental plant phenophases with specific regional durations for different species. Whether fruiting is assumed to begin somewhere during the flowering phenophase or at the end of it does not affect the total amount of photosynthate used up in flowering and fruiting. Therefore, the annual On-Off fruit-production behavior is not affected by this simplifying assumption.

2.2.1 The Model Equations

Consider the rate equation describing the dynamics of storage and usage of photosynthate in the plant:

$$\dot{P}_{net} = A - \dot{P}_{fl} - \dot{P}_{fr} \qquad \text{—eqn 1}$$

$\dot{P}_{fl}$ and $\dot{P}_{fr}$ are related to $\dot{P}_{net}$ by eqns 2 and 3.

$$\dot{P}_{fl} = -R_f \, \dot{P}_{net} \text{ , and,} \qquad \text{—eqn 2}$$

$$\dot{P}_{fr} = -R_a \, \dot{P}_{net} \qquad \text{—eqn 3}$$

Here, $$R_f = \begin{cases} R_{f_o} & t_f(j) \leq t < t_{a_i}(j) \\ 0 & otherwise \end{cases} \text{ where, } R_{f_o} > 1\text{, and,} \qquad \text{—eqn 4}$$

$$R_a = \begin{cases} R_{a_o} & t_{a_i}(j) \leq t < t_{a_f}(j) \\ 0 & otherwise \end{cases} \text{ with } R_{a_o} > 1 \qquad \text{—eqn 5}$$

Here, $j = 1, 2, 3, ..$ represents the j^{th} time the plant undergoes flowering and fruiting, and t denotes the current time and $\Delta t = 1$ is considered as the time-period of one year. R_{f_o} and R_{a_o} are both assumed to be species-specific parameters. The rates of photosynthate-usage in flowering and fruiting are directly proportional to R_{f_o} and R_{a_o} respectively. Whether the flowering and fruiting phenophases have the same rate of photosynthate-usage will depend on the internal physical mechanisms and biological signals involved. We have assumed the general case of a plant having different rates of photosynthate-usage governing the reproductive processes of flowering and fruiting. Both R_{f_o} and R_{a_o} are greater than 1 because P_{net} should decrease as the plant develops flowers or fruits which is a necessary condition for alternate bearing to be exhibited by the plant.

Substituting eqns 2 and 3 in eqn 1, we have,

$$\dot{P}_{net} = \frac{A}{1-R_f-R_a}$$ —eqn 6

The variation of R_f and R_a with time is shown in Figs. 2a and 2b respectively.

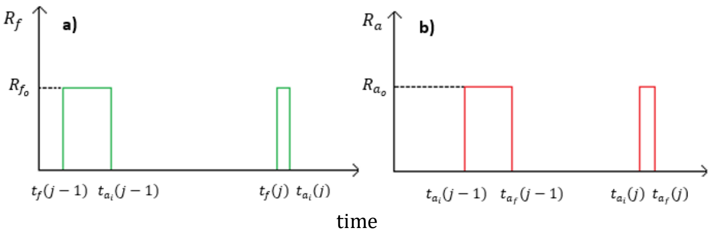


Fig. 2: Variation of R_f and R_a with time. a) R_f vs time. $t_f(j)$ and $t_{a_i}(j)$ are the j^{th} times of the onset of flowering and the end of flowering (or the onset of fruiting) respectively. **b)** R_a vs time. $t_{a_i}(j)$ and $t_{a_f}(j)$ are the j^{th} times of the onset of fruiting (or the end of flowering) and the end of fruiting respectively.

While $P_{net}|_{t_f(1)}$ is known as the initial condition, $P_{net}|_{t_f(j>1)}$ are determined by using the model's assumption that flowering is initiated in the plant only if, at the annual flowering-time (taken to be a yearly constant in the model), the amount of stored photosynthate is greater than the threshold. $t_{a_i}(j)$'s and $t_{a_f}(j)$'s are all derived constants, as shall be clear from the solution of eqn 6 given in the next section.

2.2.2 The Model Solution

The solution of eqn 6 is piece-wisely evaluated over the time-intervals $\left[t_f(j)\,, t_{a_i}(j)\right)$, $\left[t_{a_i}(j)\,, t_{a_f}(j)\right)$ and $\left[t_{a_f}(j)\,, t_f(j+1)\right)$. The case of $t_f(j) \le t < t_{a_i}(j)$ is considered first along with the initial condition:

$$P_{net}\big|_{t_f(j)} = L_T + C_{f_j} \qquad \text{—eqn 7}$$

where $C_{f_j} = C_f\big|_{t_f(j)}$. For this case, eqns 6 and 2 reduce to $\dot{P}_{net} = \frac{A}{1-R_{f_o}}$ and $\dot{P}_{fl} = -R_{f_o}\,\dot{P}_{net}$ respectively. These two eqns when solved within the integration limits $\left[t_f(j)\,, t_{a_i}(j)\right)$ give the following two expressions.

$$P_{net}\big|_{t_{a_i}(j)} = \left(1 - \frac{1}{R_{f_o}}\right) C_{f_j} + L_T \qquad \text{—eqn 8}$$

$$t_{a_i}(j) = t_f(j) + \frac{C_{f_j}}{A}\left(1 - \frac{1}{R_{f_o}}\right) \qquad \text{—eqn 9}$$

For the time-interval $t_{a_i}(j) \le t < t_{a_f}(j)$ which follows the end of flowering, eqns 6 and 3 reduce to $\dot{P}_{net} = \frac{A}{1-R_{a_o}}$ and $\dot{P}_{fr} = -R_{a_o}\,\dot{P}_{net}$ respectively. The two equations when solved within the integration limits $\left[t_{a_i}(j)\,,t_{a_f}(j)\right)$ give the following expressions.

$$P_{net}|_{t_{a_f}(j)} = P_{net}|_{t_{a_i}(j)} - \frac{R\,C_{f_j}}{R_{a_o}} \qquad \text{—eqn 10}$$

$$t_{a_f}(j) = t_{a_i}(j) + \frac{R\,C_{f_j}}{A}\left(1 - \frac{1}{R_{a_o}}\right) \qquad \text{—eqn 11}$$

The equation $C_{a_j} = RC_{f_j}$ was used to represent eqns 10 and 11 in terms of C_{f_j}. The next integration limit is $\left[t_{a_f}(j)\,,t_f(j+1)\right)$, for which eqn 6 reduces to $\dot{P}_{net} = A$. Solving this eqn within the integration limits gives:

$$P_{net}|_{t_f(j+1)} = P_{net}|_{t_{a_f}(j)} + A\left(t_f(j+1) - t_{a_f}(j)\right) \qquad \text{—eqn 12}$$

The possible values of $t_f(j+1)$ are given by $t_f(j) + i$, where i takes positive integer values. The lowest value of i at which $P_{net}|_{t_f(j+1)}$ exceeds L_T determines $t_f(j+1)$ which is then used in eqn 7 to obtain $C_{f_{j+1}}$. Alternatively, eqns 7, 8, 9, 10, 11 and 12 were used to obtain the following recursive equation.

$$C_{f_{j+1}} = A\big(t_f(j+1) - t_f(j)\big) - RC_{f_j} \qquad \text{—eqn 13}$$

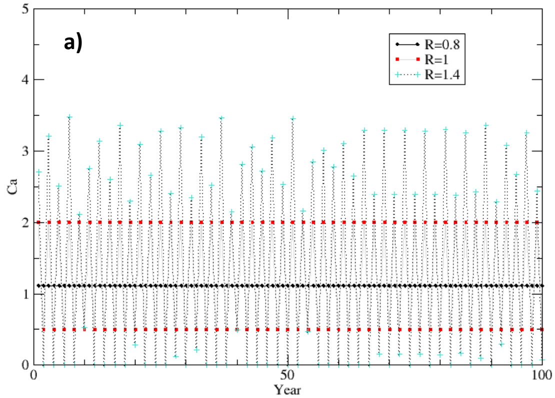
$t_{a_i}(j)$s and $t_{a_f}(j)$s are derived constants that are evaluated by using the known values of respective C_{f_j}s which are in turn evaluated using the initial condition $C_f\big|_{t_f(1)} = C_{f_1}$. The solution time-series may, in principle, be found for the entire real positive number line. However, it is obtained for a limited number of time-steps to account for the limited lifespan of a plant.

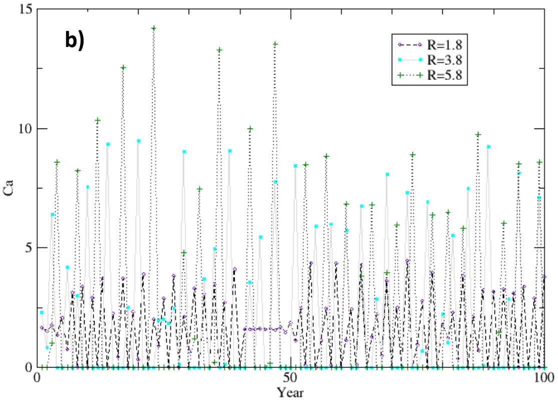
3. Results & Discussion

3.1 The Effect of Changing the Ratio of Cost of Fruiting to Flowering

The ratio of cost of fruiting to flowering, R, is a direct measure of the average size, volume and mass of the fruit as compared to the flower. A change in the ratio is also reflected in the fruit-bearing pattern of the plant species because of a change in the resource allocation to the process of fruiting. To observe the change in the fruit-bearing due to a change in the species R value, the model was numerically simulated to obtain fruit-bearing time-series (C_a vs. year of end of fruition) for different R values, where eqns 7, 8, 9, 10, 11, and 12 were recursively used to evaluate C_{f_j}s. The years with no yield were assigned the C_a value of zero.

It was observed that the model exhibited constant solutions for $R < 1$ (Fig. 3a), a period-2 solution for $R = 1$, and solutions with increasing number of Off years between consecutive On years with an increase in R (Figs. 3a, 3b and 3c). The results were in agreement with the discrete model (Isagi et al., 1997).


a)
R=0.8
R=1
R=1.4
Ca
Year
0
1
2
3
4
5
0
50
100


b)
R=1.8
R=3.8
R=5.8
Ca
Year
0
5
10
15
0
50
100

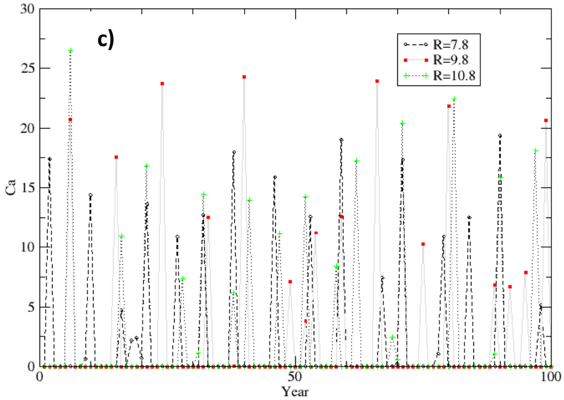


Fig. 3: Plot of C_a vs year of end of fruition for different R values. a) C_a vs year of end-of-fruition for $R = 0.8$, 1, 1.4. **b)** C_a vs year of end-of-fruition for $R = 1.8$, 3.8 and 5.8. **c)** C_a vs year of end-of-fruition for $R = 7.8$, 9.8 and 10.8. The years with no yield were assigned a C_a value of zero. The parameters C_{f_1}, L_T, A, R_{f_o} and R_{a_o} were fixed to 2.0, 5.0, 2.5, 1.08 and 1.1, respectively, and $t_f(1)$ was set to 1.125 ($\Delta t = 0.125$ corresponds to mid-February), in all the plots. Results were included after the initial 200 years.

Figure 3 shows that the RBM produces results with alternate bearing behaviour for a wide range of R values. Perennial plants produce fruits with a consistent annual variability where the fruit-production observed during any considered duration of years is never exactly repeated. However, an On-Off cycle consisting of a more or less consistent number of years is what is observed, where different plant species have different number of years in their characteristic cycle of alternate bearing (Monselise & Goldschmidt, 1982). This fruit-bearing characteristic of a perennial plant having a species-specific duration of its alternate bearing cycle is well captured by RBM. Though RBM has been modified by Esmaeili et al. (2021) to exhibit period-2 solutions for a wide parameter-range, the modified model helps in capturing some aspects of the masting phenomenon but is not a good comprehensive representation of the ‘chaotic’ alternate bearing fruit-production perennial plants exhibit.

Additionally, the bifurcation diagram of the continuous model was plotted and compared with the discrete model. For both the models, the presence of fixed-point solutions was observed for $R < 1$; at $R = 1$, a period-2 bifurcation occurred after which chaotic bands were observed for $R > 1$ (Fig. 4). These results were in agreement with the detailed study of the bifurcation diagram of the discrete model plotted using a parameter other than C_a (Prasad & Sakai, 2015).

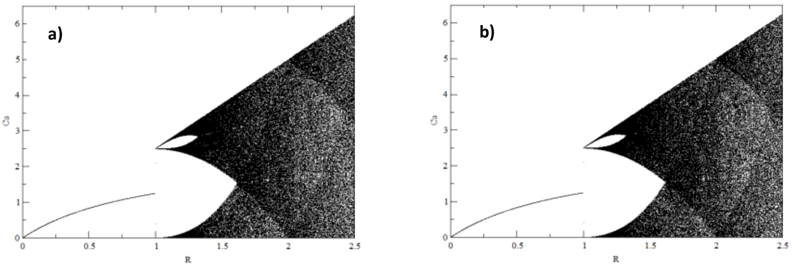


Fig. 4: Bifurcation diagrams for the continuous and discrete RBMs. a) Bifurcation diagram for the continuous model is shown. The years with no yield were assigned a C_a value of zero The parameters L_T, A, R_{f_o} and R_{a_o} were fixed to 5.0, 2.5, 1.08 and 1.1 respectively. C_{f_0} and $t_f(1)$ were set to 2.1 and 1.125 respectively. **b)** Bifurcation diagram for the discrete model is shown. The parameters L_T, P_s and C_{f_0} were fixed to 5.0, 2.5 and 2.1 respectively. P_s denoted the annual amount of photosynthate stored in the plant and was considered a constant.

3.2 Physical Significance of the New Parameters R_{f_o} and R_{a_o}

Equations 2, 3 and 6 in section 2.2.1 were used to obtain the following equations: $\dot{P}_{fl} = \frac{A}{(1-1/R_{f_o})}$ and $\dot{P}_{fr} = \frac{A}{(1-1/R_{a_o})}$. Therefore, the rates $\dot{P}_{fl}$ and $\dot{P}_{fr}$ decreased with increasing R_{f_o} and R_{a_o} respectively which implied that the duration of the phenophases increased with the respective parameters. The durations of flowering and fruiting phenophases are given by $t_{a_i} - t_f$ and $t_{a_f} - t_{a_i}$ respectively, and the corresponding years of onset are given by the greatest integer functions $[t_f]$ and $[t_{a_i}]$ respectively. The durations of flowering and fruiting were plotted against their year of onset for different values of R_{f_o} and R_{a_o} respectively (Fig. 5) and it was found that the durations increased with the respective parameters for the same value of photosynthate used. However, the parameters of the species need to be chosen in the range where the phenophases are completed within the annual duration of favorable weather conditions, as too high values would imply unnaturally extended flowering and fruiting durations.

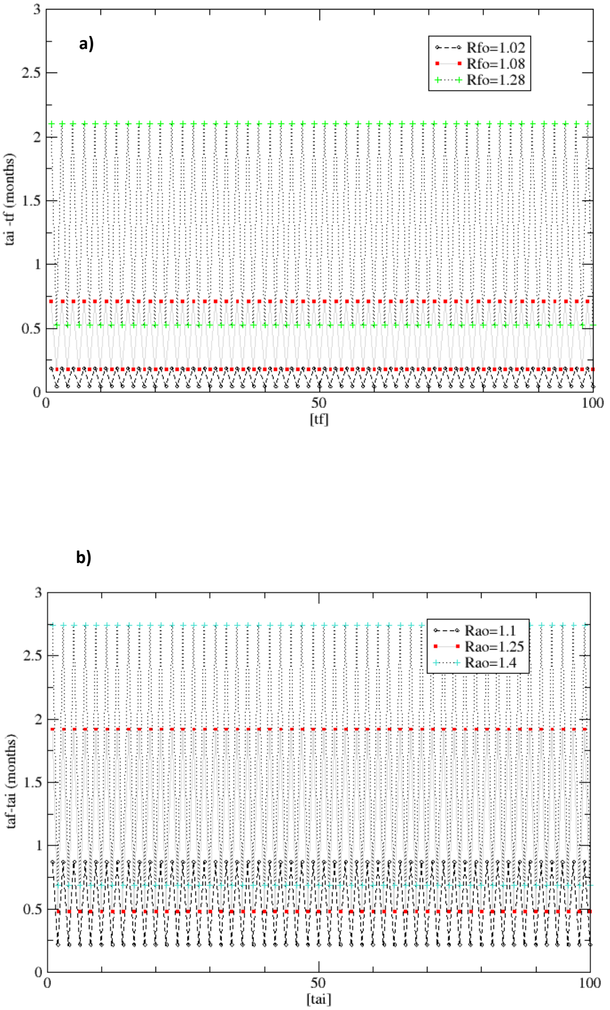


Fig. 3: Plot of C_a vs year of end of fruition for different R values. a) C_a vs year of end-of-fruition for $R = 0.8$, 1, 1.4. **b)** C_a vs year of end-of-fruition for $R = 1.8$, 3.8 and 5.8. **c)** C_a vs year of end-of-fruition for $R = 7.8$, 9.8 and 10.8. The years with no yield were assigned a C_a value of zero. The parameters C_{f_1}, L_T, A, R_{f_o} and R_{a_o} were fixed to 2.0, 5.0, 2.5, 1.08 and 1.1, respectively, and $t_f(1)$ was set to 1.125 ($\Delta t = 0.125$ corresponds to mid-February), in all the plots. Results were included after the initial 200 years.

The form of the functions R_f and R_a varies according to the flowering and fruiting patterns of different species. Experimental methods can be developed to determine the parameters based on the observed durations and rates.

3.2.1 Factors that Affect R_{f_o} and R_{a_o}

The fact that plants usually reproduce during a certain time of the year specific to their species suggests the presence of an internal signaling mechanism that follows the plant's reproductive clock set by regional climatic conditions. The plant signals the onset of flowering and fruiting at the favorable annual time which leads to R_{f_o} and R_{a_o} being non-zero and to photosynthate-usage in the respective processes. Whether R_{f_o} and R_{a_o} share a common or two different signaling mechanisms which decide their temporal behavior is subject to experimental studies. In addition, whether all perennial species follow a common signaling mechanism for R_{f_o} and R_{a_o} to be non-zero and whether R_{f_o} and R_{a_o} vary within a range in a species-specific manner, both are subject to experimental analysis as well. In this study, we've considered R_{f_o} and R_{a_o} as known constants, where the conditions $R_{f_o} > 1$ and $R_{a_o} > 1$ are necessary for a plant to exhibit alternate bearing.

It is known that abrupt severe weather changes during a year lead to crop loss or failure. R_{f_o} and R_{a_o} can therefore vary as a result of bad weather conditions. This is so in the case of crop failure where the parameters are zero and flowering doesn't onset. Therefore, a plant's internal signals that decide when R_{f_o} and R_{a_o} are non-zero are themselves subject to external weather conditions besides the internal biological clock of the plant. In the case of an insufficient amount of resource available in the plant for fruiting, only a fraction of the flowers may develop into fruits as the plant sheds off the surplus number of flower buds. The time-duration in which R_{a_o} is non-zero therefore depends on the amount of accumulated resource available in the plant.

3.3 Effect of Changings the Rate of Photosynthate-Storage on Model Solutions

Continuous model solutions were plotted for different photosynthate-storage rates (A-values) in Fig. 6, for $R = 1$. The value of $R = 1$ was chosen because the model exhibits a period-2 solution for $R = 1$ and therefore the effect of any change in A is directly proportional to C_a and can be clearly seen in the C_a time-series. It is seen in Fig. 6 that the periodic solution of $C_a = 2$ is exhibited by all the three time-series corresponding to the three A values of 2.5, 3.5 and 5.5, and $R = 1$. This is because the initial condition of $C_f = 2$ is also one of the two period-2 solutions for $R = 1$.

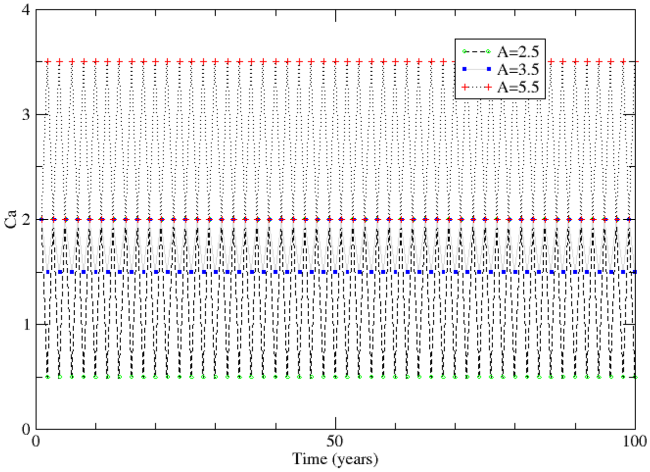


Fig. 6: Plot of C_a vs year of end of fruition for different A values. The parameters C_{f_1}, L_T, R, R_{f_o} and R_{a_o} were fixed to 2.0, 5.0, 1.0, 1.08 and 1.1, respectively, and $t_f(1)$ was set to 1.125. Results were excluded for the initial 200 years.

Therefore, if the plant is assumed to start flowering during a year with the initial condition $C_f = 2$, the excess amount of photosynthate stored above the threshold is reflected in the cost of flowering/fruiting during the next year. This explains the increase in the other periodic solution seen in Fig. 6 which leads to an out-of-phase fruiting behavior of $A = 5.5$ time-series with the other two time-series. This also shows that a year that would otherwise have been an Off-year may be an On-year depending on the value of A. The direct proportionality of C_a with A was expected because an increase in the rate of photosynthate-storage leads to an increase in the amount of photosynthate accumulation above the threshold at the time of flowering which should lead to an increase in the fruit production. This suggests that environmental stochasticity may be a major contributing factor to the On-Off fruit-bearing pattern seen in perennial plants. However, the presence of resource budgeting upon which the model is based has already been experimentally confirmed (Crone et al., 2009), and the annual environmental conditions for most crops stay more or less the same unless there is a drastic weather change during a certain year.

Amidst similar annual weather conditions, alternate bearing is still exhibited by a perennial plant. This rules out environmental stochasticity as the main contributing factor to alternate bearing.

The model solutions correspond to the fruit-bearing behavior of ‘one’ individual tree for different species characterized by different R values, which doesn’t take into account any kind of coupling which may be present between trees planted in the same field, or among widely separated tree populations. The effects of coupling between plants and changes in the environment need to be incorporated into the model. The environmental fluctuations for a single tree can however be modelled by considering annually averaged and annually changing values of A which are known constants.

4. Conclusion

The behavior of the solutions of the continuous model with change in the parameter R agreed with the discrete model. This was confirmed by the bifurcation diagrams of the two models which agreed with each other and exhibited chaotic bands for $R > 1$ that merged at around $R = 1.6$ (Fig. 4). This was because the form of relationships between stored resources and reproduction at annual scales didn't change in the extension of budgeting of photosynthetic resource as a continuous process. Also, a linear relationship between the cost of flowering and fruiting was assumed as a simplifying assumption in compliance with the discrete version. To know if there were any specific regions in the parameter space for $R > 1.6$ that led to annual periodic and chaotic reproduction, a detailed study of the bifurcation diagram of the continuous model would need to be done which we have not addressed in this work.

It should be noted that the size of a fruit of most plant species is usually many times bigger than its parent flower and the fruit production behavior of a plant/tree is chaotic in general, therefore the R-values of real-world plant species are expected to be greater than 1, and lying in the chaotic regime of the bifurcation diagram. The R-values for different species as the average ratio of the amount of photosynthate constituting a fruit to that constituting a flower for different species can be attributed to have been set during the evolutionary time-period of separation of different seed types or fruit crops.

The new features that the continuous model explained were related to the duration of flowering and fruiting phenophases which couldn’t possibly be incorporated in the discrete model. This was because of the parameters $R_{f_o}$and R_{a_o} which were inbuilt in the formulation of the continuous model. $R_{f_o}$and R_{a_o} were understood to be set by the plant’s internal biological clock (section 3.2.1) and decided the rate of photosynthate usage in flowering and fruiting phenophases of the plants which were found to be directly proportional to the parameters. The parameters, therefore, explain the varied temporal flowering and fruiting behaviour of different plant species which can’t be incorporated into the discrete model.

In this model, we considered $R_{f_o}$and R_{a_o} as constants. However, in actual practice, they may change due to abrupt environmental changes or according to the values of C_f and C_a so that the phenophases complete within the annual duration of favorable weather conditions. Additionally, two plants of different species may have comparable or different R_{f_o}’s and R_{a_o}’s depending on the respective C_f’s and C_a’s, and the duration of favourable weather conditions for the phenophases.

It should be noted that we have considered the averaged effect of the factors that might affect the resource dynamics within a season, such as climate (day length, precipitation), predators, and molecular controls, and we have assumed that effect to be an annual constant by assuming the photosynthate rate A as a constant annual parameter. However, the model allows for a time-dependent functional form of A instead of annually-averaged values considered as constants, and a non-limiting change in the environmental factors affecting the photosynthate production in the plant leads to a change in A and will affect its fruit yield.

The attempt to understand resource budgeting in plants as a continuous process by extending Isagi’s discrete RBM to a continuous model has introduced the role of evolution, environment, and plant’s biological clock in the fruit-bearing of a plant in the form of parameters $R_{f_o}$and R_{a_o}, and therefore has added a new dimension of understanding to the model, and helped in better understanding the internal physical mechanism of the storage and usage of a plant’s resource. The introduction of different kinds of intra and inter-species couplings, within plants of the same or widely spatially separated fields, in the model, is a prospect for future research.

Author’s Contributions

K.P. conceived and derived the continuous RBM’s equations, performed the numerical simulations, analysed the results and wrote the manuscript.

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Data Availability

No empirical data was used.

Author Declarations

I have nothing to declare.

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