J. AMER. SOC. HORT. SCI. 122(1):53–62. 1997.

Modeling the Sylleptic Branching on One-year-old Trunks of Apple Cultivars

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ADDITIONAL INDEX WORDS. breeding, feathers, stochastic modeling, hidden semi-Markov chain

ABSTRACT. **The structure of 1-year-old trunks resulting from sylleptic branching are compared among apple (*Malus domestica* Borkh) cultivars with diverse branching and fruiting habits. The 1-year-old trunks developing from a graft are described as a succession of metamers whose structure refers to location, distribution, and length of sylleptic axillary shoots. We used a stochastic process called hidden semi-Markov chain to capture the embedded structure resulting from mixing of different types of axillary shoots developing along the trunks. The models, corresponding to the different cultivars, are composed of a first transient nonbranched state, a succession of transient states that cover the median sylleptic branching zone, and a final absorbing nonbranched state. They are interpreted with regard to complexity, extent, and branching distribution of the median sylleptic zone. Main results deal with the balance between long and short sylleptic shoots and the distribution of long sylleptic shoots along the trunks. Results suggest that sylleptic branching could be used as an early characteristic to evaluate the later branching behavior of cultivars.**

For several years, French apple breeding programs have considered tree growth habits in addition to more usual characteristics, such as disease resistance and fruit quality (Lespinasse, 1992). Selection criteria derive from a classification of tree forms based on four main characteristics: presence of strong branches at the trunk base, presence of long branching on the terminal part of annual shoots, branching angles, and fruiting habits (Lespinasse, 1977).

Among these characteristics, the presence of strong branches at the base of the trunk results from sylleptic (or immediate) branching (Costes et al., 1995). Sylleptic branching refers to the growth of axillary meristems while the main shoot is still growing without a protected or resting phase (Champagnat, 1954, 1961). On several species, it seems to be related to the fast growth rate of the main shoot (Champagnat, 1954, 1965a, 1965b, 1965c; Génard et al., 1994). Sylleptic branching, occurring mainly during the early developmental years of tree life, indicates tree vigor (Crabbé, 1987) and usually is considered as an advantage for young tree establishment (Maggs, 1960; Van Oosten, 1981). As sylleptic branching is expressed early in tree life and differs among cultivars, we investigated whether it is a characteristic that breeders could use for characterizing and identifying cultivars.

In this study, we compared the sylleptic branching structure of the 1-year-old trunks for a set of cultivars with diverse branching and fruiting habits. Kinetic aspects were not considered as previously discussed (Costes and Lauri, 1995), but instead, the focus was on the trunk structure at the end of the growing period. The 1-year-old trunk is considered as a succession of metamers, as defined by White (1979), composed of a node, the subjacent internode, and the corresponding axillary leaf(ves) and bud(s). In our context, the term "structure" refers to the location, distribution, and length (in terms of the number of metamers) of the axillary sylleptic shoots.

Hidden semi-Markov chains that belong to the class of discrete–time, discrete–state–space stochastic processes were used to capture embedded structure resulting from the mixing of the different types of axillary productions encountered along the 1-year-old trunks (Guédon et al., 1997). This modeling approach originates from the field of speech recognition (Baum et al., 1970; Guédon, 1992; Rabiner, 1989). This family of models is mainly used to model sequences of events (sequences of phonemes in the spoken language, molecular sequences, etc.). The power of these models lies in the availability of efficient estimation algorithms that enables the automatic building of models from samples of observed sequences.

Materials and Methods

PLANT MATERIAL AND OBSERVATION METHOD. Six apple cultivars corresponding to four basic growth and fruiting habits, described as type I–IV by Lespinasse (1977), and the spur mutant 'McIntosh Wijcik', exhibiting a compact growth type (Lapins, 1974, 1976), were planted at the Arboriculture Laboratory of Institut National de la Recherche Agronomique, Montpellier, France. The six cultivars were 'Belrène' (Type I); 'Reinette Blanche du Canada' (Type II); 'Imperial Gala' (Type III); and 'Granny Smith', 'Elstar', and 'Fuji' (Type IV). Twenty trees per cultivar, bench-grafted on M.7 rootstock, were planted in the field in 1991. After the first year of growth, the shoot that developed from the grafted bud was cut back to one bud, and the trees were transplanted in blocks of 20 trees with spacing at 6×4.5 m. Trees then were allowed to develop without pruning. On the shoot developing the following year from the retained bud, the number of metamers, and the location and the length of the sylleptic shoots were recorded.

We classified the sylleptic shoots into two types according to their ability to develop more or less than 12 nodes. This ability corresponds to the usually accepted number of preformed organs in the resting bud (Rivals, 1965). Because in tree training only shoots with >12 nodes can be used, we focused on the number and the layout of long shoots.

Received for publication 16 July 1996. Accepted for publication 12 Aug. 1996. We gratefully thank P.E. Lauri and G. Garcia for their contribution to field observations and data input. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

The trunks were particularly vigorous because the corresponding root system was 1 year old. Broken or injured trunks were not included in the samples. The number of trunks described per cultivar varied from 15 to 19. The average number of metamers varied from 57 ('McIntosh Wijcik') to 90 ('Belrène'). Because the corresponding standard deviations were low, we considered that trunks of the same cultivar have a similar growing behavior.

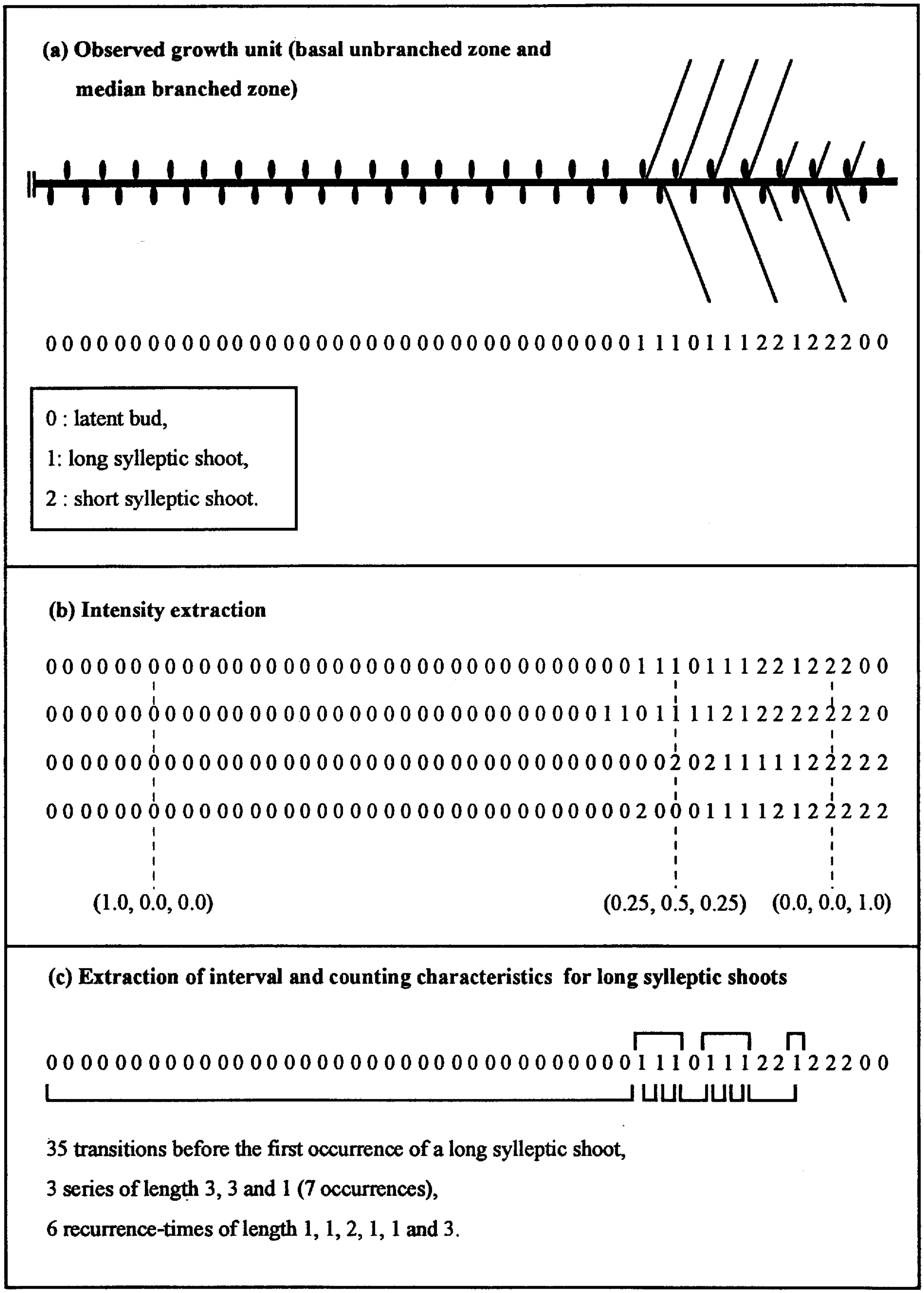


Fig. 1. Extraction of different points of view from a sample of sequences. (**a**) Coding of the successive axillary shoots along the trunk, (**b**) intensity: empirical distribution of the different symbols per rank, (**c**) interval and counting characteristics: examples on long sylleptic shoots.

MODEL. A 1-year-old trunk is described as a succession of metamers and is represented by a sequence of qualitative variables, named sequence of events (Fig. 1a). Each node bears an axillary production of a given type represented by a symbol: 0 for latent bud, 1 for a sylleptic axillary shoot composed of >12 nodes (long sylleptic shoot), and 2 for a sylleptic axillary shoot composed of ≤12 nodes (short sylleptic shoot).

The sample of sequences of events can be interpreted through different characteristics organized according to the three following points of view. The "intensity" point of view consists of extracting the empirical distribution of the different symbols for each possible rank of a node from the sample of sequences (Fig. 1b). This family of empirical distributions, thus, can be visualized as a set of curves, each curve representing the evolution of the empirical probability of a given symbol with the rank of the node (Fig. 2). The change in distribution of symbols with rank makes it possible to evaluate the dynamics of the studied phenomenon. The "interval" point of view consists of extracting three different types of intervals from the sample of sequences that constitute three types of characteristics (Fig. 1c): the number of transitions before the first occurrence of a given symbol, the number of transitions starting from a given symbol to return to it, named recurrence-time, and the number of successive occurrences of a given symbol, named series. The "counting" point of view consists of counting the number of occurrences of a given "pattern" (Fig. 1c) for each sequence. The two patterns of interest are the number of occurrences of a given symbol per sequence and the number of series of a given symbol per sequence. For example, the number of occurrences of symbol 2 per sequence represents the number of short sylleptic axillary shoots per 1-year-old trunk.

These characteristics take the form of families of empirical discrete distributions, one distribution per rank for the intensity point of view and one distribution per possible symbol for the interval and counting points of view.

To give an intuitive idea of the biological relevance of the proposed model, we chose three strongly structured sequences measured on 'Imperial Gala':

000000000000000000000000000000201012100000021222\
2222200000000000000000
000000000000000000000000000002211111110000022122\
1220000000000000000000
000000000000000000000000000000011121210002222222\
2220000000000000000

These three sequences exhibit a succession of five differentiated zones. The difficulties arise from the fact that each zone is not characterized by a single axillary production but by a given mixture of axillary productions: 0 for the first zone; 0, 1, 2 for the second; 0 for the third; 1, 2 for the fourth; and 0 for the fifth. Therefore, we propose a hierarchical model with two levels of representation. At the first level, a semi-Markov chain represents the succession of zones and the lengths of each zone. The second level consists in attaching a discrete distribution that represents the corresponding mixture of axillary productions to each zone. The whole model is a hidden semi-Markov chain.

We will detail this hierarchical building of a hidden semi-Markov chain and give the formal definition of each component of this model. The succession of zones along the annual shoot is modeled by a Markov chain, which is composed of a set of states representing the different zones and a set of transitions between states. In the following, $S_n = j$ means that the process is in state j at rank n.

A J-state, first-order Markov chain is defined by the following parameters:

1) initial probabilities (probabilities to be in a given state at the beginning of the sequence):

$$\pi_j = P(S_0 = j),\ 0 \leq j < J, \text{ with } \sum_{j=0}^{J-1} \pi_j = 1,$$

2) transition probabilities (probabilities of moving from state i at rank n - 1 to state j at rank n):

$$p_{ij} = P(S_n = j \,/\, S_{n-1} = i),\ 0 \leq i < J,\ 0 \leq j < J, \text{ with} \sum_{j=0}^{J-1} p_{ij} = 1.$$

Hence, $(p_{i0}, \cdots, p_{ij}, \cdots p_{iJ-1})$ is the transition distribution attached to state i.

In the case of a semi-Markov chain, the transition probabilities of the underlying first-order Markov chain are subject to the following constraints: non-absorbing state, $p_{ii} = 0$, and absorbing state, $p_{ii} = 1, \forall j \neq i, p_{ij} = 0$. State i is said to be absorbing if, entering in state i, it is impossible to leave it.

This first-order Markov chain only represents transitions between distinct states except in the absorbing state case. A first-order Markov chain can be interpreted as a graph (i.e., a set of vertices, representing the states, and a set of oriented edges, representing the possible transitions between states) (Fig. 3c). In the first-order Markov chain case, a strictly positive probability is associated with each edge so that the sum of the probabilities associated with the edges leaving a given state is equal to 1.

An occupancy distribution, which represents the length of the corresponding zone in terms of number of metamers, is associated

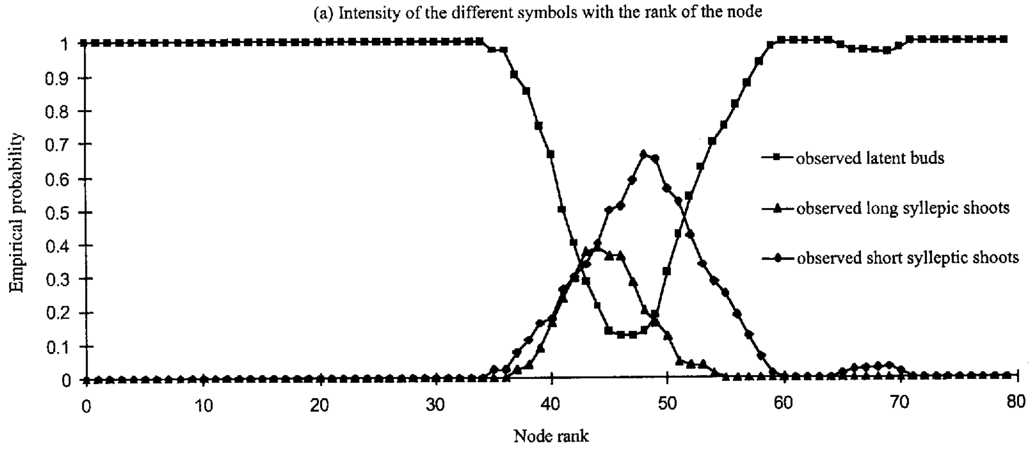


Fig. 2. Evolution of empirical probabilities of the different types of axillary shoots with the rank of the node (rank 0 is at the bud union end), example of 'Gala Imperial'.

with each non-absorbing state of the first-order Markov chain (Fig. 3c):

$$d_j(u) = P(S_{n+u+1} \neq j, S_{n+v} = j, v = 2,\cdots,u / S_{n+1} = j, S_n \neq j)\ u = 1,2,\cdots$$

The possible state occupancy distributions are usual parametric distributions [i.e., binomial distributions B(d, n, p), Poisson distributions P(d, λ), and negative binomial distributions NB(d, r, p)] with an additional shift parameter d ($d \geq 1$), which defines the minimum state occupancy. The whole (Markov chain + occupancy distributions) constitutes a semi-Markov chain.

The mechanism associated to a semi-Markov chain can be

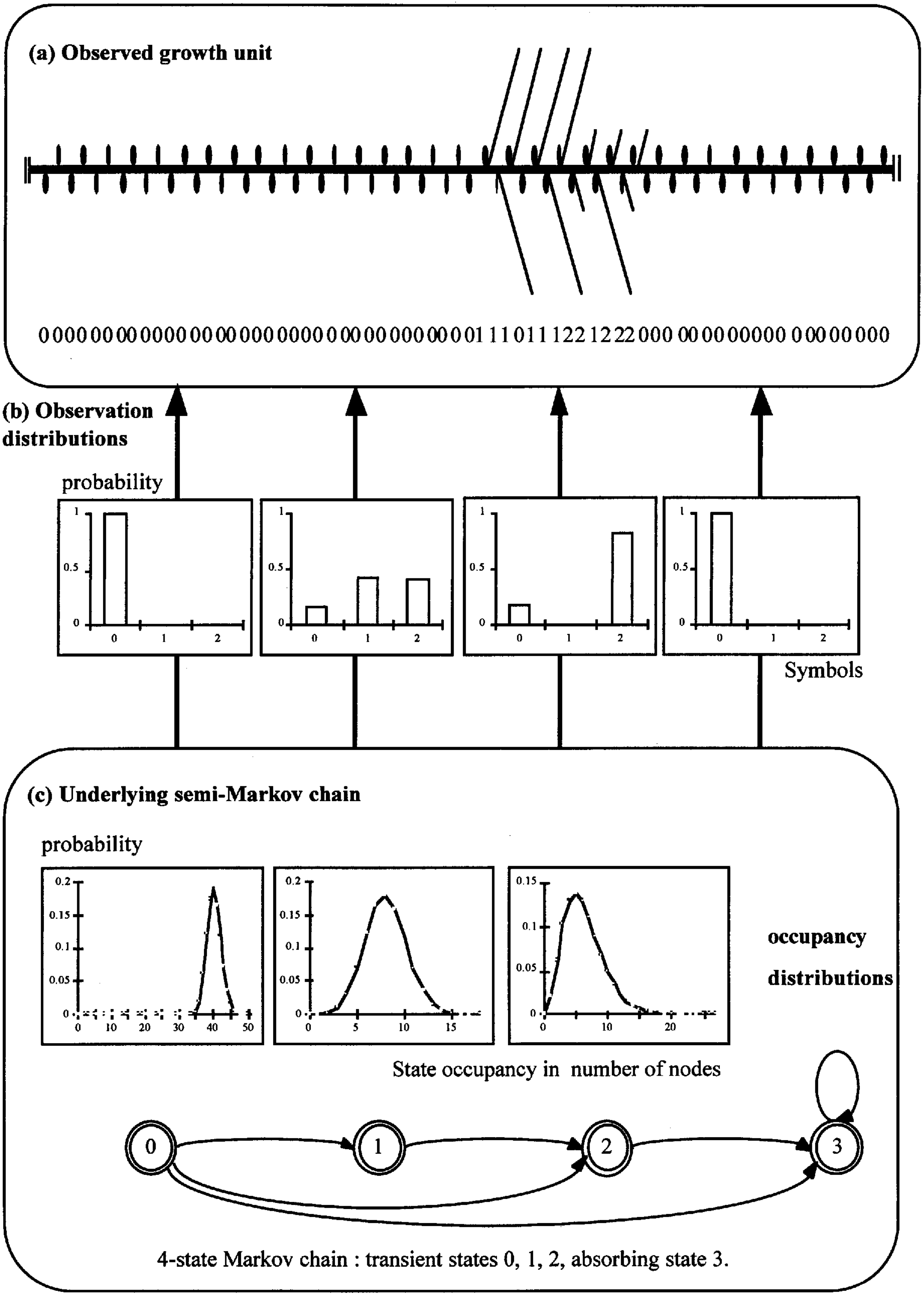


Fig. 3. Modeling the sylleptic branching structure of 1-year-old trunks by a hidden semi-Markov chain, example of 'Reinette Blanche du Canada'

described as follows: suppose that between two consecutive rank, a transition occurred between state i and state j ($i \neq j$) with probability p_{ij}. Then, the process remains in state j for a period u determined randomly by the corresponding state occupancy distribution d_j. The process then moves to another state according to the transition distribution $(p_{j0},\ldots,p_{jk},\ldots,p_{jJ-1})$.

The states of this semi-Markov chain cannot be observed directly but are related to the observed symbols by the "observation" probabilities that represent the types of axillary production in the corresponding zone (Fig. 3b):

$$b_j(y) = P(X_n = y / S_n = j),\ 0 \le y < Y,\ 0 \le j < J, \text{ with } \sum_{y=0}^{Y-1} b_j(y) = 1.$$

$X_n = y$ means that the symbol y, which represents a given type of

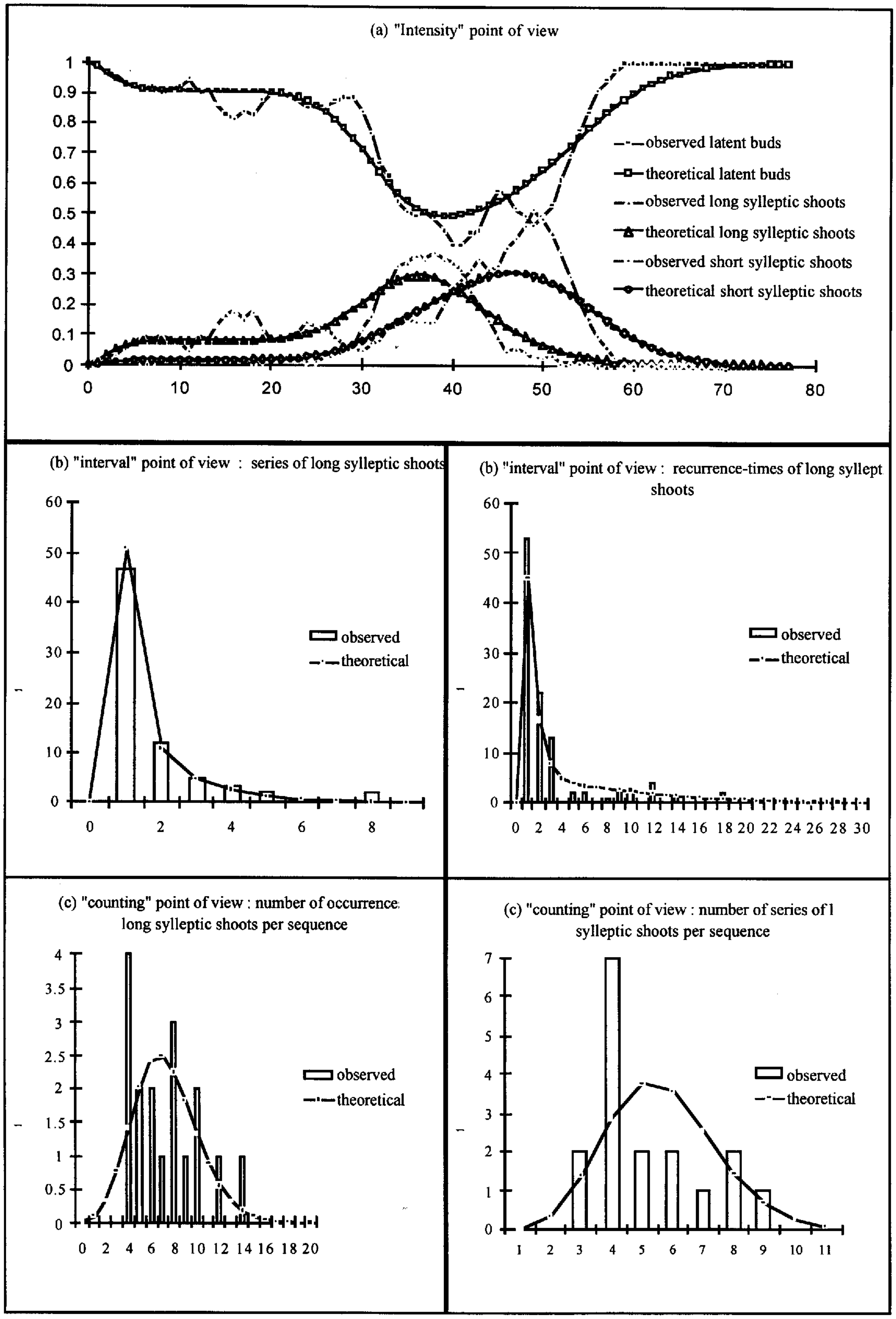


Fig. 4. Comparison of characteristics extracted from sequences and characteristics computed from the model parameters: (**a**) intensity, (**b**) interval, and (**c**) counting points of view, example of 'Imperial Gala'.

axillary production, is observed at rank *n*. This definition of the observation probabilities expresses the assumption that the observed variable at rank *n*, X_n, depends only on the corresponding hidden variable S_n. For each state, the observation probabilities constitutes a nonparametric distribution defined on the set of possible symbols. The complete model (underlying semi-Markov chain + observation probabilities) is a hidden semi-Markov chain.

As the probabilities of the symbols at the different ranks of the node (Fig. 2) exhibit a succession of transient phases, we modeled the resulting structure by a left–right-oriented Markov chain (Fig. 3). This is expressed by constraints on the transition probabilities of the underlying Markov chain: the transitions from a given state to the previous states are forbidden (for example from state 3 to states 0, 1, and 2). The model, then, is composed of *i* transient states, representing the *i* successive zones of the shoot, and a final absorbing state. These two types of states are defined according to the following structural property: if there is a positive probability that, starting from state *i*, the first return to state *i* never occurs after a finite number of transitions, state *i* is said to be transient and if, entering in state *i*, it is impossible to leave it, state *i* is said to be absorbing.

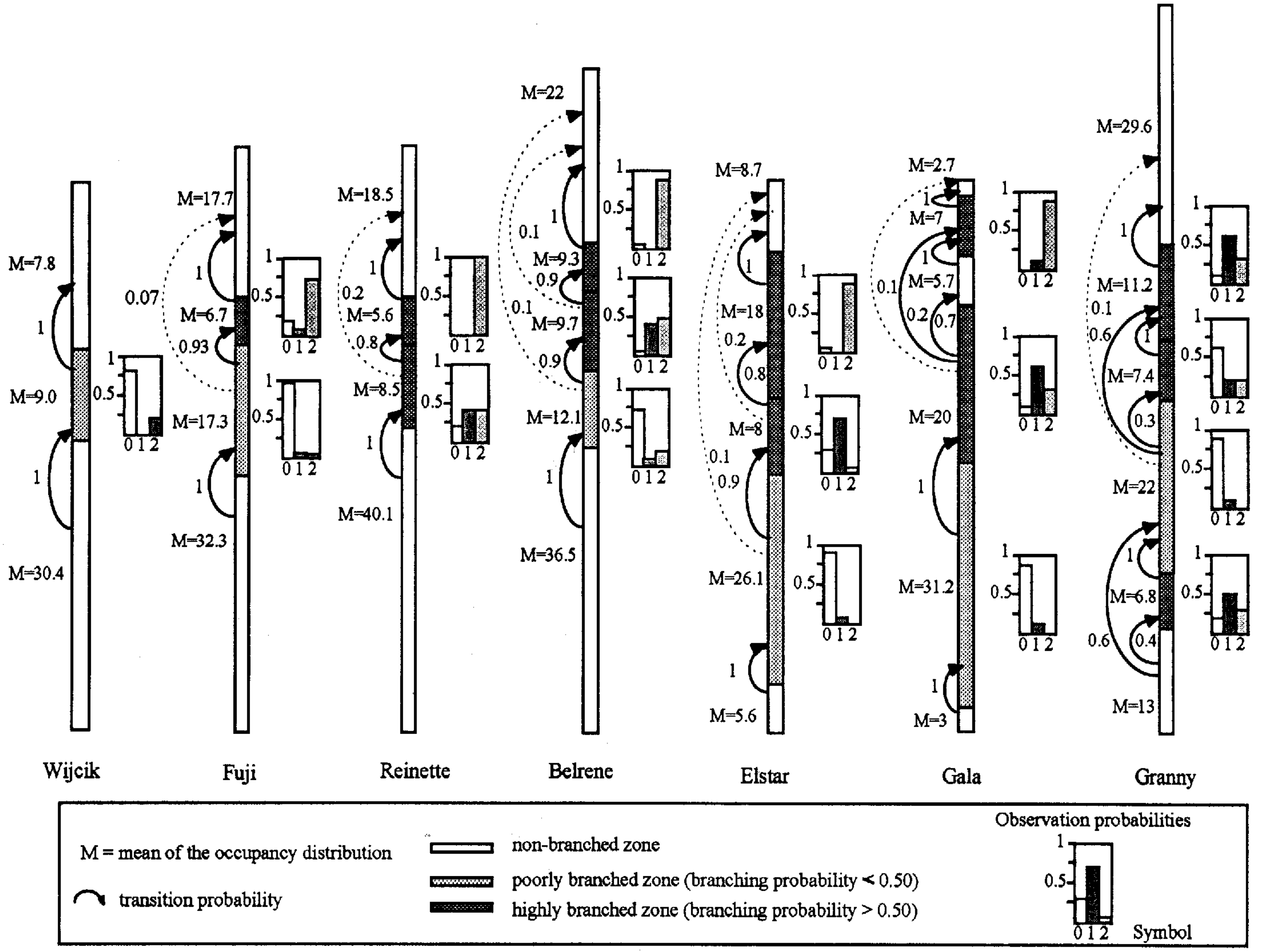
This hierarchical structure of the model provides a separation of the structural part of the model only represented in the underlying semi-Markov chain from its stochastic part partly represented in the underlying semi-Markov chain but mainly represented in the observation distributions. By structural parts of the model, we mean structural properties of the underlying first-order Markov chain.

This type of model necessitates making a hypothesis on the causality of the studied phenomenon to determine in what direction the sequences have to be described. As the sylleptic branching develops simultaneously with growth [i.e., from base to top (of the carrier shoot)], we chose the same direction to describe the succession of nodes.

Constraints can also be expressed on the observation probabilities, forbidding the observation of a given symbol in a given state. This helps to differentiate the states with regard to observations and to interpret the sylleptic branching. Therefore, only symbol 0 (latent bud) can be observed in the first and last states, which represent the basal nonbranched zone and the apical nonbranched zone, respectively.

The parameters of the model are estimated by an iterative algorithm, which maximize the likelihood of the observed sequences (Guédon, 1992; Guédon and Cocozza-Thivent, 1990). Constraints on the transitions probabilities and the observations probabilities are expressed in the form of an initial model definition. Then, at each iteration, the parameters of a new model are estimated from the preceding one respecting the constraints on the

Fig. 5. Interpretation of the models corresponding to each cultivar.



transition probabilities and the observation probabilities. The theoretical characteristics, taking the form of families of discrete distributions, are computed from the estimated parameters. These theoretical characteristics, organized according to the three points of view (intensity, interval, and counting), then can be compared to the corresponding characteristics extracted from the observed sequences (Fig. 4). This comparison enabled us to evaluate the accuracy of the model and, possibly, to modify the initial hypothesis expressed in the constraints on the transition probabilities and the observation probabilities.

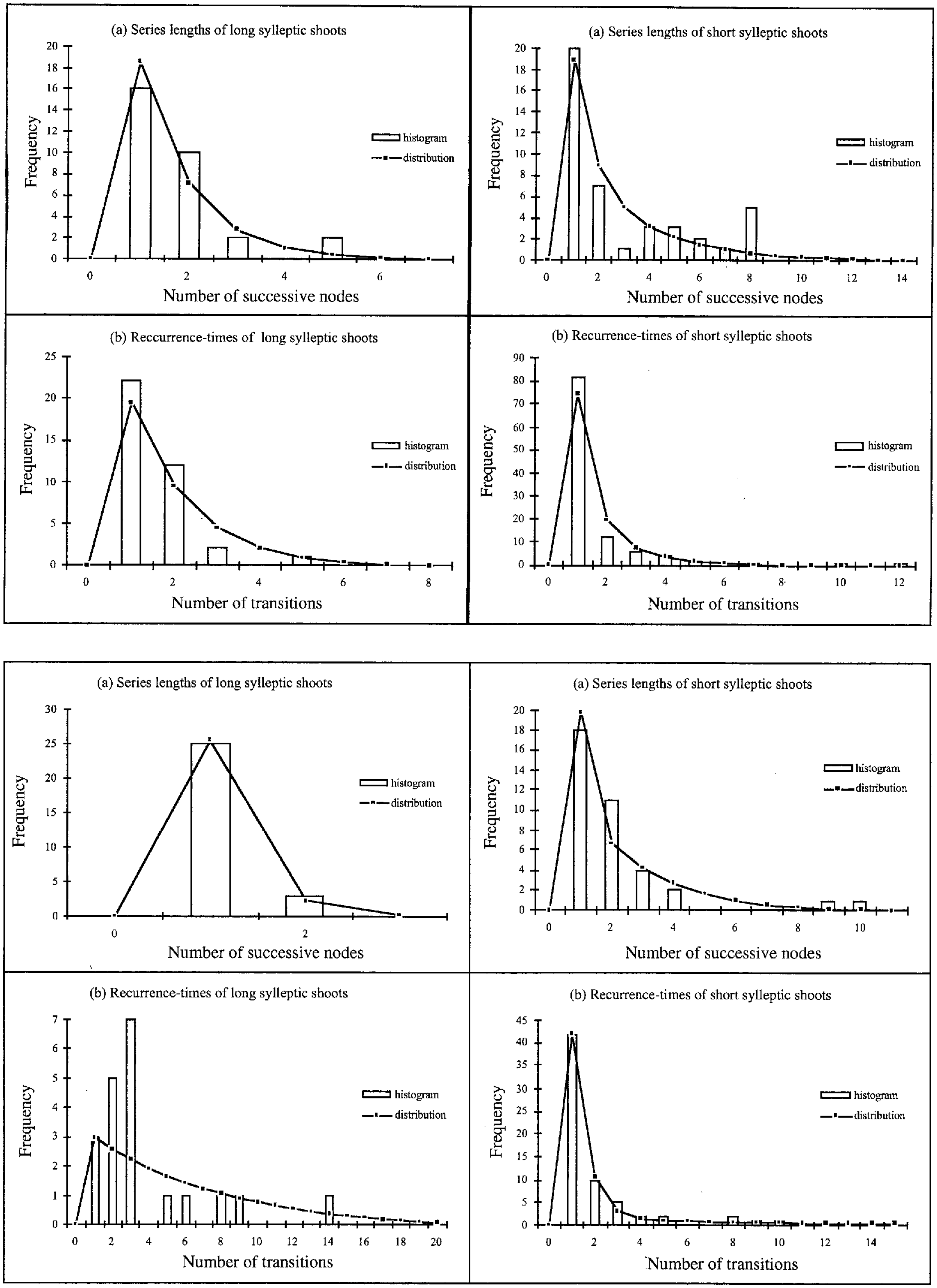


Fig. 6. Comparison of 'Reinette Blanche du Canada' (**1**) and 'Fuji' (**2**) sylleptic branching by interval characteristics: (**a**) series; (**b**) recurrence times. NB: scales are different for each graphic.

Results and Discussion

For each sample of sequences of a given cultivar, the parameters of the model were estimated, and the theoretical characteristics were computed from these parameters. Each model is composed of a first transient nonbranched state, a succession of transient states that cover the median sylleptic branching zone, and a final absorbing nonbranched state. We compared the median sylleptic branching zone of the different cultivars by the following three features: the number of states, which expresses the complexity of the zone; the occupancy distributions, which express the extent of the zone; and the branching distribution, which is expressed by the observation probabilities. It also can be evaluated considering interval and counting characteristics: series, recurrence-times, and number of occurrences per sequence.

The main results obtained for the different cultivars are shown in Fig. 5, increasing the complexity of the models from left to right. The observation probabilities are represented by histograms, while the possible transitions are represented by oriented edges (the associated probabilities are noted nearby).

STRUCTURES OF THE MODELS OF THE DIFFERENT CULTIVARS. The simplest underlying Markov chain is composed of three states representing the three successive zones: basal nonbranched, median sylleptic branching, and apical nonbranched. Such a structure is only found on ‘McIntosh Wijcik’. This cultivar is characterized by the smallness of the median sylleptic zone and its low branching probability: the long sylleptic shoots are almost absent and the short sylleptic shoots are present on only 19% of the nodes of the median zone whose mean length is nine nodes (Fig. 5).

A second configuration corresponds to a median sylleptic branching zone divided in two parts that differ by their branching probability. In this case, the model is composed of four states. Such a structure characterizes ‘Reinette Blanche du Canada’ and ‘Fuji’ (Fig. 5). The structures of these two cultivars are similar, looking at the transition probabilities and the occupancy distributions. For both cultivars, the first nonbranched zone is long, but the balance between the two types of sylleptic shoots differs. ‘Reinette’ is more highly branched, with more long sylleptic shoots than ‘Fuji’. More details are provided by interval characteristics on the differences of branching distributions. Figure 6 illustrates that ‘Fuji’ has a shorter series of branched nodes and longer recurrence times for either long or short sylleptic shoots than ‘Reinette Blanche du Canada’.

The sylleptic branching zone of ‘Belrène’ and ‘Elstar’ is composed of a lower poorly branched part, followed by two highly branched parts that can be differentiated by the balance between the two types of sylleptic shoots. The corresponding models have five states (Fig. 5). The transition probabilities are similar, but these cultivars differ by their occupancy distributions: the sylleptic branching zone of ‘Elstar’ begins near the bottom of the 1-year-old trunks and is notably longer than that of ‘Belrène’. However, the median sylleptic zone of ‘Belrène’ presents similarities with that of the ‘Reinette Blanche du Canada’: both have a short sylleptic branching zone, mainly represented by short shoots at the end of the sylleptic branching zone.

Finally, the most complex underlying first-order Markov chain is composed of six successive states. This complexity results from the extent of the sylleptic branching zone, which is found on ‘Imperial Gala’ and ‘Granny Smith’. For both cultivars, the beginning of the sylleptic branching zone is near the bottom. ‘Imperial Gala’ has the particularity of presenting a nonbranched zone inside the sylleptic median zone on 70% of the sequences. Consequently, only three states are branched, and ‘Imperial Gala’ appears to be close to ‘Elstar’. Other characteristics for the ‘Imperial Gala’ cultivar, such as the series and the recurrence times (Fig. 4b and c), highlight an interesting distribution of long sylleptic shoots for training (many well-separated long shoots). Therefore, ‘Imperial Gala’ presents the most interesting structure for training.

Additional characteristics per cultivar are presented in Table 1. The total mean number of metamers of the median zone is given as a summation on the different symbols. The overall balance between short and long sylleptic shoots can be interpreted as a degree of “spurriness.” The number of short sylleptic shoots is greater than the number of long sylleptic shoots for ‘McIntosh Wijcik’, ‘Reinette Blanche du Canada’, ‘Belrène’, and ‘Fuji’. ‘Imperial Gala’ has an equal proportion of short and long sylleptic shoots, while ‘Elstar’ and ‘Granny Smith’ have an inverse proportion (i.e., more long shoots than short shoots). As types I and II are usually considered spurred types compared to types III and IV, this classification is coherent with the fruiting types, except for ‘Fuji’. Therefore, the balance between short and long sylleptic branching appears to predict the later branching behavior relatively satisfactorily.

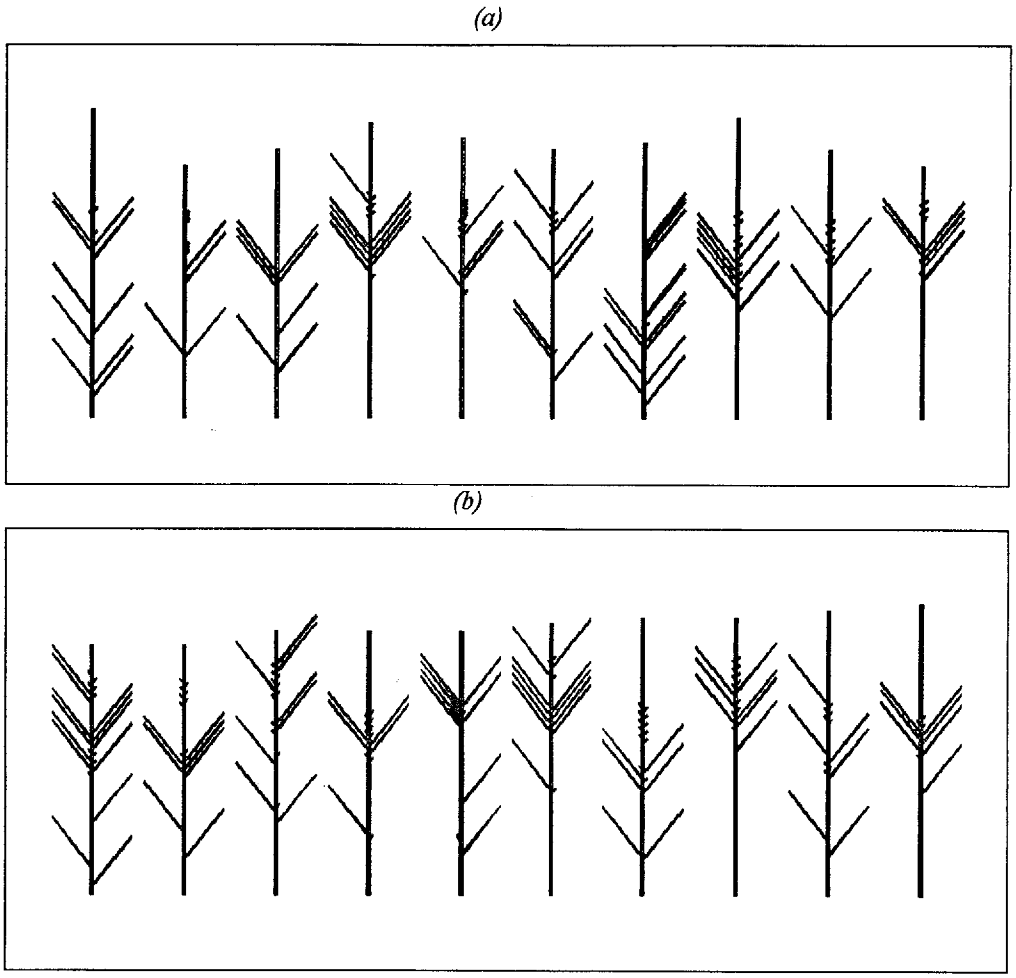
Table 1. Main characteristics on the median sylleptic branching zone.

Cultivar (fruiting type)	States involved (no.)	Mean no. metamers as sum of mean no. of symbol occurrences: T = x (0) + y (1) + z (2)	Mean first occurrence of symbol 1
McIntosh Wijcik (compact)	1	8.5 = 6.75 (0) + 0.05 (1) + 1.7 (2)	29.0
Reinette Blanche du Canada (I)	2	12.7 = 0.0 (0) + 3.2 (1) + 7.6 (2)	42.5
Fuji (IV)	2	21.7 =14.3 (0) + 2.1 (1) + 5.3 (2)	39.3
Belrène (II)	3	27.3 = 8.7 (0) + 4.7 (1) + 13.9 (2)	43.5
Elstar (IV)	3	36.3 = 25.3 (0) + 7.3 (1) + 3.7 (2)	19.2
Imperial Gala (III)	4	48.2 = 33.4 (0) + 7.3 (1) + 7.5 (2)	20.4
Granny Smith (IV)	4	37.4 = 24.2 (0) + 8.1 (1) + 5.1 (2).	20.4

Table 2. Recognition rate of 1000 simulated sequences of a given cultivar for each cultivar model (sum on a line equals 100%).

Model sequences	Belrène	Elstar	Fuji	Imperial Gala	Granny Smith	Reinette Blanche du Canada	MacIntosh Wijcik
Belrène	83.1	0.6	4.7	0.4	1.4	6.7	3.1
Elstar	0.9	87.9	0.2	3.8	5.0	0.7	1.5
Fuji	3.5	0.1	85.3	0.3	0.9	1.7	8.2
Imperial Gala	1.0	7.5	0.4	87.7	3.2	0.2	0.0
Granny Smith	0.6	3.9	1.5	1.6	89.5	1.0	1.9
Reinette Blanche du Canada	1.4	0.0	1.3	0.2	0.1	90.0	7.0
MacIntosh Wijcik	1.4	0.0	0.4	0.0	0.3	0.0	97.9

Fig. 7. Graphic representation of (**a**) observed and (**b**) simulated sequences.



Another characteristic usually used to classify the cultivars is the presence of strong branches at the bottom of the trunks, sometimes called "basitony" (Lespinasse, 1977), which result from sylleptic branching (Costes et al., 1995). Among the studied cultivars, 'Elstar', 'Imperial Gala', and 'Granny Smith' have a strong basitony, which appears in the models (Fig. 5) and in more global variables, such as the first occurrence of long sylleptic shoots (Table 1). The basitone characteristic leads to the same classification of cultivars as the spurriness characteristic.

COMPUTATION OF DISTANCES BETWEEN CULTIVARS. Thus far, we have detailed the different components and characteristics of the models and propose interpretations about the differences among cultivars. An additional approach consists in evaluating the overall adequacy of an observed sequence for a given model. This evaluation can be repeated for different models in the aim of classifying the sequence. The log-likelihood of an unknown sequence $y_0,\cdots,y_{N-1}$ for an estimated model can be computed as follows:

$$L(y_0,\cdots,y_{N-1};\theta) = \frac{1}{N} \log P(Y_0 = y_0,\cdots,Y_{N-1} = y_{N-1};\theta)$$

where θ denotes the parameters of an estimated hidden semi-Markov chain (i.e., the initial probabilities and the transition probabilities of the underlying first-order Markov chain), the occupancy distributions, and the observation probabilities.

We interpret this log-likelihood as a pseudo-distance between the cultivar corresponding to the sequence and the cultivar corresponding to the model. This distance is not a distance in a mathematical sense as the symmetry property is not verified (Table 2).

A methodologically correct recognition test would consist in computing the log-likelihood of observed sequences not used in estimating the model parameters. We do not have enough observed sequences per cultivar to split up each sample into two subsamples, one for estimating the model parameters and one for the recognition test. Therefore, we generated 1000 sequences per cultivar by simulation and performed the recognition test on these simulated sequences.

Ten simulated and 10 observed sequences have been reconstructed using a graphic software (Godin et al., 1997). This reconstruction gives an overview of the branching distribution diversity inside a cultivar and allows a visual comparison between simulated and observed sequences (Fig. 7).

The recognition test consisted in computing the log-likelihood of a simulated sequence for each cultivar model and then in ordering the cultivars according to these resulting log-likelihood. Then, the joint log-likelihood of a sample of sequences for a given model and the associated rank of the simulated sequences for the different models (Table 3) as well as the recognition rates (Table 2) provide a global summary of the results of the recognition test. The errors of classification express the overlap of cultivars, while the comparison of the joint likelihoods of simulated sequences for different models (on a line) expresses the distance between the corresponding cultivars. The order of magnitude of the recognition rates (between 83% and 98%) suggests a good separability of cultivars using only the sylleptic branching information. The comparison of joint log-likelihoods and associated ranks of simulated sequences for different models emphasizes the proximity of three cultivars ('Imperial Gala', 'Granny Smith', and 'Elstar'). The ranks of a model for the different samples of simulated sequences suggest a central location for 'Belrène', while 'McIntosh Wijcik' is the most outlying cultivar.

The next step would consist in synthesizing the information contained in the joint log-likelihood matrix either by a principal component analysis or by a clustering method to emphasize the proximities between cultivars.

Conclusion

Despite of the small sample size, the studied sequences were sufficiently structured to emphasize the differences among cultivars and to build accurate models. Using these models provides an answer to our initial aim of being able to characterize and distin-

Table 3. Joint log-likelihood and associated rank (in brackets) of 1000 simulated sequences of a given cultivar for each cultivar model.

Model sequences	Belrène	Elstar	Fuji	Imperial Gala	Granny Smith	Reinette Blanche du Canada	MacIntosh Wijcik
Belrène	–0.31 [1]	–0.54 [5]	–0.48 [4]	–0.47 [3]	–0.46 [2]	–0.61 [6]	–1.15 [7]
Elstar	–0.53 [4]	–0.33 [1]	–0.72 [5]	–0.44 [2]	–0.44 [3]	–1.17 [7]	–0.99 [6]
Fuji	–0.28 [2]	–0.38 [5]	–0.23 [1]	–0.33 [4]	–0.31 [3]	–0.41 [6]	–0.48 [7]
Imperial Gala	–0.66 [4]	–0.54 [2]	–0.77 [5]	–0.41 [1]	–0.54 [3]	–1.13 [6]	–1.36 [7]
Granny Smith	–0.55 [4]	–0.52 [3]	–0.83 [5]	–0.48 [2]	–0.37 [1]	–1.06 [6]	–1.12 [7]
Reinette Blanche du Canada	–0.25 [2]	–0.34 [6]	–0.29 [3]	–0.30 [4]	–0.32 [5]	–0.20 [1]	–0.60 [7]
MacIntosh Wijcik	–0.18 [2]	–0.20 [3]	–0.22 [5]	–0.27 [6]	–0.21 [4]	–0.33 [7]	–0.11 [1]

guish the different types of behaviors of the studied cultivars by an early observation. The modeling provides more than a mere summary at the observation level because the successive zones represented by the states of the underlying semi-Markov chain can be viewed as a new description level intermediate between the metamer level and the growth unit level.

The main results are consistent with previous knowledge on cultivar branching habit. The particular behavior of the compact type has been clearly identified and isolated from others. The closeness of 'Imperial Gala', 'Granny Smith', and 'Elstar' (types III and IV) seems to result from their strong basitony, the dominance of long sylleptic shoots, and a great extent of the median sylleptic zone. 'Belrène' and 'Reinette Blanche du Canada' (both type II) have a similar behavior for sylleptic branching: a short sylleptic branching zone, mainly represented by short shoots at the end of the sylleptic branching zone, first sylleptic shoots situated around the third or the middle of the main shoot. 'Fuji' is the only cultivar whose sylleptic branching does not correspond to its subsequent behavior. Although it is usually considered as a type IV, it presents characters close to those of types I and II.

Finally, in most cases, sylleptic branching appears to be an appropriate character to make a first and early diagnosis of branching behavior. The balance between short and long sylleptic shoots or the rank of the first long sylleptic shoot could be used as early characters to evaluate hybrid behavior. Nevertheless, it would be necessary first to study how branching is modified by grafting and by the choice of a given rootstock. (Does it only affect the values of the parameters or does it change the structure of the model?) In addition, the prefiguration of adult tree branching and fruiting habit has to be investigated further.

The pseudo-distance computation appears to be a useful tool for the overall comparison of cultivars. It could be applied using more complex characteristics, especially branching, which occurs after a winter period. In a longer term, we are looking for adaptations of this method in breeding programs to locate within genetic diversity unknown sequences, which represent hybrids, with reference to previously modeled cultivars. The heritability of branching characters could be investigated comparing the hybrid sequences with modeled parents.

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