A Model for Simulating Structure-Function Relationships in Walnut Tree Growth Processes

Séverine Le Dizès, Pierre Cruiziat, André Lacointe, Hervé Sinoquet,
Xavier Le Roux, Philippe Balandier and Patrick Jacquet

An ecophysiological growth process model, called INCA, for simulating the growth and development of a young walnut tree (*Juglans regia* L.) during three or four years, is presented. This tool, currently under development, aims at integrating architectural and physiological knowledge of the processes involved, in order to give a more rational understanding of the pruning operation. The model describes a simple three-dimensional representation of tree crown, solar radiation interception, photosynthesis, respiration, growth and partitioning of assimilates to leaves, stems, branches and roots. It supports the hypothesis that the tree grows as a collection of semiautonomous, interacting organs that compete for resources, based on daily sink strengths and proximity to sources. The actual growth rate of organs is not predetermined by empirical data, but reflects the pattern of available resources. The major driving variables are solar radiation, temperature, topological, geometrical and physiological factors. Outputs are hourly and daily photosynthate production and respiration, daily dimensional growth, starch storage, biomass production and total number of different types of organ. The user can interact or override any or all of the input variables to examine the effects of such changes on photosynthate production and growth. Within INCA, the tree entities and the surrounding environment are structured in a frame-based representation whereas the processes are coded in a rule-based language. The simulation mechanism is primarily based on the rule chaining capabilities of an inference engine.

Authors' addresses *Le Dizès, Cruiziat, Lacointe, Sinoquet, Le Roux* and *Jacquet*, Unité Associée Bioclimatologie-PIAF, INRA, Domaine de Crouelle, F-63039 Clermont-Ferrand, cedex 2, France; *Balandier*, Division Forêt et Agroforesterie, Cemagref, Domaine de Laluas, F-63200 Riom, France
Fax +33 73 62 44 54 **E-mail** ledizes@valmont.clermont.inra.fr

1 Introduction

In recent years, modelling of plants has received considerable attention. Models range from simple to extremely complicated. However, plant growth modelling roughly falls into three categories. First, architectural models deal with plant organogenesis and spatial position of organs, using botanical rules based on precise data (De Reffye et al. (1989)). By contrast, the mechanistic models (or physiological or process-based) are based on the physiological processes and their relation to environmental parameters (light, temperature, CO_2 ...) (Zhang et al. 1994; Korol et al. 1996). However, generally, these models aim at forecasting a detailed account of biomass production for each compartment rather than providing a realistic description of spatial structure of plants.

The combination of architectural models with knowledge of environmental interactions and physiological factors provides an opportunity to link canopy architecture, radiative transfer in the crown and physiological characteristics together into a single model for plant growth (Goel et al. 1991). In this respect, the so-called "mixed models" attempt to increase both the physiological realism of the architectural models and incorporate detailed descriptions of the morphology into the physiological models (Kurth 1994). Examples of mixed models can be found in Ford et al. (1990), Rauscher et al. (1990) and Perttunen et al. (1995).

Our approach belongs to the category of "mixed models". INCA is conceived neither for providing precise numerical simulation of tree behavior, nor for reproducing detailed architectural evolution. Its objectives are twofold. The first is to check if the different pieces of knowledge concerning physiological and morphological processes, obtained from various frameworks under different conditions and put together, lead to a consistent development of the tree. The second objective is to provide, at least partially, appropriate strategies to define, analyse and structure pruning interventions for physiologists or trainees in order to form for instance for forest trees a straight cylindrical bole.

The two goals presented above are tightly linked together. Indeed, by pruning interventions,

one aims at analyzing changes in tree form, which are induced by changes in physiological functioning, through the modification of the carbon budget (photosynthesis, photosynthates distribution...) (Faust 1989). The combination of both carbon metabolism and structural development (i.e. developing a "mixed model") are a prerequisite for modelling pruning effects. Several questions may arise from the integration of such processes. What are the consequences of combining physiological functioning and structural description on tree growth and development? What about combining quantitative and well-known processes such as light interception and photosynthesis with more qualitative knowledge such as correlations between organs?

In the present version, INCA focusses on the walnut tree (*Juglans regia* L.), a broadleaved, deciduous species, but also aims to become a more general tool for modelling structure-function relationships of different species. It attempts to simulate growth of a walnut tree during three or four years under optimal conditions.

In the following section, we describe the basic structure of our model tree and its capabilities for generating various realistic tree architectures. We also present the basic assumptions used for formalysing the following processes: (1) Budbreak, latence and mortality, (2) Hourly solar radiation interception in the tree crown to calculate the photosynthetic photon flux density on each leaf. (3) Photosynthate production of individual leaves, (4) Photosynthate allocation throughout the tree. Analysis and formalisation of pruning effects on tree growth are still in their infancy and therefore are not explicitly presented in this paper. Section 3 is devoted to the knowledge representation and the simulation mechanism implemented in the system. Section 4 provides partial results from a simulation. The last section discusses some advantages and limitations provided by this approach and the anticipated development of the project.

2 Tree Architecture and Functioning in INCA

The model INCA has the following main characteristics: (1) The simulation time-step is one hour; however, the carbon balance and growth are considered on a daily basis, (2) The present version of INCA only takes into account vegetative organs. Each organ is described in terms of topological properties (relative positions of the organs), dimensional and physiological properties (biomass, starch pools...). (3) Environmental data include daily global radiation, minimum and maximum air temperature, humidity, CO_2 concentration, and soil temperature. For simplicity, water and nutrients are assumed to be non-limiting and thus are not explicitly modelled in the present application. No insect or disease damage is considered. (4) The components of carbon demand during the growing season are respiration, growth (new structures) and reserve storage (non-structural dry matter), (5) The allocation of growth to new and existing parts of the tree is modelled at the organ level, based on sink strength, proximity to sources, and the quantity of carbohydrate available. The daily sink strength for each organ is calculated according to growth patterns which are both partly predetermined and flexible to some degree (see below). The sink strength is defined as the competitive ability of a sink to accumulate assimilates per unit time. This capacity, or demand, can be quantified by the *conditional* growth rate of a sink, i.e. the average growth rate which is usually achieved by those organs *under the same cultivation conditions*. At each time step Δt_i, the sink strength is calculated from the growth rate which was achieved at the previous time-step Δt_{i-1} by adjusting the parameters of a predefined growth pattern. Except for vegetative buds and fine roots, this pattern is described by a typical sigmoid curve using a logistic model. The partitioning model is recurrent, that is, the actual growth rate calculated by the model for time-step Δt_i, readjusts the conditional growth rate predefined for time-step Δt_{i+1} using the logistic function, and changing some of its parameters (see section 2.7.1).

2.1 Elementary Units Composing the Tree

The idea is to divide the tree into elementary units that ensure both a simple and realistic representation of the tree as a whole. In INCA, the above-ground parts are composed of nodes and internodes which are assembled in growth units (GU). More precisely, an internode is morphologically represented as a cylinder and bounded at its two extremities by nodes. Each node consists of a vegetative bud and, possibly, a leaf, a scale or a shoot. A GU corresponds to a portion of axis which has lengthened during one or two growth flushes in the same growing season. In the first case (as with short shoots of temperate fruit trees), the GU is made up only of preformed organs, and is composed of a fixed number of internodes ranging from 7 to 12 for the walnut tree. In the present application, this number is arbitrarily fixed at 10 for simplicity purposes. Sometimes, elongation may continue beyond preformed organs. The GU then consists of a preformed part and a new formed part, the number of internodes in the latter depends on the growing conditions. A group of growth units corresponds to an axis which is defined by its order: the axis of order 1 is the trunk, axes of order 2 are the branches connected to the trunk, and so on.

The root system is represented in a simplified manner, with three compartments: the taproot, the coarse roots and fine roots. The volume of the soil explored by roots can be divided into several layers in which soil temperature and moisture are assumed to be uniform. The coarse and fine roots compartment is characterized for each layer by total length (cumulative length of all individual component roots), total volume, average diameter and average distance from the collar. Geometrically, the taproot is represented as a truncated cone to which the lateral roots are attached.

2.2 General Rules of Branching Geometry

In INCA, the architectural structure of the tree is formed by simple branching rules. Each year, the terminal bud of a current GU gives rise to a new GU, and possibly, the axillary buds which break
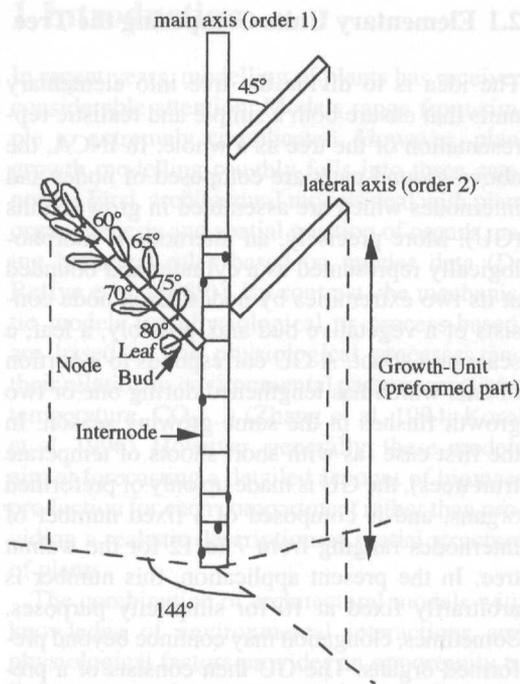
Fig. 1. Basic elements of the model tree and branching geometry from a parental growth unit (GU) (here, the main axis). The direction of the first lateral axis is determined randomly.

to give other GU's as lateral branches. The lateral GU's direction characterized by inclination and azimuth is determined according to fixed branching angles and phyllotactic distribution procedures. The insertion angle is arbitrarily 45°, for simplicity, with respect to the axis of the terminal bud and the azimuth corresponds to a divergence angle of 144° (a 2/5 phyllotaxy characteristic to the walnut tree). A GU produces a maximum number of four lateral GU's. The number of new lateral GU's depends on the budbreak probability of the lateral buds (see section 2.3). The leaf's orientation along a GU is given by insertion angle and azimuth. Leaf insertion angle is assumed to follow a constant decreasing gradient from the base to the top of the GU. Azimuth is controlled by the phyllotaxic spiral. The location of buds in three-dimensional space is also computed by using phyllotactic distribution procedures. Fig. 1 shows the spatial arrangement of the different aerial elements of the model tree.

2.3 Generating Variability in Architecture

Changes in tree form mainly caused by the three following processes:
1) Emergence of new axes defined by various dimensions, either with the continuation of existing axes, or in a different direction;
2) Death of buds;
3) Removal of existing axes (pruning).

These processes are the result of bud activity. Therefore the consideration of the three possible states of the vegetative buds, namely growth, latence or death are of primary importance to introduce variability in tree structure. In the model, the computation of a budbreak probability P_b for the one-year old buds introduces variability in tree structure. More specifically, P_b depends on the position in the GU (the apical growing bud which is dominant has a greater probability than axillary buds, and, among the latter, the median buds are more disposed to budbreak) (Ollier 1993). P_b also increases with the GU's vigour measured as the GU's volume and diminishes with the order of the axis. According to this scheme, the one year-old buds are either latent or growing buds. The number of growing buds determines the number of new GU's sprouting in spring. The final conditional size of a new GU is determined according to its position within the crown, the volume of the mother branch, its number of growing points and the amount of assimilates it earned in the previous year. The buds which remain latent may die, according to the computation of a death probability P_m which increases with tree age.

The third process which consists of cutting away parts of the tree also lead to important changes in tree structure. Pruning can break the correlative inhibitions between tree organs. In this respect, the buds which remain latent play an important role as they have greater growth potentialities than those of the growing buds. These capabilities may be expressed under special conditions such as pruning (Mauget 1984). More specifically, whenever shoot pruning is carried out, a budbreak probability P'_b is computed for each latent bud. P'_b depends on the size of cuts (the more wood is removed the greater is the number of buds able to break), the period

of pruning (the later the intervention occurs during the growing season, the less is the probability of budbreaking), and the position of each latent bud relative to the position of cuts, i.e. in terms of age and order (Mauget 1993). The final conditional size of a new GU is determined according to mother branch characteristics and the period of pruning (generally, the earlier the summer pruning is performed, the greater the amount of regrowth that occurs) (Mauget 1993). Another process involved in the pruning operation is the increase in radial growth of the lateral GU carried by the pruned stem. This process, i.e. the increase of the final conditional diameter, is determined according to the position, the period, the size of pruning and the number of growing points of the mother branch. Qualitatively, the more wood is removed and the earlier pruning is practiced during the growing season, the greater is the resulting growth. Pruning intensity and time effects on radial growth may be reduced when the GU carries many ramifications. The number of growing points is introduced here to take into account, for a given GU, the available "growth potential" which is shared among the different sinks.

2.4 Bud-break, Latence and Mortality

On 1 January, which is assumed to correspond to the dormancy release of vegetative buds, the budbreaking probability P_b is calculated for each one-year old bud as described above. In order to translate this probability into actual events for the simulation process, each bud is assigned a value T randomly sampled from a uniform distribution between 0 and 1. If $T > P_b$, the bud is assumed to remain latent. If $T < P_b$, the bud grows until it breaks in spring. Its developmental rhythm from 1 January to budbreak is measured by using heat-unit accumulation. A certain amount of exposure to warm temperatures above a given threshold termed Growing Degree Hours (GDH) or the heat unit requirement, is required for budbreak (Richardson 1974). The GDH parameter must be given as input to the model, in order to deal with early or late-breaking cultivars of walnut at a specific location. In INCA, it corresponds to the heat unit requirement for terminal

buds. The temperature threshold is arbitrarily 4.5 °C. The way temperature affects bud growth until budbreak is exponential (Henaut 1985 cited by Mauget 1993). In our model, the exponential law of action of temperature on the rate of budbreak varies with bud position, the axillary buds require higher temperatures than the terminal bud to grow after release from dormancy. This depends on the temperature-dependent increase of the bud volume and water content (defined as the ratio of water weight to dry matter weight). By assuming that 90 % of the bud volume is composed of water, each bud's dry weight can be calculated every day. The bud water content is strongly correlated to its phenological stage (Ollier 1993). A bud is scored as broken when bud development is at stage Df in the walnut phenological scale of Germain (Germain 1973), that is when the water content exceeds 6 g per g dry weight (Ollier 1993). At this stage of development, a new leafy GU starts sprouting. The further conditional developmental patterns of leaf surface area and stem length and diameter are described in section 2.7.1.

A similar reasoning as described above is used to determine whether the older buds are latent or dead: in January, the bud-death probability P_m is calculated. Then, each bud is assumed to be either dead (i.e. $T < P_m$) or latent (i.e. $T > P_m$). In case of pruning, the budbreak probability P'_b is computed for the buds which remained latent. As mentioned in section 2.3, P'_b depends on the size of the cuts, the period of pruning and the position of each latent bud (Mauget 1993). If $T < P'_b$ the bud starts growing and follows the same dependance on temperature as the rate of budbreak. In the other situation, the bud remains latent.

2.5 Solar Radiation Interception

Incident photosynthetically active radiation (PAR) greatly influences photosynthesis of single leaves, and thus explains part of the variability of growth and biomass production (Goel et al. 1991). We are developing a model that allows both sufficient realism and relative simplicity in estimating light interception. Direct and diffuse PAR are considered in this model, at hourly intervals.

First, hourly positions of the sun (elevation and azimuth) during the day and the daylength for specified days and a given location are computed using standard astronomic equations (Goudriaan 1977). Daily diffuse incident radiation (*Rd*) is derived from the daily amount of the incident solar radiation depending on sunshine duration (Bonhomme 1993). The daily courses of the two components, direct-beam solar radiation (*Rb*₀) and diffuse radiation (*Rd*₀), of the global solar radiation (*Rs*), are given using the Perrin de Brichambaut (1976) formulae (Bonhomme 1993). Two optional subroutines are available in the model, i.e. mutual shading between leaves is or is not taken into account. In both situation, the diffuse solar radiation is determined by assuming an isotropic luminance distribution, according to the Uniform Overcast Sky model (Moon and Spencer 1942).

2.5.1 Subroutine 1: No Mutual Shading between Leaves (Young Tree)

The mean direct radiation intercepted by a leaf Rb_i (which corresponds to the shadow cast by the sunlit leaf) depends on the hourly direct radiation above the canopy Rb_o and the angle β between the leaf normal and the sun direction Ω_s (characterized by an elevation H and an azimuth A). The diffuse solar radiation Rd_i depends only on the hourly diffuse radiation above the canopy Rd_0 and the leaf inclination α (Varlet-Grancher 1975). The global leaf irradiation is computed as the sum of the direct and diffuse components.

2.5.2 Subroutine 2: Mutual Shading Between Leaves (Fig. 2)

The tree canopy is represented by an ellipsoïd of vertical axis. It is assumed to have a uniform foliage density with a spherical distribution of leaf inclination (De Wit 1965). The attenuation P_0 of radiation within the canopy is expressed by a Beer's law. It is a function of the leaf area density and the path of the solar beam within the ellipsoïd. P_0 is compared to a value T randomly sampled in a uniform distribution between 0 and 1. The leaf is assumed to be shaded if $T > P_0$, or
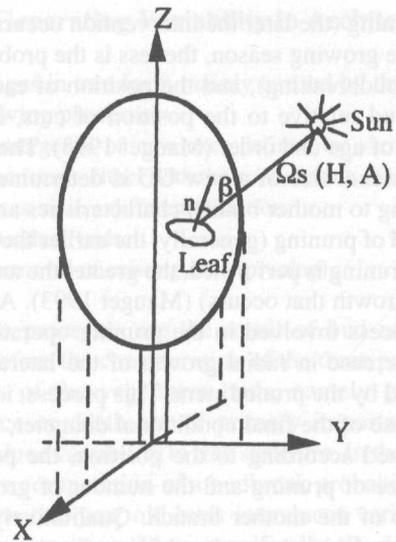
Fig. 2. Solar beam encountering the ellipsoïdal tree canopy (*n* = leaf normal; $\Omega_s(H,A)$ = sun direction defined by elevation *H* and azimuth *A*).

it is sunlit if $T < P_0$. In this case, the direct radiation received by sunny leaves is the same as defined in subroutine 1.

Diffuse incident radiation is treated as a set of directional sources, i.e. integrating directional interception contributions over the whole sky (de Wit 1965). For this purpose, the sky is divided into solid angle sector according to azimuth and zenith angle classes (azimuth A_j, elevation H_j). This requires knowledge of the luminance of the incident diffuse radiation over the sky. The beam path within the canopy and its intersection with the ellipsoïd are computed by applying the above considerations for each solid angle direction Ω_s. We then use the Goudriaan approximation (Goudriaan 1977) in which correction factors introduced in the extinction coefficients account for leaf scattering. Finally, the mean fraction of a beam coming from a solid angle sector to reach a leaf is a function of the uniform leaf area density, the path of the beam within the ellipsoïd and the leaf scattering coefficient. The integration of the contributions of each solid angle sector gives the fractional diffuse radiation received by a leaf *i*.

2.6 Leaf Photosynthate Production

The photosynthesis production submodel is based on concepts and calculations developed in the mechanistic model of Farquhar et al. (1980) whose parameters have been determined for a walnut tree in Clermont-Ferrand. The key model parameters (maximum carboxylation rate V_{cmax}, maximum electron transport rate J_{max} and respiration rate R_d) are defined for each leaf, based on its nitrogen content N expressed on an area basis (Le Roux and Grand, unpublished data):

$$V_{cmax} = 23.75N + 2.0$$
$$J_{max} = 47.1N + 10.8$$
$$R_d = -0.364N + 0.03$$

where V_{cmax}, and R_d are expressed as µmol CO_2 m^{-2} s^{-1}, J_{max} as µmol electrons m^{-2} s^{-1} and N as gN m^{-2}.

These empirical relationships are valid for N ranging from 0.9 to 3.6 gN m^{-2}. N is a function of the local radiation regime experienced by each leaf (Le Roux et al. 1997):

$$N = \frac{N_0 I}{I_0}$$

where I_0 is the time-integrated PAR intercepted by full sunlit leaves, I is the time-intergrated PAR intercepted by the leaf and N_0 is the nitrogen content in full sunlit-leaves ($N_0 = 3.64$ gN m^{-2}). This formulation allows to account for self shading effect within the tree foliage. However, the model runs presented in this paper were performed for a young walnut tree (2–3 years old). Since all its leaves were sunlit ones, leaf nitrogen content, and therefore photosynthetic parameters, were assumed to be constant for all the leaves.

Model inputs are incident PAR flux density, air CO_2 (assumed to be constant and equal to 350 ppm) and leaf temperature (assumed to be equal to air temperature). The output is the hourly average net photosynthetic rate of each leaf within the crown which allows to compute the daily supply of carbohydrate for each GU. Leaf ageing is taken into account so that leaf photosynthate supply per surface area increases from budbreak until late July and decreases during September and October due to senescence (Kajji 1992). In the present version, leaves fall is arbitrarily set on 1 Nov.

2.7 Photosynthate Allocation

2.7.1 The Dynamics of Demand

Generally for walnut trees, reserve storage occurs simultaneously with growth during the growing season (Kajji 1992); hence reserve accumulation also contributes to sink demand. Thus, the three components of carbon demand are respiration, growth (new structures) and reserve storage (non-structural dry matter).

Maintenance Respiration

The maintenance respiration rate for each organ depends on temperature, organ type and structural dry weight (i.e. the organ biomass minus the reserve pool). The component of respiration usually associated with ion uptake is neglected in the current version of the model. In INCA, the user can manipulate the respiration vs temperature relation by entering values of Q_{10} for several temperature intervals. Temperature dependance of leaf respiration and photosynthetic rates were characterized in a walnut tree by Le Roux and Grand (unpublished data). These relationships are used to infer the effect of temperature on leaf net carbon gain. The lack of field measurements for the other organs of walnut prompted us to use the maintenance respiration rates (gCO$_2$ g^{-1} dry weight day^{-1}) derived from studies conducted on peach trees (Grossman and DeJong 1994). The hourly respiration rates are summed over the day to compute a daily average respiration rate. The daily carbon cost of maintenance respiration is then determined as the product of the daily respiration rates and the dry weights of each organ.

During the winter rest season, the energy requirement for maintenance respiration in any organ is met by the mobilization of stored reserve carbohydrate and deducted from the reserve pool of the trunk, branches, tap-root, coarse and fine roots. Each organ is assumed to meet its own respiration needs (see below for fine roots).

Conditional Growth

Except for vegetative buds and fine roots, the logistic growth function which is partly set a-

priori was selected as it provides a simple and accurate representation of the sigmoïdal assymptotic growth patterns described in several tree species (Remphrey 1994). In simple logistics, the instantaneous absolute growth rate dy/dt is a quadratic function of y (Riccati's differential equation). Four parameters characterize a logistic curve: the inflection point (IP) and the maximum growth rate (V_{max}) which are characteristic of each organ class (leaves, growth units, taproot...) and the initial (y_0) and final dimension (y_m) which are set for each object (leaf-1, growth-unit-1...) according to its location within the tree (see below). The inflection point IP defines the timing of the organ development; different IPs for different organs control the overlap in the growth of competing sinks. The growth model is recurrent, i.e. the conditional growth rate is readjusted at each time step according to the actual growth rate computed at the previous time-step.

When a new growth unit appears at budbreak, it has the same diameter as the bud it sprouts from. Its final conditional dimensions (length and diameter), as well as its total leaf surface area are determined by its position within the crown and the conditions of the mother branch. More specifically, as mentioned in section 2.3, the conditional final volume is determined according to the position of the bud it sprouted from, the volume of the parental GU, its number of growing points and the quantity of assimilates accumulated in the previous year. Its final diameter has been computed as a function of the initial diameter. Then, by roughly approximating the growth unit as a cylindrical volume, the equation for the volume of a cylinder can be solved for the final length. As regards the trunk and branches (more than one year old), the final diameter of each GU (cambial growth) is a linear function of its initial diameter. The conditional final leaf surface area of the current-year stem has so far been computed from its conditional final diameter. The final surface area can then be computed for each leaf, by assuming that a leaf which is located around the middle of the GU is a bit larger than a leaf located at the extreme part (Sinoquet 1996, according to unpublished data obtained on a 20-year-old walnut tree). All individual values are then converted to biomass and summed up to give the final leaf mass of the

whole tree. Regarding the root system, the conditional final dry weight is determined from the dry weight ratio between the aerial parts and the root system which is a function of tree age. Each root compartment is attributed a fraction of this total dry weight which is then converted to a final volume.

A particular function is assigned to the growing buds and the fine root compartment. Their conditional growth rate is related to daily air and soil temperature respectively. In winter, their requirements for both growth and respiration are assumed to be met by the organ's own stored carbon. They are deducted from dry weight and reserve pools of the carrying GU (for buds) or fine roots themselves. However, if the starch concentration of the fine root compartment drops below a minimum level (which is presented as an input parameter), the fine root dry weight decreases so that the reserve concentration stays at that minimum value. This simulates fine root death in winter. No further attempt has been made to account for loss of carbohydrate from the roots by fine root turnover, exudation and increased respiration during active transport of nutrients.

From the partly preset conditional growth patterns as described above, the model determines daily dry matter increment demand (including the reserve storage) for each organ, as the sum of the elementary requirements for the synthesis of one unit of volume (growth units or roots) or leaves surface area. The instantaneous growth rate ($cm^3 day^{-1}$ or $cm^2 day^{-1}$ for leaves) is converted to biomass increment ($g day^{-1}$) by multiplying by basic density ($g cm^{-3}$) or leaf mass to area ratio ($g cm^{-2}$) of the organ considered. The carbon dioxide cost of daily growth is calculated as the sum of the carbon dioxide equivalent weight of the dry weight added by growth and the respiratory cost of that growth (Grossman and DeJong 1994):

$$Cg = (CE + G) \cdot DM$$

where Cg ($gCO_2 day^{-1}$) is the carbon dioxide cost of the dry matter added, CE ($gCO_2 gDM^{-1}$) is the carbon dioxide equivalent weight of the dry matter, DM is the weight of the dry matter added ($gDM day^{-1}$), and G is the growth respira-

tion coefficient (dimensionless). The carbon equivalent weight of all the organs is calculated from carbon concentrations which are assumed to be constant and equal to 40 % for each organ. Thus, the carbon dioxide equivalent weight (defined as the ratio of carbon concentration to carbon concentration of carbon dioxide) is equal to 1.47 (= 44/30).

Carbohydrate Reserve Storage

The walnut tree stores significant amounts of assimilates in long-term reserve pools; they represent the total non-structural carbon, also referred to as available, reserve carbon. INCA accounts for carbon storage, mainly as starch (the reversible interconversion between soluble sugar and starch is neglected). Thus, carbohydrate reserves in walnut tree organs have been given a demand function. They are assumed, in our model to be close to saturation at each time-step for the growing organs. Each class of organ is attributed a minimum and maximum starch concentration (as input parameter); these are defined as thresholds, for reserve storage. At each time-step, the reserve storage requirement to reach saturation level is a function of the structural mass increment of each organ. The greater the conditional growth rate, the greater is the storage demand of the organ.

2.7.2 Partitioning

Each day, the model calculates the allocation of newly synthesized carbohydrate and/or non-structural carbon reserve to various tree organs for respiration, growth and reserve storage. The carbon requirements for growth and storage are satisfied based on the daily carbohydrate supply of the sources S_i, the conditional sink strength of the growing organs P_j and the proximity to a source. Similar approaches to partitioning have been taken in modelling the growth of peach (Grossman and DeJong 1994), citrus and other evergreen trees (Harpaz et al. 1990). In INCA, the carbohydrate flow F_{ij} between a source S_i and a sink P_j is written as following:

$$F_{ij} = k_i \cdot Demand_j \cdot Supply_i \cdot f(D_{ij})$$

where k_i is a coefficient characterising each source calculated according to the mass conservation, $Demand_j$ is the demand of the sink j, $Supply_i$ is the supply of the source i and $f(D_{ij})$ is a function which is inversely proportional to the distance between S_i and P_j. The actual carbohydrate flow incoming into each sink P_j from all the sources is given by the following equation:

$$Demand_j \cdot \sum_i \left(k_i \cdot Supply_i \cdot f(D_{ij}) \right)$$

The partitioning process makes a clear distinction between two different periods that occur successively in the annual history of the tree: for the first days after budbreak, as photosynthesis is reduced, the total daily supply of carbohydrate is not sufficient to support the total daily demand, and afterwards, when photosynthesis is maximum the total daily supply exceeds the daily demand.

In the first situation, the main source of carbone for the growing leaves, stems and fine roots are the reserve pools stored in the previous year.

The branches and trunk are modelled as being sources closest to the leaves and stem, followed by the taproot and the coarse roots which provide carbohydrate to fine roots in priority. The carbohydrate provided is deducted from reserve pools. In the second situation, leaves are essential for carbon supply (photosynthesis). The stems and branches are modelled as being closest to the sources, followed by the trunk, and finally the taproot, the coarse and fine root compartment. In both situations, the model supplies carbon for maintenance respiration requirements before supplying carbon for growth and reserve storage (Grossman and DeJong 1994). Within each organ, if daily carbon availability after maintenance respiration has been substracted is greater than the carbon cost of daily growth and storage, reserve storage occurs at the conditional rate and growth is not limited by carbon supply and may occur beyond the conditional rate if remaining resources are still available. However, when carbon is in short supply, the carbon requirement of an organ can be unsatisfied and therefore growth and reserve storage are reduced. The fraction of carbon supply that can be incorporated in both structural growth and reserve pool is in proportion to their respective carbon requirement. This fraction is multiplied by the carbon available after mainte-
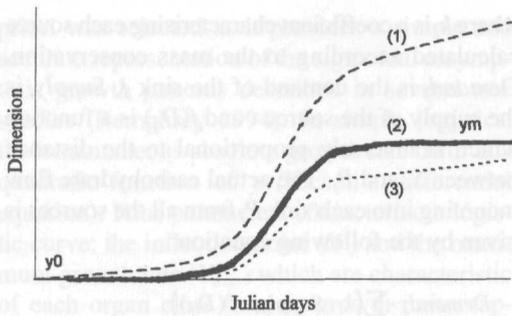
Fig. 3. Examples of actual growth rate patterns which deviate from the conditional growth rate on the logistic curve (2) according to the level of resources: when resources are abundant (1) or limiting (3).

nance respiration is satisfied, to determine both its actual growth and reserve storage. This allocation scheme causes the actual growth rate of different organs to deviate from the conditional growth rate predefined on the logistic curve, when resources are either abundant or limiting. The resulting growth pattern is then different than the predefined logistical function (Fig. 3).

2.7.3 Dry Matter Production and Dimensional Growth

The output of the partitioning model is a daily estimate of dry weight gain for structural growth and carbon storage reserve. Dimensions and starch pools are computed for all the components every day.

There is a slight overlap between lengths and diameter growth, and according to the inflection points defined as input for both diameter and length patterns of the GU class, significant diameter increase may begin before GU's reach their full length. When length expansion is finished, diameter increases as long as the carbon supply is sufficient. Above a given threshold (arbitrarily, twice the demand corresponding to the conditional growth rate in diameter) a second growth flush appears. The formation process of new GU's is currently being studied.

Internode length is assumed to be greater in the middle than in the extreme parts of a GU (Sinoquet 1996, according to empirical and unpublished data). If the leaf width/length ratio is known (a geometrical characteristic), leaf length can be deduced from leaf area.

To summarize, Fig. 4 illustrates schematically the carbon partioning in the model.

3 Knowledge Representation and Simulation with INCA

A major design constraint was to express the knowledge of the biological processes involved in a flexible framework able to accommodate well-established items with more qualitative information. In order to ease as much as possible the modification and addition of knowledge to the system it was desirable to use a simple modular representation language. INCA is implemented in the artificial intelligence programming language PROLOG II+ which is a logic programming tool extended with frame-based representation capabilities. It makes a clear distinction between the description of the tree entities and its surrounding environment on one hand and the processes that drive its evolution through time on the other hand (Jacquet 1996). The first part is represented by frames (which can be thought of as extended data records) that are organized into hierarchies structuring the components in classes, subclasses and instances of components. Inheritance helps in describing the world of interest by starting with generic descriptions and specializing them. The second part, which conveys the physiological aspects, is encoded by production rules. Associated with these representation capabilities, INCA is equipped with a simulation engine that can model the passage of time and trigger the pieces of knowledge that cause changes of state. These aspects are described now.

3.1 Representing the Elementary Units Composing the Tree

The method is to represent the tree by describing its constituent organs in a structured formalism provided by the frame-based primitives available
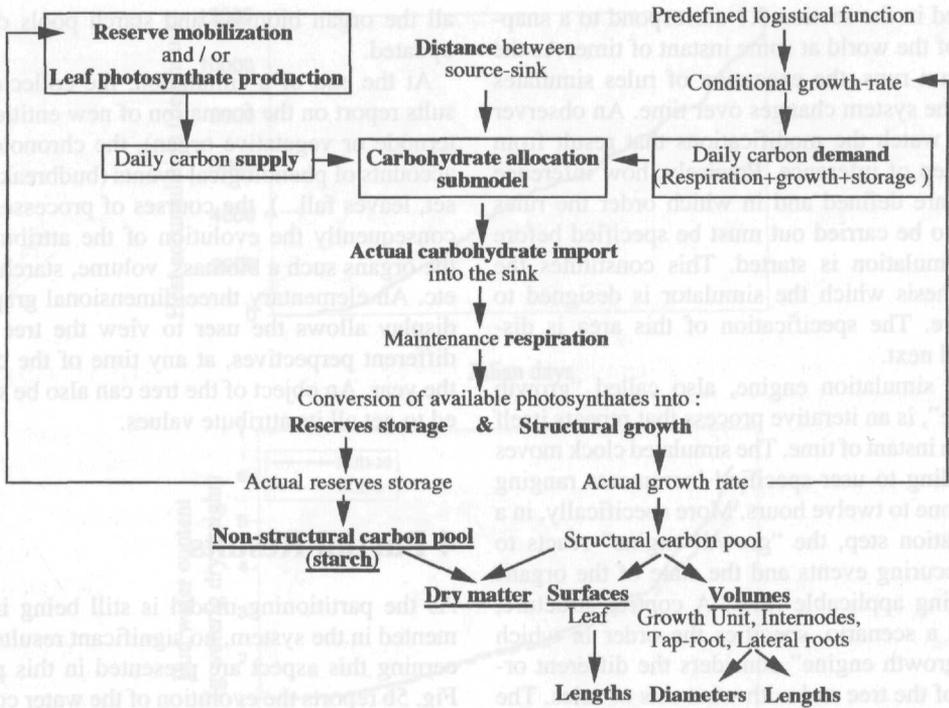
Fig. 4. Relational diagram illustrating carbohydrate partitioning by the model INCA.

in PROLOG II+. The organs are organized in hierarchies, the links of which represent class-subclass or class-instance relationships. A class represents a category of objects. The existence of members of a class is represented by instances. Each class, here an organ (e.g. a bud or a branch) or an entity of the surrounding environment (the soil and aerial volume in the vicinity of the tree), has a set of attributes that are possessed by all the objects lower down in the hierarchy. The value of each attribute can then be inherited or redefined as required. As an example of an inheritance hierachy consider the class "bud". In a specific situation under study, the system may have to deal with several instances: bud1, bud2, etc.

3.2 Representing Physiological Processes

The physiological processes of interest in the investigation domain are embedded in rules of the form "if situation, then consequence". The situation part of a rule consists of conditions to

be tested with respect to the current situation of the tree and its environment. This may include the occurrence of some events or results coming from external procedures. The consequence part states what has to be changed in the description of the situation at the next time step or what event or procedure has to be triggered (e.g. the creation of a new organ). The rule framework was chosen precisely because it allows direct representation of how a new state or event depends on the previous situation.

For clarity, the rules are distributed in distinct subsets according to the processes they represent. Each rule subset (or even each rule) represents an independent item of knowledge.

The current physiological processes represented in this way include respiration, photosynthate production and distribution, and growth.

3.3 The Simulation Engine

The values of the attributes of the objects de-

scribed in the section 3.1 correspond to a snap-shot of the world at some instant of time. As the program runs, the execution of rules simulates how the system changes over time. An observer could watch the modifications that result from one step of inference. Precisely, how inference steps are defined and in which order the rules have to be carried out must be specified before the simulation is started. This constitutes the hypothesis which the simulator is designed to explore. The specification of this area is dis-cussed next.

The simulation engine, also called "growth engine", is an iterative process that repeats itself at each instant of time. The simulated clock moves according to user-specified increments ranging from one to twelve hours. More specifically, in a simulation step, the "growth engine" reacts to the occuring events and the state of the organs by firing applicable rules. A control structure, called a scenario, specifies the order in which the "growth engine" considers the different or-gans of the tree and with what sets of rules. The basic scenario takes into account all the tree entities. However, for run time performance and focussed exploratory purposes, the user can choose the specific objects (classes or instances) on which simulation has to be performed. As an example, it is possible to distinguish the physio-logical processes to apply to the growth unit of the curent year and the older growth unit. Be-sides the order in which the tree entities have to be considered, a scenario specifies for each enti-ty the list of rule sets that have to be used. The scenario structure is basically a means to use selectively the content of the knowledge base. More detailed information of INCA is given in Le Dizès et al. (1996).

Among the events that can be triggered by a rule are those concerning the creation of organs. Each time such an event is produced, INCA calls a specific procedure to create and insert the new object shoot in the topological structure of the tree, and compute its three-dimensional location. The model computes maintenance respiration and leaf photosynthesis within each step. In a typical run, at the end of each day, the values of these attributes can be summed up and then the parti-tioning process is executed. The bud volume or leaf surface, internode length and diameter and

all the organ biomass and starch pools can be updated.

At the end of a simulation, the collected re-sults report on the formation of new entities (in-ternode or vegetative organ), the chronological accounts of phenological events (budbreak, bud-set, leaves fall...), the courses of processes, and consequently the evolution of the attributes of the organs such a biomass, volume, starch pool, etc. An elementary three-dimensional graphical display allows the user to view the tree from different perpectives, at any time of the day or the year. An object of the tree can also be select-ed to get all its attribute values.

4 Partial Results

As the partitioning model is still being imple-mented in the system, no significant results con-cerning this aspect are presented in this paper. Fig. 5b reports the evolution of the water content of the terminal bud (BUD10) and one axillary bud (BUD6) until budbreak, depending on heat unit accumulation (Fig. 5a) during the same time. Fig. 6a shows the daily course of the PAR inter-cepted by six leaves on 22 June, 1995. These patterns depends only on solar position in the sky during the day, leaf inclination and azimuth, as no mutual shading between leaves in the crown is considered in this example. Each leaf net pho-tosynthesis is given in Fig. 6b.

5 Discussion

The INCA model incorporates many processes for which a great number of parameters is need-ed. Because walnut tree is rarely studied in growth models, some parameters were either taken from other species or taken a-priori. The knowledge and numerical information concerning different processes is very different: photosynthesis or light interception have been studied intensively, while little information is available about the assimi-late partitioning between different organs of the tree. Growth partitioning in this model is mecha-nistically, not empirically defined. It uses the
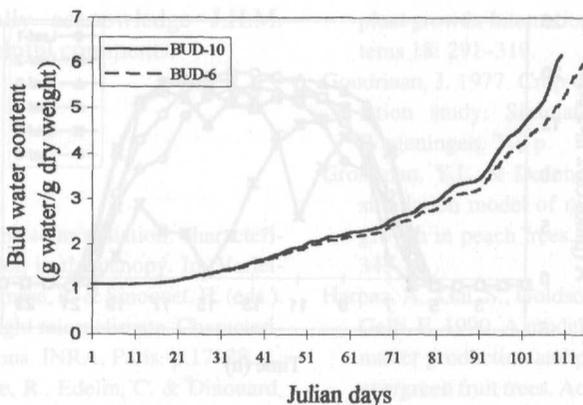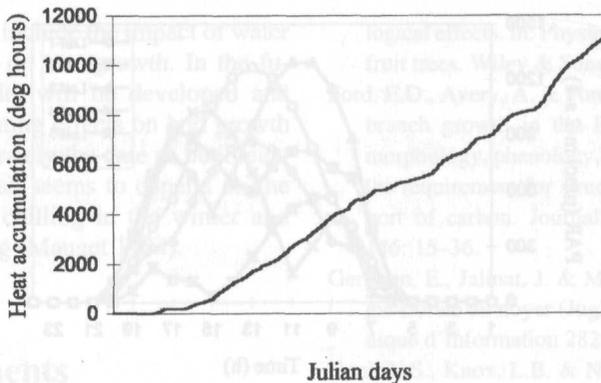
Fig. 5. Heat accumulation (a) and water content of terminal bud (BUD-10) and median buds (BUD-6) (b) from 1 Jan to 20 April. 11 000 deg.hours (an input parameter) corresponds to the heat unit requirement for budbreak.

hypothesis that tree grows as a collection of semiautonomous, interacting organs that compete for resources, based on daily sink strengths and proximity to sources. The actual growth rate of organs is not entirely predetermined by empirical data, but also reflects the pattern of available resources (Grossman and DeJong 1990). An unusual feature of this approach is that carbon partitioning coefficients to the various organs are an output of the model rather than the inputs since we use organ conditional growth rates as the primary determinants of carbon use. By contrast, some ecophysiological models such as Ecophys (Rauscher et al. 1990) are based experimentally on determined transport coefficients as inputs to their partitioning model. However, in INCA, the estimation of the "demand" of the various organ sinks is a hypothetical quantity which is indirectly approximated. At this stage of development, we are not able to grasp all the potentialities and limitations of the partitioning model, as no significative simulations have been run so far.

Validation in the strong sense as can be done with simple models is not possible in this model because of the lack of appropriate data and the great number of processes involved. This situation, however, is not an obstacle for modelling. In simulation runs the model structure and hypotheses can be checked and additional research may be initiated by the questions which arise from the simulations. It must also be kept in
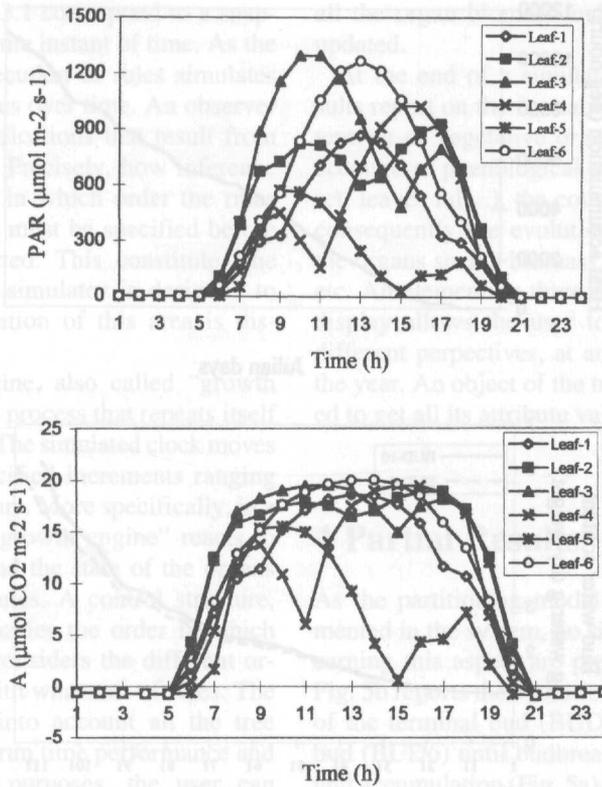
Fig. 6. (a) Daily variation of the PAR flux density intercepted by 6 successive leaves on the same GU along the phyllotaxic spiral. (b) Daily variation of the net photosynthesis (A) of the same leaves. Leaf 1 is at the bottom of the GU (insertion angle = 80° and azimuth = 0°). The insertion angle from leaf 2 to leaf 6 is respectively 75°, 70°, 65°, 60°and 55°. The azimuth is respectively: 144°, 288°; 72°; 216° and 0°. Inputs: Daily global radiation = 26 MJ m^{-2} day^{-1}, sunshine duration = 53 %, daily average air temperature = 20.5 °C.

mind that data acquisition on such processes like assimilate partitioning and growth, are difficult and expensive. Nevertheless, experimental research is necessary to improve these and other parts and parameters of the model which require better confirmation.

From a methodological point of view, the approach used in INCA system offers advantages by facilitating updates and the extension of the knowledge base because it is based on a modular representation. INCA also allows the re-use of the knowledge base for different species as the

knowledge items correspond to elementary objects and principles of physiology. Moreover, the model enables simulations to be run under different initial and run-time conditions which allow the user to experiment with different growing conditions or specific attributes. In the present application, many parameters are assumed to be constant (the basic density of wood for instance). In order to determine the relative importance of different physiological, morphological, and environmental model input variables, a sensitivity analysis is required. Further improvements of

the model could also include the impact of water and nutrient stresses on tree growth. In the future, a chilling model will be developed and coupled with the heating effects on bud growth to predict more accurately the date of budbreak, since walnut budbreak seems to depend on the interaction between chilling in the winter and warming in the spring (Mauget 1984).

Acknowledgments

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