

A Biological Model of Apple Tree Production

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Abstract Dynamic simulation models of deciduous perennial fruit tree behaviour over time are of significant use in understanding relationships that are crucial to optimal tree growth. A biological model that simulates the basic physiological processes of photosynthesis and dry matter partitioning of an apple tree is presented in this paper. The model is specified at a level of aggregation which is appropriate for incorporation into an optimising model of apple orchard management. This paper presents the development of the model and accounts for important environmental and management variables and their effect on the quantity of output produced.

1. INTRODUCTION

Management of deciduous perennial fruit crops requires a good understanding of the many environmental, physiological and horticultural factors that influence tree growth, fruit production and fruit quality. Of particular importance for apple tree management is knowledge of how the growing environment and horticultural manipulation of past years affect current and future growth habits and productivity of the tree.

A model of the growth cycle and fruiting habits of an individual apple tree is presented in this paper. The model takes into account the vegetative and reproductive physiology of apple trees, factors affecting the quantity of apples produced, and the interrelationships between these factors. Leaf, root, stem and branches (wood) and fruit growth are simulated through a series of submodels which allow the incorporation of alternative apple cultivars and canopy architectures. Processes that are unique to deciduous perennials, including the development of winter hardiness, physiological rest, and the accumulation of stored materials to fuel renewed growth following rest are also accounted for in the model.

2. MODEL

Apple tree growth is described using a carbon balance model, where change in tree mass depends on leaf (L), wood (W), fruit (F), and root (R) growth. For a given tree, the gain in mass of each tree component is defined as:

$$(1) \quad \frac{dw_j}{dt} = [(P_d - R_d)\psi + CHO]\rho_j$$

for $j = L, W, F, R$

where w_j represents dry matter mass (g) of component j , P_d is daily photosynthesis, R_d is the total respiration of the tree, CHO represents carbohydrate reserves, ρ_j is the proportion of assimilates partitioned to the various tree components, and ψ is a conversion factor between carbon and dry matter (DM). The following subsections describe the model in detail and parameter values are given in Table 1.

2.1 Photosynthesis

Daily photosynthesis ($\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) is given by (Lakso and Johnson, 1990):

$$(2) \quad P_d = \frac{\alpha S h P_{\max} [1 - \exp(-K LAI)]}{\alpha K S + h P_{\max}}$$

where α is a constant that measures the efficiency of leaf photosynthesis ($\mu\text{g CO}_2 \text{ Joule}^{-1}$), S is the daily integral of total radiation on a horizontal surface ($\text{MJ m}^{-2} \text{ day}^{-1}$), h is daylength (seconds), P_{\max} is the rate of light saturated leaf photosynthesis ($\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), LAI is the leaf area index of the tree and K is a coefficient that represents the extinction of light as it passes through the canopy.

The environmental parameters, daylength daily radiation and temperature, are determined using cosine equations: Daylength is calculated from:

$$(3) \quad X = X_m + X_r \cos\left[\frac{2\pi(u - X_d)}{365}\right]$$

where X represents either h , S or T . Subscripts m and r represent the mean and range in X respectively, d is the day of the year when the maximum value of X occurs and u is the day number (January 1 = 1).

Table 1: Parameter values used

Parameter	Value	Units	Source	Equation
Ψ	1.54	$\text{m}^2 \text{DM} (\text{CO}_2)^{-1}$	Proctor et al. (1976)	(1)
K	0.6		Jackson (1978)	(2)
α	14600	$\mu\text{g CO}_2 \text{Joule}^{-1}$	Proctor et al. (1976)	(2)
P_{max}	0.00075	$\text{g m}^{-2} \text{s}^{-1}$	Watson et al. (1978)	(2)
h_m	45000	seconds		(3)
h_r	18000	seconds		(3)
h_d	355	seconds		(3)
S_m	6.13	$\text{MJ m}^{-2} \text{day}^{-1}$		(3)
S_r	2.9	$\text{MJ m}^{-2} \text{day}^{-1}$		(3)
S_d	355	$\text{MJ m}^{-2} \text{day}^{-1}$		(3)
T_m	10	$^{\circ}\text{C}$		(3)
T_r	15	$^{\circ}\text{C}$		(3)
T_d	15	$^{\circ}\text{C}$		(3)
ϕ	80	g m^{-2}	Barritt et al. (1991)	(5)
a	2.16	$\text{g m}^{-2} \text{d}^{-1}$	Butler and Landsberg (1981)	(6)
β	0.09		Butler and Landsberg (1981)	(6)
θ_L	0.18		Heim et al. (1979)	(8)
λ_L	-0.085		Heim et al. (1979)	(8)
τ_L	6.85		Heim et al. (1979)	(8)
θ_w	0.41		Heim et al. (1979)	(8)
λ_w	-0.30		Heim et al. (1979)	(8)
τ_w	6.05		Heim et al. (1979)	(8)
θ_F	0		Heim et al. (1979)	(8)
λ_F	0.86		Heim et al. (1979)	(8)
τ_F	9.6		Heim et al. (1979)	(8)
TB	4	$^{\circ}\text{C}$	Anderson et al. (1986)	(11,12)
TU	25	$^{\circ}\text{C}$	Anderson et al. (1986)	(11,12)
TC	36	$^{\circ}\text{C}$	Anderson et al. (1986)	(11,12)

Leaf area index is defined as:

$$(4) \quad LAI = \frac{LA}{GA}$$

where LA is leaf area per tree (m^2) and GA is ground area per tree (m^2). Leaf mass (g DM) is converted to where LA is leaf area per tree (m^2) and GA is ground area per tree (m^2). Leaf mass (g DM) is converted to leaf area (m^2) using:

$$(5) \quad LA = \frac{w_L}{\phi}$$

where ϕ converts g DM into leaf area. The maximum leaf mass (L_{max}) attainable by the tree is set at a predetermined level appropriate to the age of the tree. Once L_{max} is attained in the model leaf mass remains constant until leaf fall.

2.2 Respiration

Respiration rates of apple trees are low when the trees are dormant, rise rapidly during spring to reach a maximum as leaves emerge from their buds, and then decline steadily through the season (Butler and

Landsberg, 1981). Daily respiration of the tree ($\text{g CO}_2 \text{m}^{-2} \text{day}^{-1}$) is based on an exponential response to temperature:

$$(6) \quad R_d = a \exp(\beta T)$$

where a is respiration at a temperature of zero $^{\circ}\text{C}$, β is a coefficient, and T is temperature ($^{\circ}\text{C}$).

2.3 Seasonal Effects and Dry Matter Partitioning

The production, partitioning and use of dry matter in apple trees follow specific seasonal patterns according to tree activity. During late autumn, apple trees enter a dormant period where vegetative and reproductive buds require a period of non-growth and chilling temperatures if bloom, growth and development are to occur in the spring. In early spring, leaf and fruit growth are triggered by favourable temperatures which cause growth to occur. Initial development utilises stored reserves of carbohydrates and nutrients until leaf area is sufficient to sustain growth of the tree and fruit:

$$(7) \quad CHO = \zeta R$$

where ζ is a coefficient denoting the release of reserve carbohydrates into the tree. If the chilling requirement has not been satisfied or full bloom has been reached ζ has a value of zero. In the period after the chilling requirement is satisfied and before full bloom occurs ζ is assumed to have a value of 0.03. This arbitrary value was considered a reasonable initial estimate.

Following budbreak, leaf area develops rapidly up to a maximum value. Evidence from Forshey et al. (1983), Porpiglia and Barden (1980) and Ferree (1980) indicates that the foliage canopy of an apple tree is complete at three weeks after full bloom. Leaf area becomes stable during midseason and then declines in autumn. Leaf senescence occurs over a period of 6 weeks during autumn following the onset of cooler temperatures and the tree once again enters a period of rest. These events are implemented in the model by defining triggers activated by various events.

Fruit continues to increase in size throughout the season resulting in significant demand for energy and is harvested during late summer and early autumn. Whether or not a tree is producing fruit has a significant effect on the allocation of assimilates to other tree components. One noticeable effect of fruit growth is a reduction in root growth (Heim et al. 1979). A heavy fruit load affects photosynthesis through a reduction in leaf area (shoot growth) when compared with trees having no fruit (Faust, 1989).

The proportion of assimilates partitioned to tree components during a growing season is determined using the following equations which were calibrated using data presented by Heim et al (1979):

$$(8) \quad \rho_j = \theta_j + \frac{\lambda_j F_L}{\tau_j + F_L} \quad \text{for } j = L, W, F$$

$$(9) \quad \rho_R = 1 - \rho_L - \rho_W - \rho_F$$

where F_L represents fruit load (fruit number per m^2 leaf area).

3. FRUIT GROWTH

Fruit development and growth can potentially occur when the chilling requirement of the tree has been satisfied. The chilling requirement to break dormancy varies between apple tree cultivars, with most genotypes requiring between 800 and 1200 chill units (Hauagge and Cummins, 1991). For deciduous fruit trees one chill unit is defined as an exposure to the optimum temperature (6°C) for one hour, with temperatures above or below the optimum contributing less to chilling time according to the following formula adapted from Linvill (1990) and Faust (1989):

$$(10) \quad CU = \begin{cases} 0 & \text{if } TH \leq 0 \\ \sin\left[\left(\frac{2\pi}{28}\right)T\right] & \text{if } 0 \leq TH \leq 21 \\ -1 & \text{otherwise} \end{cases}$$

where CU represents the number of chill units and TH is the hourly temperature. Positive chill units begin to accumulate in autumn thus, the date of dormancy release can be determined from hourly temperature data.

The rate of subsequent bud growth is also a function of temperature. The heat requirement to trigger bud break and growth is generally expressed in growing degree hours (GDH). The GDH model of Anderson et al (1986) outlined below illustrates how the date of full bloom can be predicted:

$$(11) \quad \text{if } TB \leq TH \leq TU :$$

$$GDH = \frac{FA}{2} \left[1 + \cos\left(\pi + \pi\left(\frac{TH - TB}{TU - TB}\right)\right) \right]$$

$$(12) \quad \text{if } TU < TH < TC :$$

$$GDH = FA \left[1 + \cos\left(\frac{\pi}{2} + \frac{\pi}{2}\left(\frac{TH - TU}{TC - TU}\right)\right) \right]$$

otherwise $GDH = 0$

where GDH is the accumulation of growing degree hours, at temperatures equal to TH, TB is the base temperature below which little growth or development occurs, TU is the optimum temperature at which the maximum amount of growth and development occurs, TC is the critical temperature above which little or no growth occurs, $A = TU - TB$ and represents the amplitude of the GDH curve, and F is a stress factor, assumed to be 1 unless the tree is under stress. Stress may arise from water deficit, or if the tree is attacked by pests and diseases. While the GDH requirement for apples varies according to variety and orchard location, Shaltout and Unrath (1983) estimate the GDH requirement for 'Starkrimson Delicious' apples at base temperatures of 4.4°C and 6.1°C to be approximately 7000 and 6200 hours respectively.

Following fruitset, growth of the fruit is caused by two processes, cell division and cell enlargement. During the first four to five weeks after full bloom cell division dominates growth. For the remainder of the season cell expansion is the most important factor in apple fruit enlargement (Faust, 1989). While the fruit growth pattern has generally been described as sigmoidal (Faust, 1989), others have suggested a curvilinear growth phase followed by a linear growth phase (Blanpied, 1966) or an exponential growth

phase followed by a linear growth phase (Lakso et al. 1995).

Fruit ripening dates vary substantially between cultivars, ranging from 70 to 90 days after full bloom (DAFB) for early varieties to between 200 and 250 days for late varieties. Fruit yield varies according to the age of the tree and the number of fruits that remain on the tree until harvest. Fruit yield per tree increases nonlinearly as the fruit number per unit of leaf area increases, but average fruit weight decreases (Heim et al. 1979). Fruit load is calculated as:

$$(13) \quad F_L = \frac{N_F}{LA}$$

where N_F is the number of fruits that remain on the tree until harvest.

The number of fruits on the tree at harvest can be influenced by the orchardist through a process known as thinning. Under optimal conditions apple trees will set more fruit than can be supported to grow to a commercially desired size and quality and it usually becomes necessary to thin fruit or buds in order to improve the average size of each piece of fruit remaining on the tree. The results of thinning are explained biologically by the existence of intra plant competition. By removing excess fruit and increasing the leaf to fruit ratio, more nutrients become available to develop the remaining fruit to a larger size. The relationship between N_F and average fruit size for a given tree has not been incorporated into the model yet.

4. TREE MANAGEMENT

For the model to be useful as a management tool, variables which can be affected by horticultural management to improve orchard productivity need to be identified. Important management practices include thinning, pruning and training.

An apple tree is composed of a piece of a particular cultivar called a scion, that is grafted or budded onto a rootstock. A specific rootstock is normally chosen for the ultimate tree size it will produce. The large number of dwarfing rootstocks now available means that trees can be pruned and trained to achieve almost any size or degree of dwarfness.

Pruning and training are used to alter the growth and fruiting habits of the tree. Techniques that control the shape, size and direction of tree growth are known as training, and the removal of particular parts of the plant are known as pruning. The practice of pruning an apple tree occurs throughout its lifetime. As a young tree, pruning is undertaken with the aim of

training the tree to produce a certain shape and structurally sound framework that can hold heavy crops, allow easy access to the picker and pruner, allow thorough penetration and tree coverage to orchard sprays and, importantly, to produce a shape that allows light to enter all parts of the tree. Light interception thus depends on the tree form that results from pruning and training.

The two methods of tree pruning and training are either to allow the tree to grow to its natural form, or to restrict tree canopies to certain geometric forms, examples include training trees to thin restricted single planes of foliage such as narrow hedgerows, tree walls, and trees trained to the A, V and T forms.

The value of the light extinction coefficient, K , is used as a proxy for the shape of the tree. The value of K depends on leaf clumping and leaf arrangement which vary depending on the pruning and training that takes place (Jackson, 1978; Jackson, 1980). Trees in which the pruning techniques do not allow light to enter all parts of the tree would have higher values of K , while trees that have been pruned to allow good light penetration would have lower values of K .

Thinning, either by hand or by chemical means, may be captured in the simulation model through N_F (see equation 13).

5. EXPERIMENTAL DESIGN AND MODEL IMPLEMENTATION

Tree growth and fruit production over one year was simulated for a three year old Granny Smith apple tree on a dwarfing rootstock (EMLA.26) trained as a free standing central leader (CL). The initial conditions for each tree component, w_i , were: $w_L = 0$; $w_W = 200$ g DM; $w_F = 0$; and $w_R = 300$ g DM. The fruit load was arbitrarily set to 5, thus output will be in terms of weight rather than number of apples. A base run, setting L_{max} to 300 g DM, K to 0.6, and GA to 2, was simulated. These values were chosen from actual measured data for a similar tree (Barritt, 1989). L_{max} was then varied in accordance with Barritt's data on maximum leaf area for the same tree when pruned to vertical axis (VA) and slender spindle (SS) forms, the values of L_{max} were 270 and 330 g DM respectively. Fruit production from the simulation model for the three tree forms was compared to data from Barritt (1989). Fruit production was also simulated for different pruning and training practices by varying K . A thinning experiment was not undertaken due to the lack of a satisfactory equation relating fruit number with average fruit weight for a given tree.

Fruit weight in g dry matter was converted to kilograms of fresh weight per tree by assuming the

portion of dry matter in fresh weight is around 15 percent (Schechter et al. 1993).

Environmental parameters appropriate to Southern Hemisphere locations were used in the model. Rather than using the temperature triggers described in section 3, day number was used as the trigger for dormancy release in the spring and for leaf senescence in late May. The trigger for growth following dormancy release was 15 September, an appropriate date for orchards in eastern Australia.

The model was implemented using the Simulink® add-on for the Matlab® dynamic simulation software package and numerically integrated using the Runge Kutta method (Matlab, 1992).

6. MODEL OUTPUT AND DISCUSSION

Results for leaf area index and fruit production from the base simulation are plotted against date in Figure 1. Leaf area index increases rapidly to a maximum value from mid-September, with all leaves falling from the tree during June. Fruit growth is triggered once maximum leaf area has been achieved, and fruit mass increases steadily over the season after an initial rapid increase in weight. The harvest date of Granny Smith apples is approximately 180 days after full bloom, which occurs during late April, around a month before the leaves begin to fall.

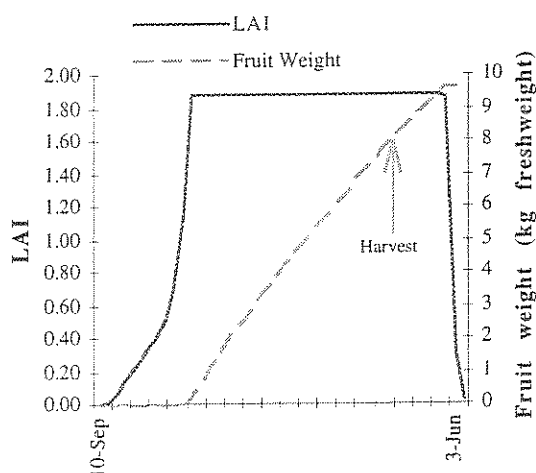


Figure 1: Simulation results for leaf area index (LAI) and fruit weight over time for a three year old Granny Smith apple tree

Leaf area index and fruit production for the three training methods from the simulation model and Barritt (1989) are compared in Table 2. While the model overestimated fruit production for each training system by between 1.3 and 2 kg, model output for each training system is comparable with the measured data. The overestimation is the likely result of ignoring respiration of the fruit in the simulation model.

Table 2: Leaf area index and fruit production for a three year old Granny Smith apple tree, using three training techniques.

Tree form	Tree leaf area index		Fruit output ^a (kg fresh weight)	
	Barritt	Model	Barritt	Model
CL/26	1.9	1.9	7.8	9.1
VA/26	1.4	1.7	5.6	7.6
SS/26	1.6	1.8	7.4	8.8

^a Apples harvested at 180 DAFB

A second series of simulations was undertaken, using changes in the value of K as a proxy for pruning and training techniques. Fruit production for varying values of K and LAI are given in Table 3. When less light penetrated the tree (higher values of K), fruit production was below that of trees where light penetration was higher. While values of K have not been directly related to specific pruning and training methods, they give an idea of the differences in fruit output that can occur over a range of realistic K values.

Table 3: Values of fruit production (kg fresh weight)^a under increasing values of K at different values of LAI

K	LAI		
	2	3	4
0.44	11.7	16.0	19.2
0.6	9.5	12.7	14.3
0.76	8.2	10.2	13.4

^a Apples harvested at 180 DAFB

7. CONCLUSIONS

The biological model developed in this paper represents a preliminary attempt to model apple tree growth over a year. The simulation model produced realistic fruit production data for a young apple tree in a high density orchard system over a period of one year. The inclusion of fruit respiration in the model is likely to reduce the slight overestimate of fruit production for a given maximum leaf area. Extending the model to allow for thinning to take place is also necessary.

The model was used to simulate fruit production as values of K changed. Results showed that good light penetration has a positive impact on the amount of fruit a tree can produce. Relating different values of K to different pruning and training methods available

would contribute significantly to the usefulness of the model as a management tool.

Other necessary extensions of the model are the inclusion of the non-linear relationship between fruit number and weight, and the inclusion of the relationship between growth of the tree frame and leaf area over an extended period of time. Modelling tree growth over time would enable the simulation of the long term impacts of pruning strategies and specific fruit loads on tree development.

Allowing dormancy release and leaf fall to be triggered by temperature rather than by date will enable the model to simulate fruit production for any location and tree variety.

In the future, the biological model will be incorporated into an optimising model of apple orchard management. As such, the model will allow comparison of income levels associated with different horticultural management strategies.

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