Carbon Supply From Starch Reserves to Spring Growth: Modelling Spatial Patterns in Kiwifruit Canes

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The remobilization and transport of reserve carbon from a kiwifruit (Actinidia delicosa) cane to developing axillary shoots was modelled using a simple pool structure and mass flow process. Manipulative experiments with mature kiwifruit plants are compared with simulation results. The model uses detailed architectural information rather than explicit partitioning functions, achieving carbon partitioning as emergent behaviour of a spatial organization. The model successfully simulated shoot growth and starch distribution patterns. © 1999 Annals of Botany Company

Key words: Carbon reserves, starch reserves, plant architecture, Actinidia delicosa, kiwifruit.

INTRODUCTION

Plant canopy architecture has been postulated to generate complex spatial patterns of carbon distribution and thus affect organ development (Watson and Casper, 1984). These patterns may arise through both interactions with the external environment and through internal plant factors. Principal among the ‘internal environment’ factors are the spatial relationships of sources and sinks, their vascular connections, and transport processes. Carbon reserves (which may be both a source and a sink) are significant for their role in supporting early season growth and for buffering the surpluses and shortages of carbon resulting from cyclical processes and the vicissitudes of environment (Wardlaw, 1990; Schnyder, 1993). They are subject to a spatial distribution within the plant, and at any point in time the principal sites of reserve remobilization or storage may be remote from sites of carbon utilization or acquisition (Chapin, Schultze and Mooney, 1990).

Perennial vines such as kiwifruit (Actinidia delicosa (A. Chev.) C. F. Liang et A. R. Ferguson) are particularly reliant on reserves (primarily starch) to support rapid seasonal growth phases (Mooney and Gartner, 1991). Starch reserves are found throughout the canopy and root system of kiwifruit (Smith, Clark and Boldingh, 1992). The focus of the current paper is carbon reserves in the canes retained over winter. In spring, shoots bearing flowers grow from a proportion of the axillary buds on these canes, the majority of shoots beginning growth in synchrony. Anthesis occurs distributed reserve to competing sites of active growth. The model successfully simulated shoot growth and starch distribution patterns with more or less cane resulted in proportionately faster or slower growth. This suggests variation in the distribution of reserves within the canopy may be a factor contributing to heterogeneity of early shoot growth (in turn linked to variation in fruit set and early fruit development). While starch concentrations are relatively uniform at any point in time within the perennial canopy (Smith et al., 1992), the physical dimensions of canes and the location of axillary buds vary considerably.

A simulation model could be a useful tool in assessing the potential significance of reserve distribution to shoot growth patterns at the canopy level. This would require combining detailed architectural information with an effective representation of remobilization and transport processes. Direct measurements could provide the architectural information necessary to model an initial spatial distribution of starch reserves, but describing the processes of storage, remobilization and transport is more problematic.

The fundamental issue of carbon partitioning between plant components has inspired many modelling approaches, often beginning on or deriving from work of Thornley (1972) describing the distribution of resources between organs based on a transport or pathway resistance concept. While this method has been employed to explore architectural influences on resource partitioning (Thornley, Gifford and Bremner, 1981), storage and remobilization associated with the transport pathway itself have had little attention.

In this paper we formulate and test a model that simulates the mobilization and transport of carbon from a spatially distributed reserve to competing sites of active growth. The model achieves realistic patterns of carbon partitioning within a cane, primarily on the basis of architectural and phenological parameters (the spatial arrangement of buds, the physical dimensions of shoots, the timing of budbreak) while operating in a manner consistent with observed and putative processes governing carbon storage, remobilization and transport.
MODEL DEVELOPMENT

System description

Carbohydrate within a stem can be thought of as being within a labile pool, a reserve pool which buffers concentration changes in the labile pool, and a structural pool (Minchin, Kyan and Thorpe, 1984; Hayes, Patrick and Utter, 1985; Thorpe and Minchin, 1996). In the work of Minchin et al. (1984) focusing on short time scales, the reserve pool was identified as being the stem apoplasm. In the current work, with time scales of days and weeks, the reserve pool will consist of both the stem apoplasm plus longer-term starch reserves within stem parenchyma tissue. A similar pool structure has been shown to describe carbon flow through leaves (Geiger et al., 1983; Kocher and Rivoit, 1987; Minchin et al., 1996). Both the labile and reserve pools must be limited in size, and it seems reasonable that this limit is related to the size of the structural pool in which they are embedded. Hence we expect that as either of these pools approach their maximum size, flow into them must reduce, i.e. they approach a state of saturation where they are unable to accommodate more carbon.

The reserve, labile and structural pools form a continuum within the cane. We modelled this system by considering the pools as spatially subdivided into a large number (within the cane. We modelled this system by considering the pools as spatially subdivided into a large number of discrete labile-reserve-structure elements, with carbon transport taking place through the labile components (Fig. 1). The value of N was constant for any particular simulation, with values of 100 or greater found to accurately represent the continuum.

This model does not include any independent functioning of xylem transported carbohydrate. The experiments of Piller et al. (1998) indicated a dominant influence of the phloem system and reserves in the immediate vicinity of the growing shoot. Current knowledge of xylem sap composition (Ferguson, 1980; Ferguson, Eisemann and Leonard, 1985) and xylem flow rates in spring (Buwalda and Smith, 1990) also support the idea that carbohydrate in xylem sap is unlikely to be other than a minor carbon source for growing shoots.

Equations and implementation

The model considers a kiwifruit cane as an independent system containing a supply of reserve carbon which becomes mobilized and available for utilization in the growth of shoots. The total mass of carbon $c_i(t)$ (symbols and units are listed in Table 1) within cane element $i$ at time $t$ is the sum of that within the reserve pool $r_i(t)$, the labile pool $l_i(t)$ and the structural pool $s_i(t)$, that is

$$c_i(t) = r_i(t) + l_i(t) + s_i(t)$$  \quad (1)

The maximum size of the reserve pool $r_i^*(t)$ and of the labile pool $l_i^*(t)$ are assumed to be simple multiples of the structural pool size $s_i(t)$, i.e.

$$r_i^*(t) = \beta_r s_i(t)$$  \quad (2)

$$l_i^*(t) = \beta_l s_i(t)$$  \quad (3)

with $\beta_r$ and $\beta_l$ being dimensionless parameters controlling the maximum size of reserve and labile carbon pools within an element.

Walton and Fowke (1995) reported carbon concentrations (on a dry weight basis) for current season’s shoots between 453 and 479 mg g$^{-1}$. In the work here we used a value of 500 mg g$^{-1}$. Total carbon within each element prior to budbreak $[c_i(0)]$ was calculated from this value using cane dimensions and dry weight (see experimental section below), and $N$. Canes were treated as either cylindrical or tapered, with their length, basal diameter and apical diameter supplied as inputs for each simulation. In the case of cylindrical canes both diameters were taken as 1.5 cm, whereas in tapered canes the basal diameter was 1.5 cm reducing linearly to an apical diameter of 0.70 cm. Cane length was 200 cm (except in the experiment with cane sections described below).

Starch reserves in canes are at their maximum level just before budbreak (Smith et al., 1992), and the labile pool was assumed also to be at its maximum level at this time. The value of $\beta_r$ was set so that the initial value of $r_i$ (if converted to a carbon concentration within element $i$) corresponded to the budbreak starch concentration (60 mg g$^{-1}$) reported for kiwifruit canes by Smith et al. (1992). The value of $\beta_l$ was more difficult to define, so in the absence of data was set to equal $\beta_r$.

During the first 3 weeks of shoot growth, the influx of carbon to growing shoots from net photosynthesis is considerably smaller than the amount acquired from reserves (Piller and Meekings, 1991). Hence photosynthesis and respiration were omitted at this stage. The processes of carbon transport, storage and growth are treated as continuous functions of time, and these carbon fluxes can be expressed as a set of differential equations:

$$\frac{dr_i}{dt} = K_i$$  \quad (4)

$$\frac{dl_i}{dt} = H_{i+1,i} - H_{i+1,i+1} - K_i - G_i$$  \quad (5)

$$\frac{ds_i}{dt} = G_i$$  \quad (6)

where $K_i$ is the net rate of transfer of carbon between labile and reserve pools, $H_{i+1,i}$ and $H_{i+1,i+1}$ are the net rates of transport of labile carbon from $i$ to $i+1$ and $i-1$ elements respectively, and $G_i$ is the rate of transfer of labile carbon to...
structural carbon (growth). \( H_{i-1} \) and \( H_{i+1} \) can only operate via the labile pool, and while \( G \) is unidirectional, \( H_{i-1} \), \( H_{i+1} \) and \( K_i \) can be bi-directional. This model therefore assumes the transport of mobilized reserves through the cane can occur in both basipetal and acropetal directions with equal facility (Lai, Woolley and Lawes, 1989).

The net transfer of carbon between the labile and reserve pools is modelled using modified first-order kinetics, i.e.

\[
K_i = k_{lr} l_i - k_{rl} r_i
\]

and was modified to

\[
K_i = k_{lr} \left( 1 - \frac{r_i}{r^*} \right) l_i - k_{rl} \left( 1 - \frac{l_i}{l^*} \right) r_i
\]

so that for \( r_i \ll r_i^* \) and \( l_i \ll l_i^* \) the flow follows first-order kinetics, while for \( r_i \sim r_i^* \) and \( l_i \sim l_i^* \) the flow into the respective pools saturates.

Growth occurs by movement of carbon from the labile pool to the structural pool in turn driving a concomitant flow from the reserve pool into the labile pool. Consequently the reserve pool maintains or buffers the labile pool. The greater the ratio \( k_{lr}/k_{rl} \) the stronger the buffering, i.e. the greater the ability of the reserve pool to control changes in the labile pool. To ensure substantial buffering of the labile pool \( k_{rl} \) and \( k_{lr} \) were initially set at 1.0 and 0.01 \((d^{-1})\), respectively. The rapidity with which buffering takes place is governed by the actual values of \( k_{rl} \) and \( k_{lr} \).

Having defined the saturated level of the labile carbon pool using eqn (3), growth \((G_i)\) as limited by carbon supply, can be described by

\[
G_i = g_s \left( \frac{l_i}{l^*} \right)
\]

where the parameter \( g \) is the potential relative growth rate of the element and corresponds to the intrinsic ‘vigour’ of a meristem. Consequently when the labile pool is empty growth is zero, and when the labile pool is full, growth occurs at the potential rate. The initial value of \( g \) was set at 0.1 \((d^{-1})\) from the data of Piller and Meekings (1997), but its influence on model behaviour was tested in simulations. Further, eqn (11) can be rewritten using eqn (3) as

\[
G_i = a l_i
\]

where \( a = g / \beta_i \), from which it can be seen that \( G_i \) follows first-order kinetics.

A finite-difference code (Crank-Nicholson numeric scheme) implementing this model was written in the C programming language. This code was integrated with a graphic interface in which a stylized cane and shoots are redrawn after each numerical iteration. Note that although the cane is drawn as a curve (purely for visual similarity with real canes), the transport process described [eqn (8)] is strictly correct only for a straight rod and all calculations in the model are on this basis. Relative carbon concentration in the reserve pool \((r/r^*)\) along the cane is mapped to colour so that as reserves are depleted, the colour of the cane changes (from brown to white). This provides a dynamic visualization of changes in reserve levels throughout the

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Definition</th>
<th>Unit</th>
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<tbody>
<tr>
<td>( c_i(t) )</td>
<td>Total mass of carbon within element ( i ) at time ( t )</td>
<td>mg</td>
</tr>
<tr>
<td>( r_i(t), l_i(t), s_i(t) )</td>
<td>Mass of C within the reserve, labile and structural pools of element ( i ) at time ( t )</td>
<td>mg</td>
</tr>
<tr>
<td>( \beta_i, \beta_i )</td>
<td>Maximum size of reserve and labile pools as fractions of the structural pool size</td>
<td></td>
</tr>
<tr>
<td>( K_i )</td>
<td>Net rate of transfer between reserve and labile pools</td>
<td>mg d(^{-1})</td>
</tr>
<tr>
<td>( H_{i-1} )</td>
<td>Net rate of transport of labile carbon from element ( i ) to ( i+1 )</td>
<td>mg d(^{-1})</td>
</tr>
<tr>
<td>( G_i )</td>
<td>Rate of transfer of labile carbon to structural carbon</td>
<td>mg d(^{-1})</td>
</tr>
<tr>
<td>( h )</td>
<td>Transport coefficient</td>
<td>mg cm(^{-1}) d(^{-1})</td>
</tr>
<tr>
<td>( A_{i-1} )</td>
<td>Area of the interface between elements ( i ) and ( i+1 )</td>
<td>cm(^2)</td>
</tr>
<tr>
<td>( \Delta x_{i-1} )</td>
<td>Distance between the centres of adjacent elements</td>
<td>cm</td>
</tr>
<tr>
<td>( k_{lr}, k_{rl} )</td>
<td>Labile to reserve, reserve to labile transfer coefficients</td>
<td></td>
</tr>
<tr>
<td>( g )</td>
<td>Growth rate coefficient</td>
<td>d(^{-1})</td>
</tr>
</tbody>
</table>
cane (Fig. 2). Shoots growing from the cane are drawn as extending arcs with their length being directly proportional to accumulated structural carbon. All model parameters and initial conditions are set from a graphic screen and a simulation can be interrupted, parameters changed, and then restarted at any time.

EXPERIMENTAL MATERIALS AND METHODS

The model described above was designed to stimulate axillary shoot growth and reserve partitioning within a single isolated cane, demanding experimental data describing shoot growth patterns and starch remobilization under comparable conditions. The following experiments used mature kiwifruit vines grown on research orchards in the Waikato and Bay of Plenty districts of New Zealand. These vines received standard commercial management, except that they were not treated with the budbreak enhancing material hydrogen cyanamide (Henzell and Briscoe, 1986). Measurements of shoot extension growth were employed throughout as an index of carbon accumulation (Piller and Meekings, 1997).

Shoot growth patterns

This study was designed to test the validity of modelling an isolated cane. Forty matched pairs of canes were selected prior to budbreak (on ‘T-bar’ trained vines; Sale and Lyford, 1990). The phloem tissue of one cane from each pair was severed at the base of the cane by girdling (removing a 5 mm wide strip of bark with minimum damage to the underlying tissue). At weekly intervals until anthesis the length of all axillary shoots on the canes was recorded. Shoot length data for the treated and control canes were compared using a residual maximum likelihood analysis of log transformed data.

Canes trained on a ‘T-bar’ system are normally tied down at an angle below horizontal, and relatively little is known about the influence of cane angle on shoot growth in kiwifruit. We therefore trained a further set of canes horizontally and recorded the length of all shoots at anthesis (by which time the growth of most shoots had terminated).

Starch remobilization

Spatial patterns of starch remobilization in isolated canes were similarly measured in a set of cane pairs matched in diameter and length. These were selected just prior to budbreak (one pair per vine, 28 pairs in total) and one cane of each pair was girdled at the base. At this time, and subsequently at 3, 7 and 10 weeks from budbreak, seven cane pairs were removed at random from the vines and divided into four sections of equal length. Their dimensions were recorded and the starch content of individual sections determined using the method of Smith et al. (1992).
**Inter-shoot competition**

In an experiment using isolated pairs of shoots we attempted to determine if overt competition exists between adjacent shoots during the period of reserve dependence. One week after budbreak when the majority of shoots were approx. 5 cm long, 20 closely matched pairs of adjacent shoots were tagged, each shoot pair on a separate cane, and the pairs divided into two treatment groups. In one treatment the parent cane was girdled 30 cm above and 30 cm below the pair of shoots (Fig. 3), so that the shoots were centrally located in a section of cane and within each pair could be expected to experience similar reserve availability. In the second treatment the parent canes were girdled 54 cm above and 6 cm below each shoot pair, so that the shoots were offset in an otherwise similar section of cane. In this case it could be expected that within each pair the shoots would experience different reserve availability, with the apical member of each pair being at a disadvantage.

Both these treatments were intended to limit each shoot pair to accessing the reserves in a total of 60 cm of cane, an amount shown to be adequate to support normal growth (Piller *et al.*, 1998). Shoot extension growth was measured at weekly intervals after treatment application as an index of carbon gain. This experiment was initially carried out 7 d after budbreak and repeated 50 d post budbreak.

**MODEL EVALUATION AND EXPERIMENTAL RESULTS**

The model described uses simple representations of the physiological processes believed to govern the supply of carbon from perennial reserves to early spring growth. These local mathematical rules are coupled with architectural information to create a carbon allocation model at a higher spatial scale. We now show that the spatial complexity of this model is sufficient to produce complex dynamics and subtle interactions similar to some of those observable during development of axillary shoots on a kiwifruit cane.

As described earlier, the transport coefficient ($h$) and the parameters controlling buffering of the labile pool by reserves, $k_{rl}$ and $k_{lr}$, could not be directly estimated from experimental data. Our initial step in model evaluation therefore tested the model’s sensitivity to these values. For these simulations an architectural layout was used that is typical of canes on managed vines with high budbreak levels (McPherson *et al.*, 1988). Ten axillary buds were located on a tapered cane, their spacings decreasing from 14 to 6 cm apart between base and apex. The apical bud was assigned an earlier ‘budbreak’ time than other buds (by > d) and a higher ‘vigour’ ($g = 0.12$ d$^{-1}$ vs. 0.10 for other buds). Simulations were run for 100 iterations with a time step of 0.01 d. With an $h$ of 1.0 (mg cm$^{-1}$ d$^{-1}$), and $k_{rl}$ and $k_{lr}$ of 1.0 and 0.01 d$^{-1}$, respectively, this simulation resulted in final shoot size progressively reducing in the acropetal direction along the cane but with an apical shoot of similar size to the most basal shoot (Fig. 4). At the completion of the simulation almost all cane reserves were partitioned into shoot growth.

Varying the transport coefficient ($h$) value between 1000 and 10 mg cm$^{-1}$ d$^{-1}$ substantially alters the growth of the apical shoot with its higher $g$ and earlier budbreak (Fig. 4). At the ‘fast’ $h$ value (100 mg cm$^{-1}$ d$^{-1}$), transport through the labile pool is enhanced and the apical shoot grows substantially larger, while the gradient in final length of the other shoots is lessened—in effect the cane has become a globally accessible carbon pool. With a ‘slow’ $h$ value (1.0 mg cm$^{-1}$ d$^{-1}$) the vigorous apical shoot rapidly exhausts the carbon reserves in its vicinity and its growth (and that of its immediate neighbour) effectively halts.

The values of $k_{rl}$ and $k_{lr}$ were varied between 1.0 and 10.0 d$^{-1}$ ($k_{rl}$), 0.01 and 0.001 d$^{-1}$ ($k_{lr}$). At the lower ratio of $k_{rl}/k_{lr}$ as growth occurs there is a slight drawdown of reserves in the vicinity of the shoots (Fig. 5). At the higher ratio, where greater buffering of the labile pool occurs, pronounced zones of reserve depletion centred on shoots are apparent. The dynamics of growth and the final pattern of carbon allocation however are little different (data not shown).

The influence of the architectural parameters on simulation results is shown in two simulations approximating the experiment with centrally located and offset pairs of shoots. Two identical shoots were placed 15 cm apart on a 60 cm cane section. The shoot pair was first centred in the cane, then offset to the apical end, while all other parameters were set to the default values described earlier. Growth rates of the centrally located pair diverged slightly as reserves were...
depleted, reflecting the gradient in cane diameter and consequent reserve distribution (Fig. 6). When the shoots were offset to the end of the cane section, this effect was increased.

The results of the field experiments where shoot growth and cane starch levels were recorded on girdled and ungirdled canes may be compared with the above series of simulations. There were no statistically significant differences in shoot extension growth between girdled and ungirdled canes at any of the weekly measurement times (data not shown). Measurement of shoot lengths at anthesis on horizontally trained canes showed an acropetal gradient in shoot length (but with a large apical shoot, Fig. 7) that is qualitatively very similar to that generated by the initial simulation.

Cane girdling however had a significant impact on starch levels. In girdled canes the starch levels of all cane sections dropped almost in unison (effectively to zero by 7 weeks from budbreak, Fig. 8) and without the development of any significant spatial gradients. In contrast, in control canes by 7 weeks there was a significant gradient in starch concentration, and less starch depletion overall. Starch levels were higher in the basal sections of the cane, reducing towards the apex (Fig. 9). The slope of a linear trend fitted to this gradient was significantly \( P < 0.05 \) greater than zero at \(-5.8 \text{ mg g}^{-1} \text{ per section} (\text{s.e.} = 1.7)\). Between 7 and 10 weeks starch levels in the girdled canes rose again, while the control canes showed no significant change.

The first field experiment with shoot pairs on a cane section was conducted immediately after budbreak. In this experiment shoot growth rate was significantly affected by the treatments. In both central and offset shoot pairs,
Apical location storage and mobilization is a dynamic equilibrium driven by \( \text{from the adjacent canopy, and that the process of starch} \). This suggests that carbon is flowing into the intact cane isolated cane shows uniform depletion (virtually to zero). Over 50 d of spring growth, starch levels in a cane develop \( \text{instarment in canes that are altered by severing the phloem.} \) show spatial gradients of starch exhaustion and replenishment in canes that are altered by severing the phloem. This results in competitive partitioning between growing shoots and the progressive development of zones of reserve depletion. In essence, this scheme formalizes much ‘verbal behaviour shown by this model and that \( \text{therefore seems reasonable to look for similarities in the}\) modelling’ in which carbon sinks are described as competing for supply, an advantage in proximity to the source translating into a competitive advantage in terms of growth and photosynthetic capability (Piller \( \text{et al.}, 1998). It}\) produces very similar results using realistic values for the parameters that can be measured and (arguably) reasonable values for the others. The conclusion from this must be that it is possible to explain some of the qualitative behaviour shown by kiwifruit canes and axillary shoots in spring on the basis of the interaction between architectural and phenological characteristics, and perennial reserves. We hypothesized that two shoots of similar size located in the centre of an isolated section of cane would have nearly equal access to reserves and would show correspondingly uniform growth, whereas offsetting comparable shoots to one end would result in uneven reserve accessibility and reduced growth of the most apical shoot. A simulation with this configuration results in the expected behaviour; there is a difference in growth between the centrally located shoots due to the effect of cane taper on initial reserve distribution, but a larger effect on the offset shoots due to inter-shoot competition. The results of the field experiments with shoot pairs were equivocal. In the experiment conducted during the period of maximum reserve dependence there was a significant difference in growth within pairs in both treatments while the predicted effect of pair location was not significant. There was a suggestion that the shoot growth differential (at 13 d from treatment) was increased by offsetting the shoots, but a more accurate experiment would be required to confirm this. The experiment conducted during the net source phase showed no treatment effects. This latter result is trivial in terms of predicted behaviour, but confirms that there is no interaction between the growth.

**Table 2. Difference in length between members of centrally and apically located shoot pairs following girdling treatments applied at 7 and 50 d from budbreak**

<table>
<thead>
<tr>
<th>Days from treatment</th>
<th>Central location</th>
<th>Apical location</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Length difference (cm)</td>
<td>LSD</td>
</tr>
<tr>
<td>Girdling 7 d from budbreak</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.1</td>
<td>1.7</td>
</tr>
<tr>
<td>6</td>
<td>6.1*</td>
<td>4.6</td>
</tr>
<tr>
<td>10</td>
<td>15.6*</td>
<td>11.7</td>
</tr>
<tr>
<td>13</td>
<td>21.0*</td>
<td>20.1</td>
</tr>
<tr>
<td>20</td>
<td>33.2</td>
<td>34.2</td>
</tr>
<tr>
<td>Girdling 50 d from budbreak</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>0.8</td>
<td>21.0</td>
</tr>
<tr>
<td>14</td>
<td>0.6</td>
<td>28.0</td>
</tr>
<tr>
<td>19</td>
<td>2.8</td>
<td>5.5</td>
</tr>
<tr>
<td>22</td>
<td>3.9</td>
<td>11.1</td>
</tr>
<tr>
<td>27</td>
<td>5.4</td>
<td>18.5</td>
</tr>
</tbody>
</table>

* \( P < 0.05. \)
of individual shoots and proximity to the injury inflicted by girdling.

The model achieves these results from a technique that has been employed with success in other efforts to model the structural and physiological complexity of plants. Simple local rules are applied repeatedly in both time and space, and their reiteration leads to complicated dynamics and structures that are emergent properties of the models. Recently this approach has been employed in models of whole-plant resource allocation (Cheeseman, 1993), plant architecture (Room and Prusinkiewicz, 1996), and complex stomatal behaviour (Haefner, Buckley and Mott, 1997). In the case of the model described here, this technique provides numeric and computational tractability, ready spatial expandability (perhaps to a whole canopy level) and ease of integration with sophisticated architecture modelling techniques (Mech and Prusinkiewicz, 1996).

Development of the model to encompass longer time scales in canopy growth would require the inclusion of photosynthesis and respiration. Given the simple mechanism used here to drive growth, the inclusion of an external carbon supply (proportional to structural pool size) within the closed system would result in continuing exponential growth. This would certainly not be realistic behaviour—in fact, the growth of the first cohort of kiwifruit shoots generally terminates about the time of anthesis. The growth rates of axillary shoots can be accounted for on the basis of local carbon availability alone for the first few weeks; beyond that other processes are involved that are outside the scope of the current model.

The salient result, the ability to mimic patterns of early shoot growth and reserve depletion, is achieved from a system requiring only the obvious and readily measurable architectural parameters, a parameter corresponding to bud potential growth rate or vigour, a transport coefficient, and two parameters describing the remobilization and storage processes. In the general context of biological modelling, this is simplicity itself, and furthermore the architectural parameters and the transport coefficient have a dominant impact on the patterns of growth.

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LITERATURE CITED


