

CHAPTER 16

FUNCTIONAL-STRUCTURAL MODELLING OF FABA BEAN

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Abstract. Crop models such as CERES and CropSyst treat canopies as homogeneous entities without attempting to define canopy geometry, other than through row structure, nor deal with growth processes at time steps shorter than one day. A functional-structural modelling approach can improve canopy simulation, in particular of indeterminate crops such as faba bean. A major challenge is to incorporate the plasticity of the canopy. Functional-structural models can accomplish this by introducing variation in several ways and at different levels of canopy composition. ALAMEDA is a functional-structural model of a faba bean (*Vicia faba* L.) crop that addresses these issues. An L-system provides the basic conceptual and program structure within which functional relationships can be connected. In this way it plays a comparable role to physical plant structure that provides the linkage between morphology and physiological processes spatially distributed over plant components. In accordance with results of previous studies with faba bean, the stem was selected as the main building module. An associated growth model is linked to calculate the lengths of the vegetative organs, and leaf allometries are used to compute leaf area. ALAMEDA is currently being extended by including a model of radiation interception and functions from classic models, for example, the variation of specific leaf area with temperature as specified in CROPGRO-legume.

CONCEPTS IN FABA BEAN MODELLING

The objective of this chapter is to present relevant concepts in faba bean (*Vicia faba* L.) functional-structural modelling as exemplified by the ALAMEDA model. For this purpose, an overview of structural and functional considerations is presented.

A detailed morphological description is needed to represent the structure of faba bean plants because of its complexity; the crop structure is of special relevance in the early stages of this crop when canopies are most heterogeneous. Faba bean plants have indeterminate growth habit and produce compound leaves with the number of leaflets per leaf increasing from the plant base to the top. Distribution of the size of vegetative organs along the stem follows the same pattern for all organs and components (petioles, leaflets, leaves, internodes) but absolute sizes vary between sowing dates (Ruiz-Ramos and Mínguez 2006). Branching occurs from the

first and second internodes of the main stem producing between 1 and 4 pod-bearing branches and up to 3 unproductive stems none of which branch further. Inflorescences of 2-5 flowers appear in leaf axils from node rank five or six upwards and produce between 1-4 pods per node. The phyllochron can be considered constant (the same value for main stem and branches) till the beginning of the grain-filling period (Ruiz-Ramos and Mínguez 2006).

The simulation of the development of this morphology over time is the objective of the functional part of the model. This simulation seeks to understand the response of faba bean and other indeterminate crops to the environment, and is not always supported by quantitative equations. For this reason, functional-structural plant models (FSPMs) often have to resort to descriptive information to be able to complete a specification of structure. In the FSPM ALAMEDA, a limited part of the general relationships for the faba bean crop were obtained from field experiments (Ruiz-Ramos and Mínguez 2006), using several approaches to capture variation among individual organs. The next section describes those approaches and presents results of the morphological parameterization. Current process-based models (PBMs) of faba bean that could provide the equations to increase the functionality of ALAMEDA are discussed in the section “*Sources of physiological functions: existing models*”.

Morphological parameterization and building modules

The detail of module definition in a functional-structural crop model depends on the objectives of the model. Improving the simulation of individual leaf surfaces, or of leaflets in the case of compound leaves of faba bean, requires specification of modules appropriate to the finer resolution of the model. Simulation of structure can, however, be simplified by ‘clustering’ modules according to observed repetitive patterns. A recent morphological study that revealed the crop to grow as an aggregation of stems behaving similarly (Ruiz-Ramos and Mínguez 2006), supports the choice of the stem (meaning main stem and branches alike) as the main building module for faba bean functional-structural modelling. In this work, the structural parameterization of the plant was drawn from a single stem. The allometric functions relating leaf parts and properties, the number of leaflets per leaf, the phyllochron, the leaf elevation angle, and the phytomer location of maximum organ length and leaf area per stem, were applicable to a range of sowing dates and to the main stem and branches. In contrast, information on parameters such as organ (internode, leaf, petiole, pod and flower) length, leaf area and phyllotactic angles, was valid for the main stem and branches of each single crop but varied with sowing date.

Allometric relationships between leaf parts were obtained to simulate the morphology of the faba bean leaves as leaflets and petioles (Ruiz-Ramos and Mínguez 2006). Figure 1 presents an example showing the relationship, for the main stem, between the lengths of the whole petiole (P) and the part of the petiole between the stem and the first pair of leaflets (A) for an autumn sowing. When stems 1 to 3 are considered together, the regression obtained is:

$$y = -3.46x + 82.3 \quad (R^2 = 0.77) \quad (1)$$

where y is the A/P ratio and x the leaf rank. Other morphological relationships can be found in Ruiz-Ramos and Mínguez (2006).

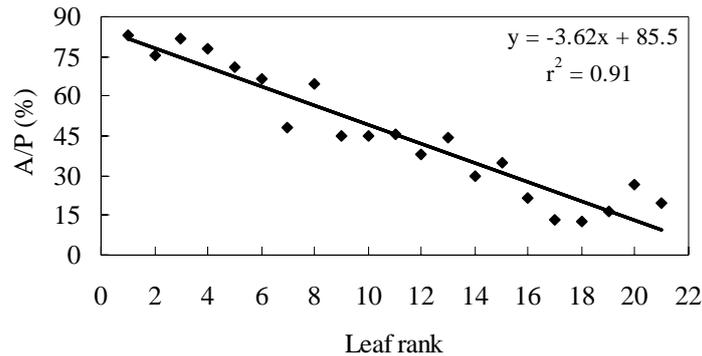


Figure 1. Ratio (%) of lengths of the first part of the petiole (A) (insertion of first pair of leaflets) to petiole (P), as a function of leaf rank for the main stem of autumn-sown faba bean

Variation and plasticity: number of organs

In faba bean, morphological variation is expressed by differences in the number, position and size of organs of individual plants of a crop. Such variation, required in FSPMs for realistic 3D simulations of crop structure (Prusinkiewicz 1994), can be observed at different levels of the canopy, viz.:

- intra-stem variation: variation in the number of leaflets per leaf, number of reproductive structures per node;
- intra-plant variation: variation in the number of leaves per stem or branch, number of nodes bearing reproductive structures, rank of the first node bearing reproductive structures, rank of the leaves where the number of leaflets per leaf changes;
- inter-plant variation: variation in the number of branches and plant height.

The morphology of plants also varies when sown in different seasons. This change, the morphological plasticity, is reflected in further variation of leaf and stem number per plant, the internode length distribution and the phytomer location of the longest internodes within the stem, and in the variation in phyllotaxis between seasons (Ruiz-Ramos and Mínguez 2006). To illustrate this, the final number of leaves can be related to the leaf appearance rate or its inverse, the phyllochron. The phyllochron remains constant and the same holds for the main stem and branches for 937 °Cd until the reproductive sinks become strong, but after this moment, leaf production rate and hence final leaf numbers differ among the stem and branches, and sowing dates (Table 1). The R^2 values for the relations between number of leaves and thermal time were high (0.85) up to 937 °Cd, falling to 0.59 afterwards.

There are several non-exclusive options able to deal with variation and plasticity in an FSPM when comparing sowing dates for variables other than those described with universal relationships. These include:

- a. variation through random variables and probabilities, building a stochastic FSPM; this method can provide a population of simulations;
- b. genotype descriptors, for instance, in variables such as stem number per plant;
- c. sowing season/date with associated sets of parameter values;
- d. plant population density with associated sets of parameter values;
- e. descriptive equations and relationships from PBMs that can capture part of the plant plasticity.

Table 1. Various features illustrative of canopy variation and plasticity

	Main stem	Branch 1	Branch 2
Phyllochron (°Cd) until 937 °Cd	57.8	59.2	66.7
Phyllochron (°Cd) from 937 °Cd	103.1	153.8	128.2
Delay between stems (°Cd)	-	116	232
Phyllochron factor	1	2	4
Phyllotactic angle			
A (°)	93.9 (29.1)a	97.9 (42.3)a	93.7 (41.9)a
W (°)	122.7(35.9)b	122.3 (21.7)b	124.6 (24.2)b

Values of angles are means with their standard deviation within brackets. When not specified, data were the average of autumn (A) and winter (W) sowings. Values followed by the same letter are not significantly different (F test at 95% of confidence level). Phyllochron factor: multiplicative factor relative to main stem phyllochron to obtain phyllochrons of branches 1 and 2. Phyllotactic angle: angle between the petioles of two consecutive leaves.

Specific experiments are required for different sowing dates and crop densities in order to implement options c) and d). The probability distribution of the number of branches can be expressed by option a) until option d) has been implemented. To illustrate, two of the methods mentioned above are used to represent the variation of the number of leaflets per leaf in a faba bean stem in Figure 2.

The first approach (Figure 2, Main stem), corresponding to method a), considers several stem regions with an increasing number of leaflets per leaf: from 2 (bottom stem region) up to 7 (upper region). The leaf ranks where regions change are defined by a random variable, with a mean and an SD, allowing for variation among stems and plants.

The second approach, corresponding to method e), descriptive equations, considers a stem in two stem regions. First a region of leaves with a constant number of leaflets per leaf (Figure 2: $y=2$, where y is the number of leaflets per leaf) where other stems arise, and a second region modelled by a logarithmic regression of the number of leaflets per leaf as a function of leaf rank ($R^2=0.95$, Figure 2). Variation can be considered here introducing random variables in the coefficients of the

regression and also to calculate the leaf rank of the transition between regions, combining methods a) and e).

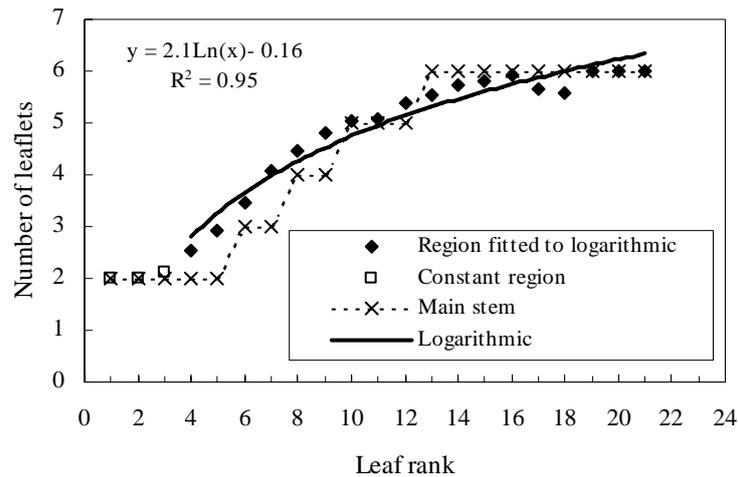


Figure 2. Number of leaflets per leaf as a function of leaf rank quantified in two ways: (i) increasing leaflet numbers for consecutive stem sections as exemplified with data from the main stem (broken line), and (ii) an initial region with constant leaflet numbers and a transition to a logarithmic relation with leaf rank number (full drawn line). Data are means of two sowing dates and, when not specified, refer to the main stem and branches 1 and 2

The driving role of structure

FSPM building offers guidance to the modeller, especially for plants without a fixed ‘final structure’, consistent with the proposition that ‘a model must look like a plant to function like one’. The more mechanistic the FSPM, the more this statement becomes valid. For an FSPM to succeed, the right steps are needed because the structure imposes limits to the application of the functions, and their outputs modify the structure. The structural part of the model establishes where an equation has to be applied, and the functional part defines which equation and under what conditions. This feedback results in the functional growth of structure, especially useful in indeterminate plants with variable branching and final structure, as in faba bean. Instead of searching for rules to stop growth, we can obtain a final structure as a result of a combination of processes and organ position. For instance, the timing of organ senescence depends among other factors on its position within the plant. Thus, “the L-system provides the basic conceptual and program structures within which functional relationships can be connected, playing a comparable role that physical plant structure provides for physiological processes”, i.e. specifying where an equation has to be applied or directing the information flow across the stem (Ruiz-Ramos and Mínguez 2006).

THE ALAMEDA MODEL

ALAMEDA is an FSPM of the faba bean canopy whose structural part uses an L-system that is stochastic, differential (i.e. the time step is defined as a differential interval of time, dt) and sensitive to environment. The complete model code can be found in Ruiz-Ramos (2003) and is available from the authors. Ruiz-Ramos and Mínguez (2006) present model parameterization and verification as well as the general methodology to assign functions to the L-system structure through the linkage to the organ growth model SAF (Durand et al. 1999). The SAF (Simulation d'Allongement des Feuilles) model is based on equations used to simulate the growth of kiwi fruit (Gandar et al. 1996) and has been applied to grass leaf elongation and phyllochron (PH) (Fournier et al. 2005). SAF consists of sigmoidal differential equations. Each organ is organized in three one-dimensional zones: division (DZ), elongation-only (EOZ) and mature (M) zones. Growth results from the allocation of assimilate fluxes from one zone to another, depending on an elongation rate function of temperature.

ALAMEDA was built according to the following assumptions: 1) the main stem and branches of a plant behave similarly; 2) all internodes and all leaves can be simulated with two sets of SAF parameters (one for internodes and another for leaves) and 3) environmental response is limited to temperature and day length.

Figure 3 describes the inputs, outputs, sub-L-systems and subroutine organization, and the relationships among these model components of ALAMEDA v.3.0 and components currently being incorporated. Four types of inputs are considered for the parameterization of the L-system and the SAF model: constants, probability distributions, random variables and functions. The L-system is organized in one main L-system that drives stem growth, one sub-L-system for the leaf growth and a second sub-L-system for reproductive organs.

Modules of vegetative organs or parts of organs of these L-systems invoke the ALAMEDA subroutine, SOLVFABA (equation SOLVer for FABa bean) at every time step. SOLVFABA considers the initial conditions of the L-system for every time step, solves the differential equations of the SAF growth model, and calculates the initial conditions of vegetative-organ dimensions for the next time step. The subroutine SOLVFABA also contains the functions used to calculate leaf area.

Organ length as a model output

In ALAMEDA, lengths of mature organs are model outputs achieved with individual subsets of parameters for leaves and internodes, respectively. There are no parameters to limit organ size; rather growth stops as each organ senesces. This contrasts with PBMs of faba bean in which maximum organ lengths are model inputs, as in Boote et al. (2002) and Pachepsky et al. (2004) for maximum leaf size, node number and plant height in soybean. The same technique is applied to maximum size of blade and sheath in an FSPM of wheat (Fournier et al. 2005).

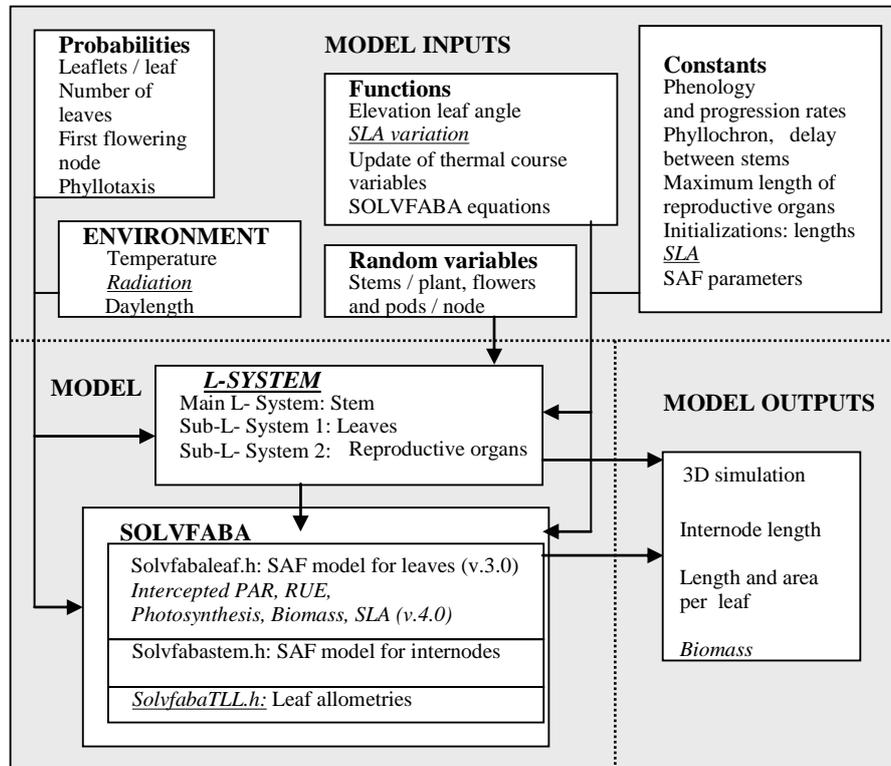


Figure 3. Components and information flow in ALAMEDA v.3.0. Components currently being modified or added are written in italics underlined while future extensions for version 4.0 are written in italics

Current extensions

Introducing other micro-environmental variables: radiation

ALAMEDA localizes the leaf area spatially, vertically through internode length and horizontally through phyllotaxis. Gautier et al. (2000) have shown the influence of local light conditions on clover leaf position and elevation, and this could be the starting point for an investigation on the role of radiation interception to explain the difference of ca 30° that has been observed between the phyllotactic angles of faba bean plants of different sowing dates (Table 1). Radiation may also help to simulate organ number more mechanistically because the light conditions can be used to explain branching in clover (Gautier et al. 2000) and tillering in wheat (Evers et al. 2005).

For these reasons, radiation is the environmental variable chosen to extend ALAMEDA with a linkage to the Nested Radiosity Model (Chelle and Andrieu 1998). The interface, Caribu (Chelle 1998), allows that model to be connected with L-system-based models under L-studio (Prusinkiewicz 2000) by means of the

environmental symbol ?E (Měch 1997) of the L-system language. This task is currently underway.

Calculation of a varying SLA

The SAF model provided simulations of one-dimensional growth and helped to develop the methodology for linking growth functions to ALAMEDA. The simulation of radiation interception (under construction), however, will allow computation of biomass using radiation-interception functions incorporated in models mentioned in the section "*Sources of physiological functions: existing model*". These can substitute the equations of SAF that are based on temperature. This new approach presents biomass as the primary growth output from which leaf area can be calculated using specific leaf area (SLA). SAF will still be retained to calculate internode growth until the simulation of biomass partitioning can be accomplished. The modification of the conceptual scheme of this approach for a new version of ALAMEDA (v. 4.0) is shown in Figure 3.

This approach requires computation of biomass at the organ level, thus avoiding the problem of translating mean crop magnitudes, usually per unit surface area, that are provided by most crop PBMs (section "*Sources of physiological functions: existing model*"). It does, however, require accurate determination of SLA and its variation within the plant and during the crop cycle. Several authors have reported such variation in SLA (Stützel 1995a; Boote et al. 2002) while the CROPGRO PBM introduces some variability by relating SLA to mean air temperature (Boote et al. 2002). This relationship has been incorporated in ALAMEDA as follows:

```
#define SLAo 0.0285 /*m2 g-1*/
if(T<2) {SLA=0*SLAo;}
if(T>=2 && T<=20) {SLA=(0.04167*T+0.16667)*SLAo;}
if(T>20) {SLA=SLAo;}}
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where *T*: daily mean temperature (°C), SLAo: initial SLA (m² g⁻¹).

Current work focuses on methods to update the value of SLA. One possibility is to calculate a new SLA as a mean of several days' values and to apply it to the biomass generated during this period. For this, more work is needed to fix the optimum interval for calculation, together with further work to establish relationships among leaf area and biomass according to leaf rank.

DISCUSSION AND PROSPECTS

Useful tips from and for other legumes

Modelling of other plants of indeterminate growth habit, and especially of other annual grain legumes, can share problems and solutions with faba bean modelling.

Soybean has been the object of numerous useful studies. For instance, the root system of soybean has been described applying, among others, a pipe model (Tanaka et al. 1994) that could be used in ALAMEDA. Morphological descriptions

of soybean also include leaf allometries and functions (Pachepsky et al. 2004) with different sets of parameters for individual soybean cultivars, one of the approaches proposed to deal with faba bean plasticity (see section "*Variation and plasticity: number of organs*"). Also for soybean, the diurnal course of leaf behaviour in response to water stress has been studied (Olioso et al. 1996), providing a reference for analogous studies in faba bean. FSPMs could reflect this diurnal course through hourly or shorter time steps. Tips for faba bean response to climate change could be extracted from impact studies on soybean response (e.g., Haskett et al. 1997).

The number of reproductive nodes has been studied in peas by Dumoulin et al. (1994), and modelled by Roche et al. (1998) depending on environmental, nutrition and genetic factors. The approaches used there are generally applicable to other indeterminate species, and could help to simulate the canopy composition of faba bean more mechanistically.

The structure of ALAMEDA, organized in sub-L-systems associated to organ types, supports that exchange and/or modification of organ responses between other legume models. For instance, the sub-L-system that simulates leaf growth in ALAMEDA can be modified to simulate leaves in other beans while the other parts of the model remain untouched. This ability contributes to the development of models for the growth of vegetative organs that have application across species, a need identified by Birch et al. (2003).

Sources of physiological functions: existing models

There are various models that can readily provide functions to be incorporated in an FSPM of faba bean such as ALAMEDA. The CROPGRO simulation model for legumes (Boote et al. 1998a; 1998b) has recently been adapted to simulate the growth and development of *Vicia faba* (Boote et al. 2002). In that work, parameters were developed for two varieties of faba bean from field experiments and data compiled from the literature. The CROPGRO subroutines, or part of them, can be linked to ALAMEDA-type models, and part of their outputs can be referred to individual organs. An example currently being implemented has been shown in the section "*Calculation of a varying SLA*".

The Stützel (1995a; 1995b) and Turpin et al. (2003) models accumulate dry matter according to radiation interception that is then partitioned to individual organ types depending upon phenological development. Manschadi et al. (1998) extended the Stützel model to include water balance and crop water stress. The interest of these models is that their relationships were developed specifically for faba bean.

Dennet and Ishag (1998) applied an expo-linear growth model to faba bean, pea and lentil, providing for contrasting growth habits, in a model in which growth rate is proportional to intercepted radiation. The interest of this model is the consideration of different sets of parameters corresponding to various crop densities (see section "*Variation and plasticity: number of organs*").

Useful functions can also be extracted from the cropping systems model CropSyst (Stöckle and Nelson 1994) since it can incorporate physiological

parameters with the characteristics of faba bean or other legumes (Díaz-Ambrona 1999).

Future extensions of ALAMEDA

When the connection with the radiation model is complete, attention will turn to the inclusion of a vertical profile of temperature within the canopy; with that it will be possible to include functions simulating other processes (photosynthesis, assimilate partitioning, water balance) of organ response to microenvironment.

Currently, ALAMEDA is able to provide values of up to ca 50 variables, referable to each of ca 3500 organs, at each time step. The current and future extensions of the program make obvious the need for a subroutine to deal efficiently with the numeric outputs.

CONCLUSIONS

The FSPM ALAMEDA is organized in sub-L-systems associated to organ types, allowing individual simulation of stems, leaves and reproductive structures that can have generic application across species. The modules define the range from leaflets (for an accurate leaf area simulation) to stem (cluster modules that compose the crop).

The functional simulation of growth provides a feedback that improves our understanding of crop processes. For this reason, success in representing faba bean plasticity will assist modelling work on other plants of indeterminate growth habit or multiple branching.

ALAMEDA is a functional-structural crop model that has been developed with a methodology that allows for incorporation of functions for a more mechanistic simulation of faba bean growth. For this, progress requires inclusion of organ microenvironment and variation within the plant and through time of plant properties such as SLA. A detailed structural simulation at organ level can provide the basis for simulation of assimilate partitioning, incorporating source–sink relationships with proximity weighing.

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