Development and growth of plant

Roux model

Example of the coffee tree

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Glossary

Vegetative axis: succession of phytomers produced by meristems.

Development axis: defined by the succession of development default (no organ produced) and development successes. During development cessation, growth continues.

Physiological age: Relates to the degree of differentiation of the structures produced by the meristem. It can be defined by a combination of morphological, anatomical and functional attributes of resulting entities.

By convention the physiological age of the trunk is 1 and the physiological age of branches is 2.

Development cycle: Unit in number of phytomers of step allowing the production of phytomers of the same generation

Phytomer: Botanical entity formed by a node, associated with its leaf (or leaves) and axillary bud(s) plus the subtending internode.

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Roux architectural model (descriptions and definitions from P. de Reffye thesis [1])

Definition of the Roux Model

The trunk is a monopodial orthotropic axis which shows continuous growth, the plagiotropic branches are inserted continuously. Flowering is lateral on the branches. (Hallé et al. 1978 Fig. 1).

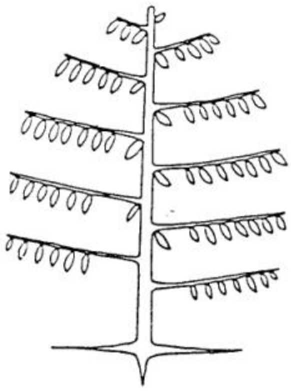


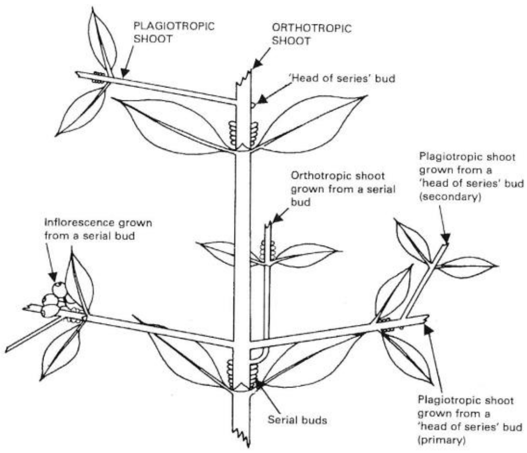
Figure 1. Roux model

Example of Roux model: the coffee tree

Coffee tree architecture is classified as a Roux model. The trunk is an orthotropic monopodia (Fig. 2). Each node bears two opposed plagiotropic branches with immediate development. The flowering is lateral on the branches and appears fleetingly after sufficient rainfall happening after the dry season. On each node of axes, supernumerary buds can develop into an axis with delayed development named secondary axis.

For robusta tree generally less than 10% of the phytomer are from secondary axes and the phenomenon is often negligible.

Figure 2. Shoot morphology of Arabica Coffee (Clifford, 1985)[2]



[1] **Verchere de Reffye P.** (1979). Modélisation de l'architecture des arbres par des processus stochastiques. Simulation spatiale des modèles tropicaux sous l'effet de la pesanteur. Application au *Coffea Robusta*. Thèse soutenue le 17 septembre 1979, Université Paris Sud Centre d'Orsay, n° d'ordre 2193.

[2] **Clifford MN, Willson KC, Cannell MGR** (1985). Physiology of the Coffee Crop. In. Coffee. Springer US, 108-34.

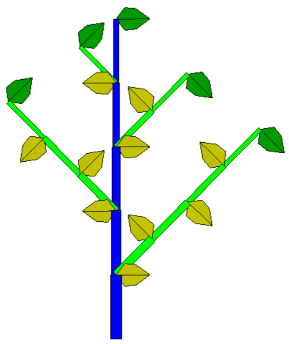
The deterministic part of GreenLab model

The case of free growth

Plant growth depends on leaves surface that intercepts light. At the beginning of growth all leaves surface intercepts light (leaves do not overlap). Interception surface is then equal to the total surface set up and production is proportional to leave surface; the growth is named free. According to leaves growth, they overlap and only a part of leaves surface intercepts light. The growth is then dependent of the square meter surface covered by the plant. A surplus of leave is then useless for production.

In the case of deterministic model (opposed to stochastic model, non-described in this tutorial) all organs are set up at each time step. A time step corresponds to a (growth) development cycle. Here, we consider the case where leaves and fruits function only during one cycle and then die.

1. Phytomer set up



At each cycle, each apical bud forms a new phytomer. In the present example one bud forms an internode and a leaf.

Figure 3. Simulating *Roux 's model*

Phytomers of physiological age 1 are colored in blue, while phytomers of physiological age 2 are colored in green.

Leaves functioning at cycle n are colored in dark green while those set up before the cycle n are colored in light green.

2. Mixte buds: reiterations set up

Total reiteration may occur on trunk phytomers

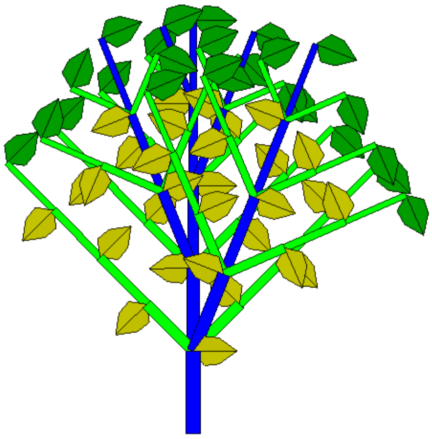


Figure 4. *Simulation with reiterations*

3. Biomass

Leaves grow at each time step. At cycle *n* the quantity of biomass given to organs (supply) is the biomass available at cycle *n-1*. At each cycle, the supply increases because the number of organs increases. However if the supply at cycle *n-1* is constant, the size of each organ produced over time will decrease.

The relationship between the produced biomass *Q(n)* at cycle *n* and the supply *Q(n-1)* at cycle *n-1* is:

$$\boxed{Q(n) = \frac{E(n)}{r\,e} N_a(n)\, p_a \frac{Q(n-1)}{D(n)}} \qquad (1)$$

<u>Demonstration</u>

$$Q(n) = \frac{E(n)}{r} S(n) \qquad (2)$$

$Q(n)$ = supply at n cycle = biomass that can be produced at n cycle

$E(n)$ = environment efficiency at n cycle (e.g. light or water availability)

r = leaves resistance to environment or conversion coefficient of environment efficiency in carbon RUE or WUE or ETP) = coefficient of supply calibration which is given by experiments

$S(n)$ = total efficient foliar surface produced at n cycle

but $$S(n) = N_a(n) \cdot s(n) \qquad (3)$$

$N_a(n)$ = total number of leaves produced at n cycle (a indicates assimilating organ)

$s(n)$ = elementary surface of a leaf produced at n cycle

$$s(n) = \frac{q_a(n)}{e} \qquad (4)$$

$q_a(n)$ = volume of a leaf produced at n cycle = demand of leave at n cycle

e = thickness of a leaf

$$q_a(n) = p_a \frac{Q(n-1)}{D(n)} \qquad (5)$$

p_a = sink strengh of a leaf = demand of a leaf

$Q(n-1)$ = total supply of biomass at $n-1$ cycle

$D(n)$ = total demand of organs at n cycle

Taking equation (2) we have

$$Q(n) = \frac{E(n)}{r} S(n) = \frac{E(n)}{r} N_a(n) \frac{p_a \frac{Q(n-1)}{D(n)}}{e}$$

Then during free growth we have the following equation:

$$Q(n) = \frac{E(n)}{r\,e} N_a(n)\,p_a \frac{Q(n-1)}{D(n)}$$

Let $$A = r\,e \frac{D(n)}{N_a(n)\,p_a} \qquad (6)$$

In the simple case where the plant is made of leaves and internodes, the demand at cycle n is:

$$D(n) = N_a(n)\,p_a + N_e(n)\,p_e \qquad (7)$$

$N_e(n)$ = total number of internodes produced at cycle n

p_e = sink strength of the internode = demand of the internode

If each internode produces one leaf at each time step we have: $N_a(n) = N_e(n)$, then

$D(n) = N_a(n)\,(p_a + p_e)$

$$A = r\,e \frac{N_a(n)\,(p_a + p_e)}{N_a(n)\,p_a} = r\,e \frac{p_a + p_e}{p_a}$$

This relationship links leaves allometry (thickness e), the environment efficiency (r) and the ratio of sink strengths. By recurrence we obtain

$$\boxed{Q(n) = \frac{E(n)}{A} Q(n-1) = \left(\frac{E(n)}{A}\right)^n Q_0 \qquad \text{(1bis)}}$$

if $N_a(n) = N_e(n)$

We can note that the number of phytomers does not influence $Q(n)$ so that $Q(n)$ does not depend on the architectural model.

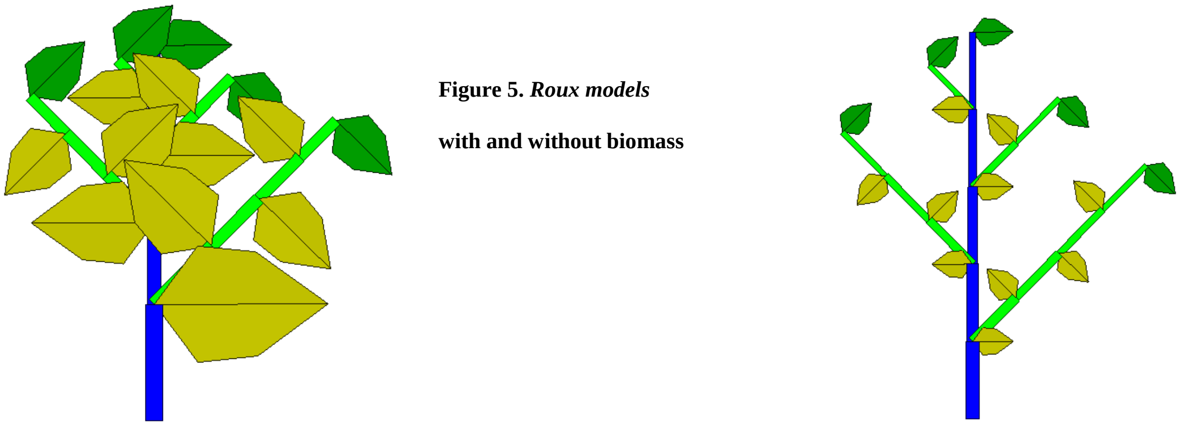


Figure 5. *Roux models*

with and without biomass

In the next sections we consider a constant environment $E(n) = E$.

4. Branching with Biomass and fruits

We aim to define the values of sink strengths for each organ when the plant is at equilibrium, that is to say when the biomass production is constant at each time step (i.e $\frac{E}{A} = 1$)?

The total demand at cycle n is : $D(n) = N_a(n) p_a + N_e(n) p_e + N_f(n) p_f$

$N_a(n)$ = number of leaves at n cycle and p_a = sink strength of a leave
$N_e(n)$ = number of inter-nods at n cycle and p_e = sink strength of an inter-nod
$N_f(n)$ = number of fruits at n cycle and p_f = sink strength of a fruit
with

$$N_a(n) = n_a \; N_{\varphi a}(n)$$
$$N_e(n) = n_e \; N_{\varphi e}(n)$$
$$N_f(n) = n_f \; N_{\varphi f}(n)$$

and

n_a = number of leaves for one phytomer (can vary from 1 to 3 in a tree) = 2 for coffee tree
n_e = number of internodes for one phytomer = 1
n_f = number of fruits for one phytomer (can vary from 0 to many)
$N_{\varphi a,e,f}(n)$ = total number of active phytomers bearing leaves (a), internodes (e) or fruits (f) at n cycle

If $N_{\varphi e}(n) = N_{\varphi a}(n) = N_{\varphi f}(n) = N_\varphi(n)$ we have

$$D(n) = N_\varphi(n) \, (n_a p_a + n_e p_e + n_f p_f)$$

Let $d_\varphi = n_a p_a + n_e p_e + n_f p_f$ be the phytomer demand

then

$$D(n) = N_\varphi(n) \, d_\varphi$$

If we take the equation that links the total biomass at n cycle and total supply at $n-1$ cycle then

$$Q(n) = \frac{E}{r\,e} \frac{N_a(n) p_a}{D(n)} Q(n-1) = \frac{E}{r\,e} \frac{n_a \; N_\varphi(n) \; p_a}{N_\varphi(n) \, d_\varphi} Q(n-1)$$

By simplifying by $N_\varphi(n)$ we obtain

$$Q(n) = \frac{E}{r\,e}\frac{n_a\;p_a}{d_\varphi}Q(n-1)$$

Let $A = r\,e\dfrac{d_\varphi}{n_a p_a}$

At equilibrium we have $\dfrac{E}{A} = 1$ Then $A = r\,e\dfrac{d_\varphi}{n_a p_a} = E$

From this relation the phytomer demand can be computed, leading to a linear relation between between internode and fruit sink strengths.

Numerical applications

1. Roux model. Each phytomer stands for an internode bearing a leaf and a fruit on the trunk and on the branches. We aim to calculate the internode and fruit sink strengths at equilibrium (we suppose is this example that sink strengths are balanced).

Let $E = 1$, $r = 10$, $e = 0.05$, $p_a = 1$. Equilibrium is supposed reached at cycle n = 10.

2. Coffee model. Each phytomer stands for an internode bearing 2 leaves and 4 fruits on the trunk and on the branches.

Let $E = 1$, $r = 13.33$, $e = 0.05$, $p_a = 1$.

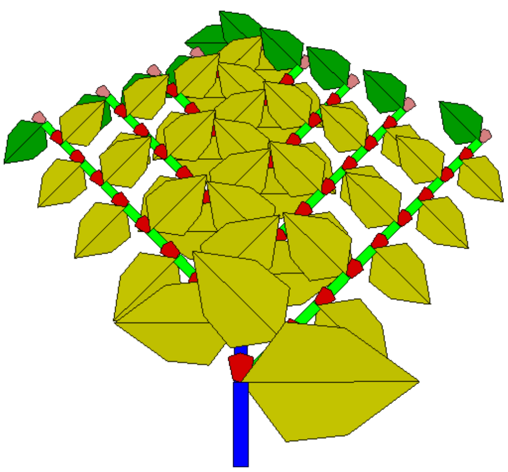


Figure 6. ***roux model at equilibrium state***

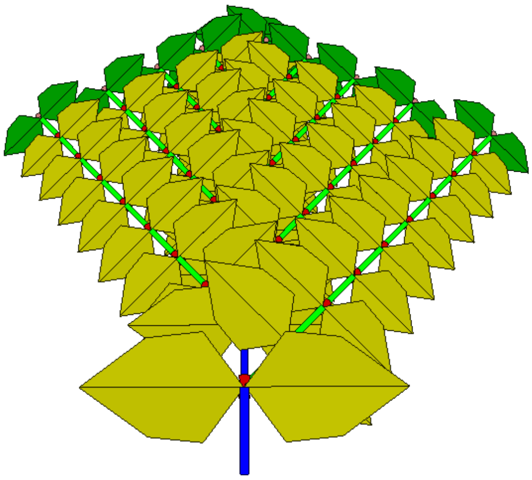


Figure 7. ***Coffee model at equilibrium state***

By introducing more and more precise examples, we take on little by little the generalization of the Q/D GreenLab equation.

5. Branching + Biomass + fruits only on branches

When trunk and branches do not bear the same number of organs[3], equation (1) is written as follows

$$\boxed{Q(n) = \frac{E}{re}\frac{N_{\varphi 1}(n)\,n_{a1}\,p_{a1} + N_{\varphi 2}(n)\,n_{a2}\,p_{a2}}{D(n)}Q(n-1)} \qquad (8)$$

Demonstration

$D_{\varphi 1}(n) = N_{\varphi 1}(n)\left(n_{a1}\,p_{a1} + n_{e1}\,p_{e1}\right)$ for organs of physiological age 1

$D_{\varphi 2}(n) = N_{\varphi 2}(n)\left(n_{a2}\,p_{a2} + n_{e2}\,p_{e2} + n_{f2}\,p_{f2}\right)$ for organs of physiological age 2 (with fruits)

$D_{\varphi 1}(n)$ = total demand of trunk phytomeres at n cycle

$D_{\varphi 2}(n)$ = total demand of branches phytomeres at n cycle

$N_{\varphi 1}(n)$ = total number of trunk phytomeres at n cycle

$N_{\varphi 2}(n)$ = total number of branches phytomers at n cycle

The total demand is :

$$D(n) = D_{\varphi 1}(n) + D_{\varphi 2}(n) = N_{\varphi 1}(n)\left(n_{a1}\,p_{a1} + n_{e1}\,p_{e1}\right) + N_{\varphi 2}(n)\left(n_{a2}\,p_{a2} + n_{e2}\,p_{e2} + n_{f2}\,p_{f2}\right)$$

Let

$d_{\varphi 1} = n_{a1}\,p_{a1} + n_{e1}\,p_{e1}$

$d_{\varphi 2} = n_{a2}\,p_{a2} + n_{e2}\,p_{e2} + n_{f2}\,p_{f2}$

$d_{\varphi 1}$ = demand of one trunk phytomere

$d_{\varphi 2}$ = demand of one branch phytomere

Then

$$D(n) = N_{\varphi 1}(n)\,d_{\varphi 1} + N_{\varphi 2}(n)\,d_{\varphi 2}$$

but

$N_{\varphi 1}(n) = 1$; only one active phytomer on the trunk at cycle n (the last internode at trunk top)

$N_{\varphi 2}(n) = n-1$; there are $n-1$ active phytomers on the branches at cycle n (corresponding to the apical internode of branches)

[3] In the following equations, phytomers numbered 1 are those of the trunk (physiological age 1), and the phytomers numbered 2 are those of the branches (physiological age 2)

We obtain $D(n) = d_{\varphi 1} + (n-1)\, d_{\varphi 2}$

If we take equation (1) that links total demand at n cycle and total supply at $n-1$ cycle

$$Q(n) = \frac{E}{re} \frac{N_{\varphi 1}(n)\, n_{a1}\, p_{a1} + N_{\varphi 2}(n)\, n_{a2}\, p_{a2}}{D(n)} Q(n-1) = \frac{E}{re} n_{a1}\, p_{a1} \frac{Q(n-1)}{D(n)} + (n-1) \frac{E}{re} n_{a2}\, p_{a2} \frac{Q(n-1)}{D(n)}$$

Let $k_1 = \frac{E}{re} n_{a1}\, p_{a1}$ and $k_2 = \frac{E}{re} n_{a2}\, p_{a2}$, we have then

$$Q(n) = \left(\frac{k_1}{d_{\varphi 1} + (n-1)\, d_{\varphi 2}} + \frac{(n-1)\, k_2}{d_{\varphi 1} + (n-1)\, d_{\varphi 2}} \right) Q(n-1)$$

When $n \to \infty$ the first term tends to 0 and the second tends to $\frac{k_2}{d_{\varphi 2}}$. Then $Q(n) \to \frac{k_2}{d_{\varphi 2}} Q(n-1)$.

$$\lim_{n \to \infty} Q(n) = \frac{E}{re} \frac{n_{a2}\, p_{a2}}{d_{\varphi 2}} Q(n-1)$$

If $\frac{k_2}{d_{\varphi 2}} = 1$ then we have progressively $Q(n) \to Q(n-1)$

And if $E = 1, n_{a2} = 1, p_{a2} = 1$ then $re = 1$ when $n \to \infty$

<u>Numerical application</u>

For this example model, trunk phytomers bear one leaf, the first internode of branches and the branches phytomers bear one leaf and four fruits. *What are the sink strengths of trunk internodes, branch internodes and fruits (of branches) at equilibrium?* ($E = 1$, $r = 10$, $e = 0.05$)

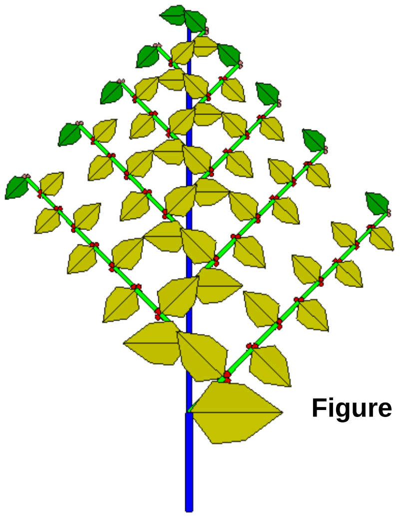


Figure 8. Roux's model at equilibrium with fruits on branches