Pascal Dabadie, Philippe de Reffye, & Pierre Dinouard*: **Modelling Bamboo Growth and Architecture:** ***Phyllostachys viridi-glaucescens*** **Rivière A. et C.**

Introduction

The purpose of this study is to describe the application of a botanical and mathematical method to determine basic parameters of plant growth and architecture. The collected information is comprehensive enough to obtain a realistic simulation, by means of complex software for plant modelling and representation [Reffye, et al., 1987]. Simulation results can be expressed by pictures of plants; they are botanically correct and reproduce individual variations. For agronomic purposes, cotton, coffee and lychee have already been studied using this method.

Although qualitative analyses can be used to describe plant growth mentally, they provide only part of the information necessary for correct computer modelling. Only mathematical analysis makes it possible to extract the basic parameters of plant architecture, otherwise unascertainable by observation only. Nevertheless, the botanical approach to the study of plant architecture is an essential prerequisite for statistical analysis, without which it is impossible to know what to measure.

Material and Methods

The study focused on *Phyllostachys viridi-glaucescens* Rivière A. & C., in the Prafrance Bamboo Plantation, at Anduze, South of France. The architectural analysis is made by observation and drawing. As the mathematical measures focus on internode numbers, field work mainly consists of noting the plant ramifications on sketches and marking the axis internode. Geometric data such as phyllotaxis, insertion angles, evolution of diameters and internode lengths are also noted. These measures required the cutting of about thirty culms. Each year, the new culms of the bamboo plantation are marked with different colours of paint spots. The knowledge of culm ages proved to be a very useful information. We thank Mr. Crouzet, owner of the bamboo plantation, for his material help and advice during the field study.

In the laboratory, data processing was made with a spread sheet connected to a micro-computer. The parameter adjustments and Monte-Carlo simulations have been calculated by the CIRAD mini-computer (DATA GENERAL MV 20000). The mini-computer was used to produce synthetic pictures with the plant simulation software; images were visualized and finalized on a high level graphic station (Silicon Graphiq's IRIS 4D). The pictures presented here were produced by a laser printer.

Principles of the Mathematical Model

This is only a brief presentation and we invite the reader to refer to previous studies regarding other plants [Reffye, 1979; Reffye, et al., 1987; Costes, 1988].

The question is to determine parameters of a general growth model for a ramified system. The plant is compared to an assembly of basic elements consisting of internodes (axis

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section) topped by nodes (ramification area including one leaf or more with axillary buds). Time is discretized into elementary clock pips. At each pip, a decision is made concerning the evolution of each apical meristem which can die, form an additional element or remain latent.

After sowing, two plants of the same species become quickly differentiated while keeping a family likeness. Originally identical axes of these two plants will develop with variable vigour. Stochastic simulation accounts well for individual variations: the evolution of each meristem is found by using the Monte-Carlo method, which involves comparing the probability of an event (death, growth, ...) with a random number between zero and one.

Method of Estimating Parameters

The "dimension" of an axis is the amount of tests to which it was submitted, which is its age expressed in clock pips. Given an axis with a dimension equal to N and an elongation probability equal to P, the length of an axis population will be distributed according to a binomial function, $B(N;P)$.

Conversely, axes of identical size can have different dimensions. The probability that an axis with K internodes is the result of N tests is given by a negative binomial function.

$$P(X=K) = C_{N-1}^{N-K} P^K (1-P)^{N-K}$$

Axes of different orders generally grow at different speeds: their clock pips are not of the same length. The W_i clock ratio is defined as the ratio between the time unit for the $n-1$ bearing axis and for the order n axis.

When the end of a ramified axis is observed, it is possible to estimate three basic parameters : P_1 and P_2 elongation probabilities for main axis and axillary axes and W_i clock ratio*. At K internodes from the top, if P_1 and P_2 and W_2 are constant, it is demonstrated (Reffye, et al., 1987) that the average theoretical variance of the pair formed by internodes of two order 2 axes separated by L internodes is equal to

$$V_i = \frac{(K+L/2)}{P_1} W_2 P_2 (1-P_2) + \frac{P_2^2 W_2^2 L (1-P_1)}{2P_1^2} + \frac{P_2^2 W_2^2 L^2}{4P_1^2}$$

V_i is estimated by using the mean of the variance of the paired axes of the sample. For practical reasons, L must be low (1 or 2) for quick convergence towards the theoretical value. Moreover, at K internodes from the top, the Expected value of x, E(x), and the Variance of x, V(x), are:

*The suffixes correspond to the axis ramification order. Conventionally the trunk of a culm is here the ramification order 1, although originating from a ramified rhizome.

$$E(X) = \frac{KP_2W_2}{P_1}$$

$$V(X) = \frac{KP_2(1-P_2)W_2}{P_1} + \frac{K(1-P_1)W_2^2P_2^2}{P_1^2}$$

From these equations, we arrive at the following estimators:

$$P_1 = 1 - \frac{1}{E^2(X)}\left\{\left[V(X)-V_l\right] + \frac{L}{2}\left[\frac{LE^2(X)}{K} + V(X)\right]\right\}$$

$$P_2 = \frac{1}{E(X)}\left\{\frac{L}{2K}\left[V(X) + \frac{LE^2(X)}{K}\right] - V_l\right\} + 1$$

$$W_2 = \frac{E(X)P_1}{KP_2}$$

The precision of these parameter estimators is measured by numerical simulation, as the method based on Maximum Likelihood is difficult to use here.

Application To Bamboo

Phyllostachys viridi-glaucescens Rivière, A. & C. is a tall bamboo from central China, where it grows approximately fourteen meters high, as at Prafrance. It is a leptomorph bamboo [Dahlan & Valade, 1987; McClure, 1966], the rhizome presenting large horizontal axes, with laterally located culms. A characteristic of the *Phyllostachys* genus is that ramified nodes generally bear two branches of unequal size (Fig. 2). The larger branch is called here "A" and the shorter "B". In fact, the B axis is a ramification of A, the first internode of which is very short; this makes it appear as though A and B come from the same axis. The internodes located at the beginning of the ramification area often bear an A axis only, while those located at the end of the axis can have three axes, A, B, and C, C being an axillary axis of B. The culm diameter is maximal not at the base, but at a height of approximately three meters. The first year, culms ramify up to the order four, sometimes five. They bear deciduous sheaths. All the axes terminally bear two to five leaves joined by their sheaths. The first year, culm development is entirely monopodial. The following spring, leaves fall, the last leaves remain joined together and carry down with them the clasped axes part. At the same time, short leafy axes grow from the axillary buds of internodes located below the leaves of the previous year (Fig. 1). Rhizome growth was studied at Prafrance for a closely related species: *Phyllostachys viridis* (Young) McClure [Dahlan & Valade, 1987].

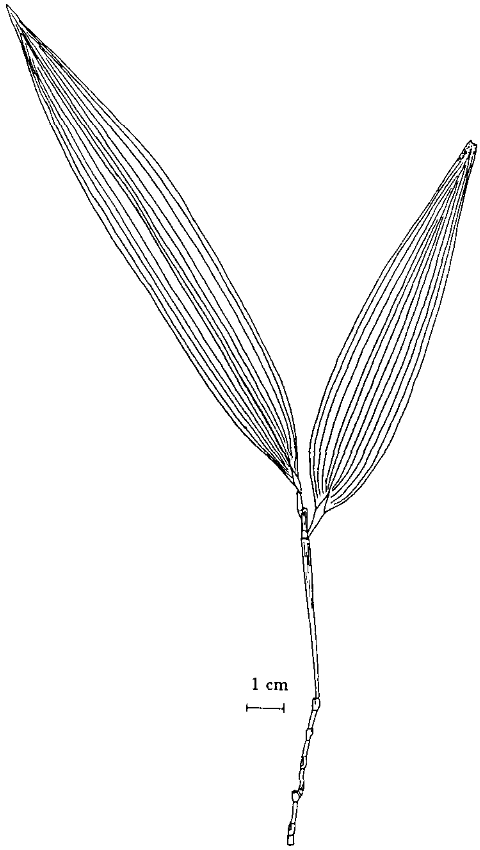

Figure 1. Short axis.

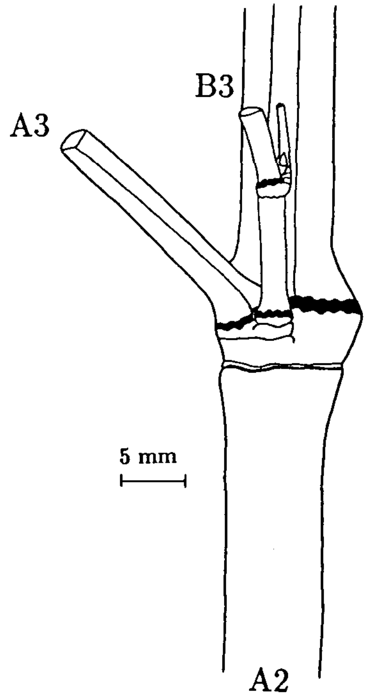

Figure 2. Node detail.

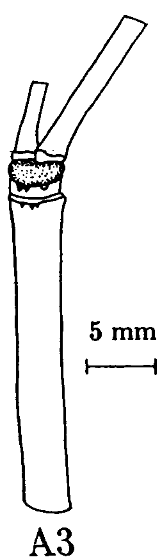

Figure 3. Axis damaged during growth.

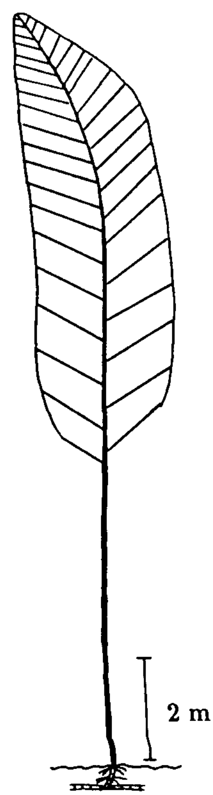

Figure 4. Culm figure.

Study of First Year Growth

The bamboo canopy is conical at its end and becomes cylindrical below (Fig. 4). All this happens as though the order 2 axes have a finite dimension and stop growing while the upper order 2 axes are still growing. Analysis of the tops requires the culm axes to be stopped simultaneously; it must be carried out for the conical part. All the axes located at the end of the canopy stop growing together and then calculations are not disrupted. The fact that plant growth is completely stopped (for example in winter) will have no influence on parameters, because the clock pips measure a biological activity and not physical time. It appears that tops are conical up to twenty internodes from the top. The internodes of the A3 axes located at K and $K+L$ internodes from the top, with K varying from 8 to 20 and $L=1$, have been counted on 13 culms, for a total of 136 axis pairs. We obtain:

$$0.59 < P_1 = 0.79 < 0.92$$

$$0.91 < P_2 = 0.94 < 0.96$$

$$0.56 < W_2 = 0.73 < 0.86$$

The asymmetrical confidence interval is given for the risk $\alpha = 5\%$. It should be noted that A2 axes grow slower than the A1 axis. This method is called the "top method."

Results for B2 Axes

Although the B2 axes are in fact ramifications of A2 axes, they are morphologically different from other axes of order 3 and they must be dealt with separately. On average, the first B2 axes only appear at 5 internodes from the top; consequently their elongation is assumed to be delayed at a rate of $\frac{4}{P_1} \approx 4$ clock pips. The bias introduced in the estimation is eliminated by replacing K with $K-4$. We obtain:

$$0.23 < P_1 = 0.74 < 0.99$$

$$0.87 < P_{2B} = 0.95 < 0.98$$

$$0.24 < W_{2B} = 0.71 < 1.04$$

The same calculation is carried out at a higher order between the A2 and A3 axes from 9 to 15 internodes from the top for 128 pairs, with the following results:

$$0.91 < P_2 = 0.95 < 0.99$$

$$0.96 < P_3 = 0.99 < 1$$

$$0.65 < W_3 = 0.67 < 0.7$$

Between the A3 and A4 axes, it it found that:

$$P_3 = 0.95$$

$$P_4 = 1$$

$$W_4 = 0.5$$

From too close to the top, the Monte-Carlo method cannot be used any longer to calculate the confidence interval, the estimation being biased by the approximation of real numbers by whole numbers.

Calculation of Maximal Dimension for A2 and B2

If the cylindrical area is generated by a finite dimension, the internode number for the A2 must be distributed according to a binomial function $B(N;P_2)$. The following values are estimated from the observed distribution:

$$N = 21$$

$$P_2 = 0.9 \pm 0.07$$

which is consistent with the P_2 estimation by using the top method. Thus, the A2 axes reach a limiting value of their dimension.

Distribution of A2 Lengths						
K	16	17	18	19	20	21
Observed Number	3	7	14	19	20	11
Theoretical Number	3.6	7.1	14.4	20.7	18.9	8.2

For the $B2$ axes, the binomial function $B(21;0.94)$ is obtained. This is a second way of estimating the probabilities of A2 axes elongation. It is profitable, and it is often possible, to apply several different methods in order to estimate the same parameter.

Death of Axes During Growth

An important number of order 1 to 3 axes are suddenly terminated at a node level (Fig. 3). However, an old axis never breaks at this place. It is in fact the scar of the abscission resulting from the death of the elongated apex. It seems that the apices die mainly because of the knocking together of culms; sometimes, they abort spontaneously.

In the case of A2 axes, the area with a finite dimension is considered. If the death probability is constant on the axis, the distribution of axis length is governed by a function which is a combination of binomial and exponential functions. The generating function is:

$$G(z) = (1-P_L)\left\{\frac{1-\left[P_L(1-P_2+P_2z)\right]^N}{1-P_L(1-P_2+P_2z)}\right\}+P_L^N(1-P_2+P_2z)^N$$

and the expression for probabilities is:

$$P(X=K) = \sum_{i=K}^{N-1} C_i^K P_2^K (1-P_2)^{i-K}(1-P_L)P_L^i + C_N^K P_2^K (1-P_2)^{N-K} P_L^N$$

and:

$$E(X) = \frac{P_2 P_L}{(1-P_L)}(1-P_L^N)$$

$$V(X) = \frac{P_2 P_L}{(1-P_L)^2}\left[1-P_L(1-P_2)-(1-P_L)(2NP_2+1)P_L^N-P_2P_L^{2N+1}\right]$$

with N = maximal axis dimension
P_2 = elongation probability
P_L = life probability

Number of Internodes	0	1	2	3	4	5	6	7	8	9	10
Samples of A2 Axes	9	5	4	0	1	1	1	6	3	0	5
Theoretical Values	5	4.8	4.7	4.5	4.4	4.2	4.1	3.9	3.8	3.7	3.6
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Simulation From The Estimated Parameters	4	4	6	3	6	2	3	6	7	2	2

Number of Internodes	11	12	13	14	15	16	17	18	19	20	21	22
Samples of A2 Axes	4	5	2	4	3	5	9	9	24	24	19	6
Theoretical Values	3.4	3.3	3.2	3.2	3.4	4.3	6.9	11.9	18.1	20.9	15.7	5.7
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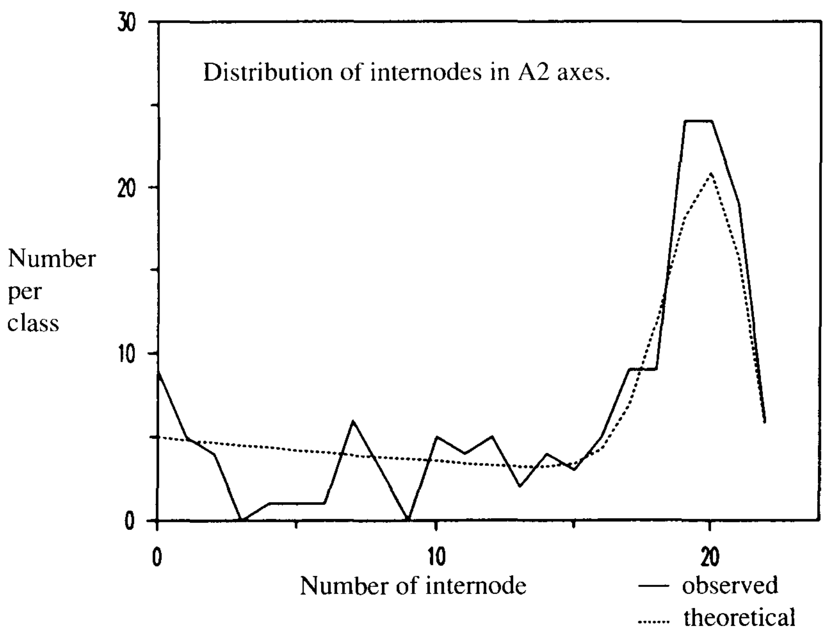
Simulation From The Estimated Parameters	5	2	4	0	2	6	5	14	16	27	17	6



Distribution of internodes in A2 axes.

The decreasing exponential function due to growth troubles at the beginning of the axis and the binomial function resulting from breaks at the end of the axis should be noted. The value of 22 is a limit for this dimension. With the value of N known, those values of P_2 and P_L are searched for that minimize the χ^2 for the comparison with the sample. A correct adjustment is found with the values:

$$P_2 = 0.89 \pm 0.02$$

$$0.995 < P_L = 0.97 < 0.98$$

Calculations have not been extended to the other types of axes, but the function is very likely identical with parameters of different values.

Dimension of the Order 1 Axis

Of course, the bamboo seed does not build a 14 meter culm during the first year, but higher and higher culms will develop each year, until they reach a maximal size. This process, frequently found among rhizomatous plants, is described as an expression of the "establishment growth" [Tomlinson & Esler, 1973].

The studied plantation is the result of cuttings planted in about 1850 which never flowered. A considerable fraction of culms are smaller (between 5 and 10m) and more spindly than the average. Given the plantation age, it is not due to the establishment growth (it is estimated that the rhizomes produce culms of maximal size after 10 years) and their positions on the rhizome are unknown. In order to work on an homogeneous population, all the calculations focused on culms considered to be of maximal size.

According to the model, the number of internodes for the A1 axes of a sample must follow a binomial function $B(N;P_1)$. By estimating N and P_1 from a sample of 16 stems, we obtain:

$$P_1 = 0.82 \pm 0.05$$

$$64 < N = 68 < 73$$

The estimation is comparable to $P_1 = 0.79$ obtained by the top method. The A1 axes therefore have a finite dimension.

Base Effect

The canopy base has the shape of a reversed cone and the length of order 2 axes gradually increases approaching the median area, the elongation and death probabilities and the dimension of which have been calculated. This phenomenon called "base effect", quite usual among trees, can be translated by a variation of the maximal dimension of the A2 axes. A regression shows that this variation is linear. The dimension of A2 axes is from 16 to 17 internodes from the top base* and increases linearly up to the limit of 22, reached at the 21st internode.

*The base is defined as the internode bearing the upper root verticil.

Study of the Second Year of Growth

After the falling of first year leaves, leading to the falling of apexes, regrowth begins at the level of the buds located on the last axis internodes. They produce short leafy axes, called "SA1"(short axes of the first generation).

Law of SA1 Appearance on A4 and A5

One to five SA1s appear at the end of the axis so that SA1s always fill the last *n* nodes of the bearing axis. Probabilities Pb_i that an axis bears *i* relays are calculated. These probabilities vary according to the height in the canopy.

Number of SA1s	0	1	2	3
Top of the Canopy	0	0.25	0.69	0.06
Middle	0	0.57	0.43	0
Bottom	0.12	0.78	0.1	0

It can be seen that the number of relays increases from the base to the top. Many SA1+s branch out at the end of the second year and bear short axes similar to SA1. Consequently there are two growth periods during the second year (Fig. 6). The SA1 bear 0 to 3 SA1+, grouped at the end as for the SA1 themselves on their bearing axis. Given Pb_i, the probability that a SA1 branch out *i* SA1+:

Number of SA1+	0	1	2	3
Top of the Canopy	0.87	0.09	0.04	0
Middle	0.18	0.44	0.26	0.02
Bottom	0	0.75	0.20	0.05

This gradient is the opposite of the previous one, the SA1's being more frequent at the canopy base. These processes have the effect of multiplying the leaf number by the following coefficients:

Top of the Canopy:	2.1
Middle:	2.9
Bottom:	2.1

That is, 2.4 on the average. This definitely shows that the first year is principally devoted to the development of bearing axes and the next years are devoted to the extension and renewal of the chlorophyllous system.

Culm Evolution After Two Years

The evolution after the second year has not been studied statistically and only a qualitative approach is considered here. A culm can live at least ten years. The foliage cannot grow indefinitely as it does during the second year. Its bulk becomes stationary at about the third year, then decreases until the culm dies. During the ageing process, axes of order 1, 2, and 3 gradually dry out from their ends, while the A2 and B2 of the base die and are self-pruned. This results in grouping together living parts into a very dense foliage ball located in the upper third of the canopy. Renewal of the foliage is provided by the previously mentioned processes, but also by reawakening of the latent buds. These buds are located at the base of the short axes and axes of order 4 (Fig. 5). Some buds can remain latent for at least ten years. The appearance of two generations of short axes in the same year has only been observed to occur during the second year. Contrary to an accepted idea, for this species at least, counting the order of the short axes is not sufficient for finding the culm age, since it is difficult to know if one or two generations of short axes have been produced each year. However, the following method, which is only valid for this species in the Prafrance plantation, can be used: the number n corresponding to the maximal piling-up of short axes is evaluated on the ramifications coming from the top. The same evaluation is made on the ramifications coming from the base, with a maximum equal to $n+1$ (because of the doubling which is common during the second year). The age is then equal to $n+1$. In practice, age determination for old culms is awkward.

Simulation of Bamboo Growth

Data collected on a plant by using this method are accurate enough to simulate its growth step by step. According to the simulation software, the apical meristems created are submitted to death, elongation and ramification tests at each clock pip. A list of interrelated internodes is therefore obtained for each given age. At the same time, the software [Jaeger, 1987] calculates the space position of each created element, using parameters such as phyllotaxis, ramification angle, internode length or wood elasticity for this purpose. Therefore, a complete space description of the plant is available at the end of the calculation. This can be used to obtain an image or begin calculations so as to evaluate wood production or solar interception, for example. The image, in conjunction with statistical adjustments, allows for a very efficient validation of the model (a lifelike picture does not prove that the modelling is right, but a bad picture indicates a deficiency of the modelling).

The software was created by Philippe de Reffye for the agronomic study of coffee [Reffye, 1979]. It was then further developed by Marc Jaeger (Jaeger, 1987), in order to make it more efficient and capable of producing synthetic images.

Conclusion

As the graphical and numerical simulation results have proven satisfactory, the original hypotheses (elongation per internode, time quantification, Monte-Carlo) are therefore valid. If the quantitative study of culm architecture has been completed, the studies of the rhizomes, of the early stage and of the flowering stage, remain to be done. The analysed data are characteristic of the studied plot. They can therefore be different in other places or at other development stages. Compared to plants previously studied using this method, the original feature of the bamboo is the finite dimension of its axes. Moreover, there is a sudden change from a quick monopodial growth to a slow sympodial one. Processes of culm building and leaf renewal are probably similar to those of other bamboos. Indeed, the problem to be solved is identical: how to build a tree without cambium?

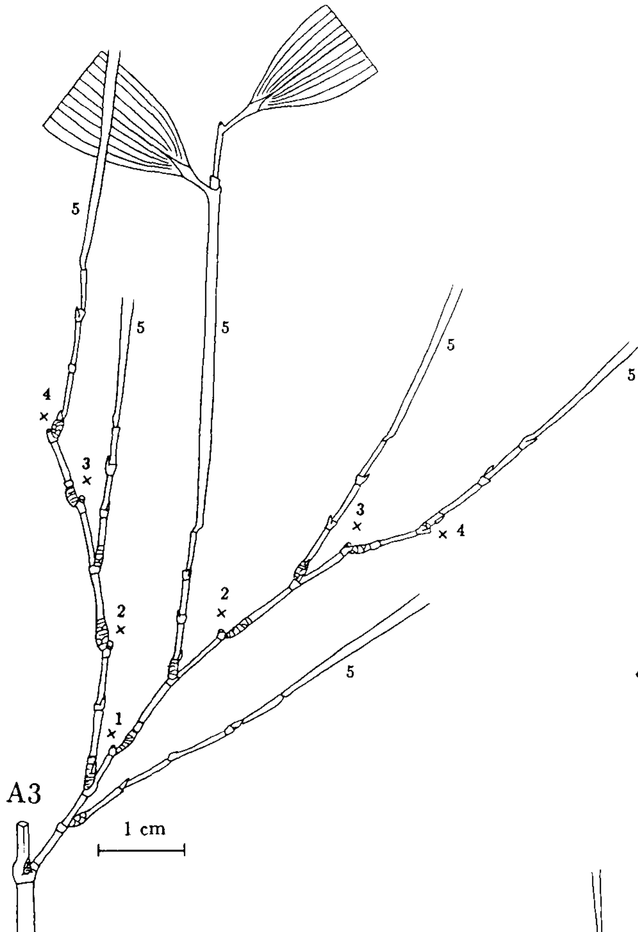


Figure 5. Five year old branch, (only one short axis grows the second year). It can be seen that some buds stay latent for several years.

Numbers stand for the year of axis formation.

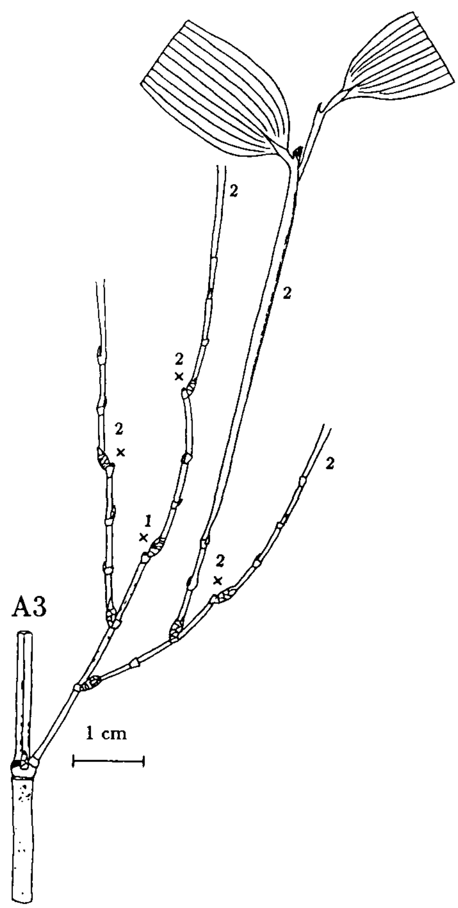
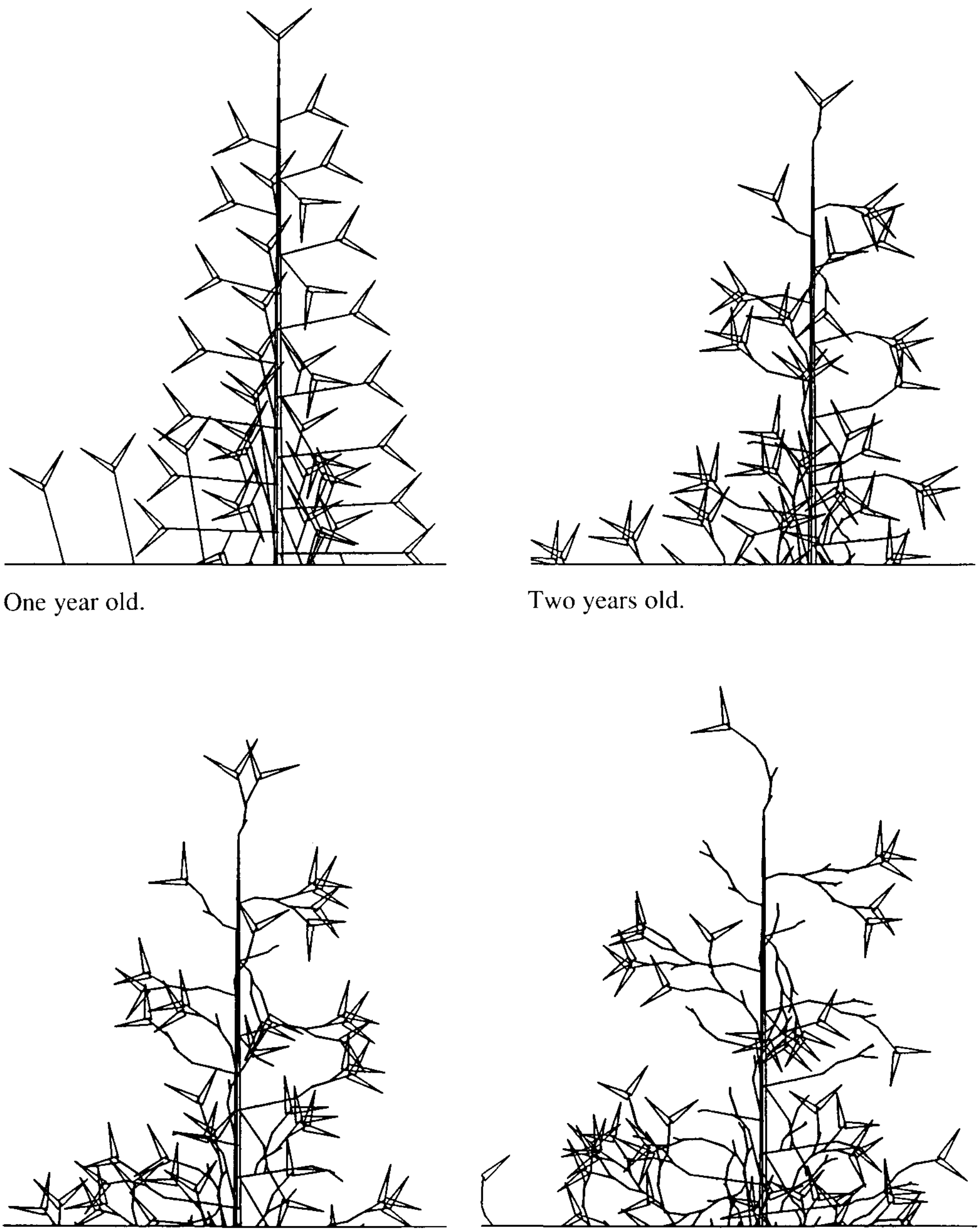


Figure 6. Two year old branch (two short axes the second year).

Images Produced by the Simulation Software

These representations integrate all the results of the measures made in the field.



One year old. Two years old.

Three years old. Four years old.

Figure 7. Evolution of an order 2 axis and its ramifications. Top view.

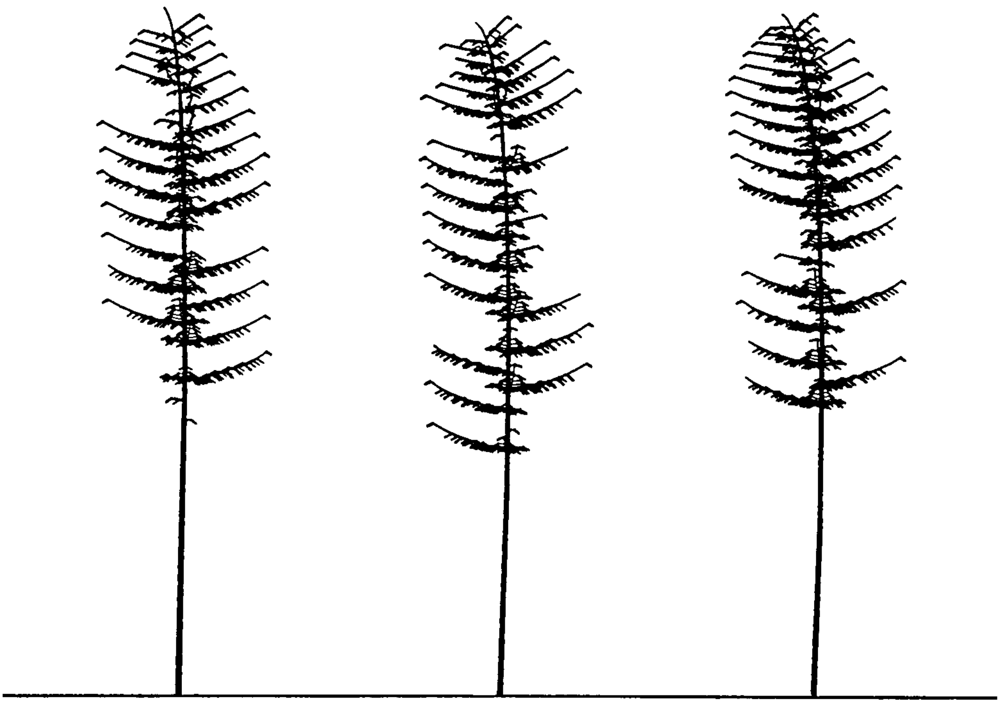


Figure 8. Three different culms of one year old. The three culms have been built according to the same functions; only the random number generation varies. Accidents on the order 2 axes are clearly visible.

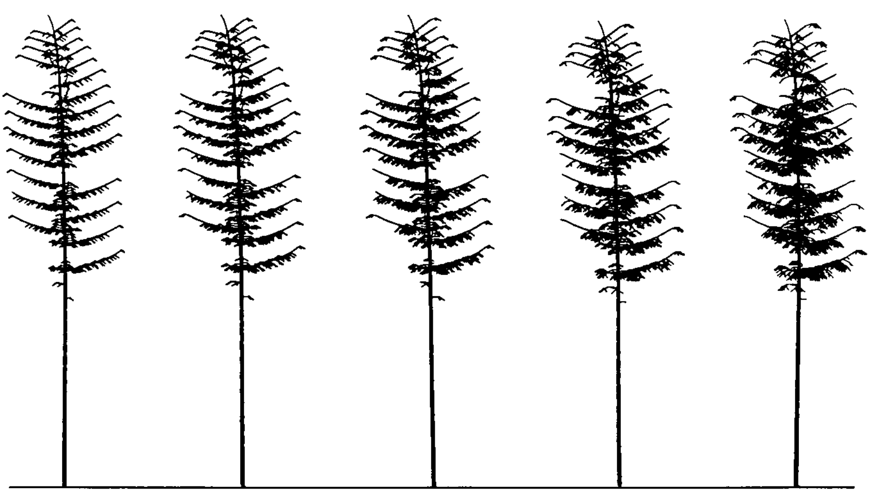


Figure 9. Ageing of a culm. The increase in the amount of leaves is obvious.

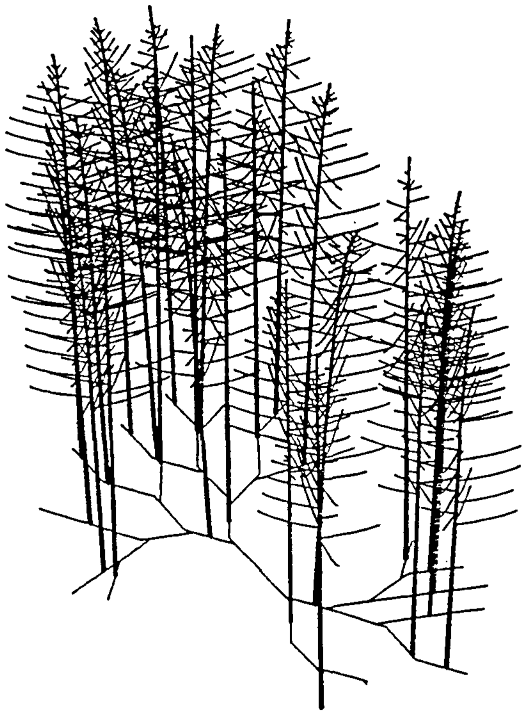


Figure 10. Rhizome system. The currently studied rhizome [Dahlan & Valade, 1987] is still too poorly known, particularly in a quantitative way, to be properly represented. Gradual development of creeping axes is not taken into account here and the conditions of appearance on the rhizome are unknown.

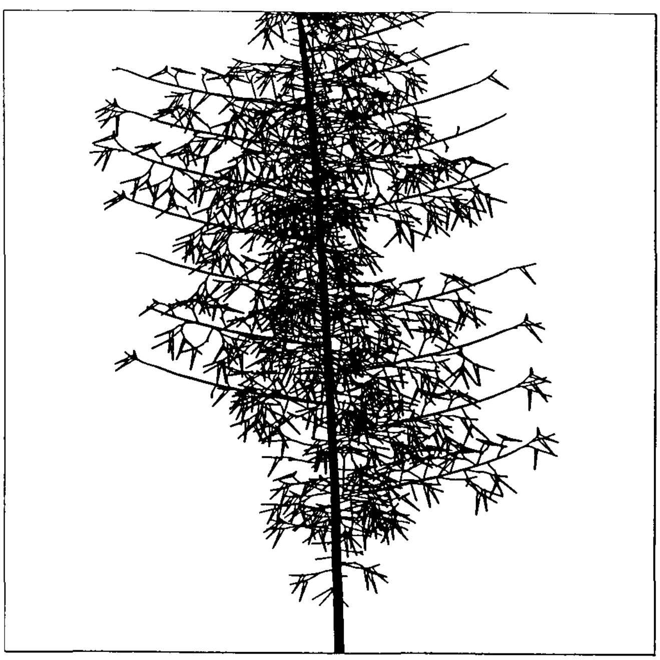


Figure 11. Detail of the top.

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