Analysis and modelling of fruit tree axillary shoot and flowering distribution

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Abstract — Introduction. To characterize the behaviour of various fruit tree varieties from morphological features, the distribution of axillary production along shoots were compared. Vegetative shoots borne along apple tree trunks and the associations between vegetative and floral buds on 1 year-old shoots of *Prunus* were studied. **Methodological aspects**. The growth units are represented by sequences whose index parameter is the rank of the node. The nature of the axillary production and several qualitative or quantitative variables are taken into account at each successive node. The computation of a distance between individual sequences is proposed which leads us to analyze the variability of the sequences within each sample. In addition, from an exploratory analysis of the observed sequences, parametric models may be built to summarize and to characterize the organization of the growth units. **Applications**. The homogeneity and separability of the behaviour of branching for seven varieties of apple trees were studied with a paired comparison of the sequences, taking into account the given variety to which they belonged. Results of the comparison are given. Moreover, the flowering distribution on various types of peach tree shoots was analyzed using a model. **Conclusion**. When applied to the branching of young scions, the approach presented makes it possible to characterize the zones where the nodes bear long shoots. It thus becomes possible to evaluate the growth and branching potential of scions as of the nursery and to specify what interventions are necessary to the plant training. In the second example, the fruiting peach shoots differ by the characteristics of the model. An analysis of the "vigor effect" on the shoot structure is proposed through the occurrence of particular floriferous zones. © Éditions scientifiques et médicales Elsevier SAS

France / *Malus* / *Prunus* / growth / branching / plant anatomy / plant vegetative organs / flower / plant model

Analyse et modélisation de la répartition des rameaux axillaires et des floraisons chez les arbres fruitiers.

Résumé — Introduction. Pour caractériser le comportement de diverses variétés d'arbres fruitiers à partir de caractères morphologiques, la distribution des productions axillaires le long de rameaux de pommiers a été comparée. Des rameaux végétatifs répartis le long des troncs et des associations de bourgeons végétatifs et floraux sur des rameaux de pêchers d'un an ont été étudiés. **Aspects méthodologiques**. Les unités de croissance sont représentées par des séquences dont l'index est le rang du nœud. Le type de production axillaire et d'autres variables qualitatives ou quantitatives ont été considérées à chaque nœud successif. Le calcul d'une distance entre séquences est proposé ; il permet d'analyser la variabilité des séquences d'un même échantillon. Par ailleurs, sur la base d'une analyse exploratoire des séquences observées, la construction de modèles permet de synthétiser et de caractériser l'organisation interne des unités de croissance. **Applications**. L'homogénéité et la séparabilité du comportement de ramification de sept variétés de pommier ont été étudiées à partir de la comparaison des séquences deux à deux, en tenant compte de leur appartenance à une variété donnée. Les résultats de cette comparaison sont donnés. Par ailleurs, la répartition des floraisons sur différents types de rameaux de pêcher est analysée à l'aide de modèles. **Conclusion**. Appliquée à la ramification de jeunes scions, la démarche présentée permet de caractériser les zones où les nœuds portent des rameaux longs. Il est alors possible d'évaluer, dès la pépinière, le potentiel de croissance et de ramification des scions et donc de préciser les interventions nécessaires à une formation des plants. Dans le second exemple, les rameaux fructifères de pêchers diffèrent par les caractéristiques du modèle. Une analyse de l'effet de vigueur sur la structure du rameau est proposée à partir de l'occurrence de zones particulièrement florifères. © Éditions scientifiques et médicales Elsevier SAS

France / *Malus* / *Prunus* / croissance / ramification / anatomie végétale / organe végétatif des plantes / fleur / modèle végétal

1. introduction

To characterize and compare the behaviour of various fruit tree varieties on the basis of morphological features, we directed our interest towards the distribution of axillary production along shoots. Two types of axillary production were analyzed: on the one hand, vegetative shoots borne along the trunks were studied due to their importance to tree perennial structural development; on the other hand, the associations between vegetative and floral buds on 1 year-old shoots were studied, in light of their importance in the fruit production.

The distribution of axillary production[1] along an axis reflects the development of the bud(s) situated on the successive metamers[2] of which the axis is composed. This distribution is expressed in the form of discrete sequences, indexed according to the rank of the bearer node. The analysis of these sequences aims at bringing to light any noticeable form of organization to their existence. Plus, if such an organization is found, the analysis will help in characterizing it. Several previously developed methodological aspects [2–4] are briefly presented herein. The approach is then illustrated using previous studies on the comparison of apple cultivars [2, 5] as well as on the distribution of flowering-fructification on 1 year-old *Prunus* shoots [6, 7].

2. methodological aspects

2.1. observation method

Data was collected on axes located within tree canopies and which were considered to be morphologically comparable, e.g., 2 year-old trunks or 1 year-old long fruiting shoots. On trees subject to rhythmic growth, shoot distribution depends on the growth rhythm, whether the development is immediate or differed by winter dormancy [8, 9]. In the second case, the distribution of axillary production was studied on sections of axes, called "Growth Units" or GUs [10], developed between two given resting periods.

Once the shoots had been chosen, descriptive variables were attributed at the ranks of the bearer nodes (*figure 1*). The first variable, which is qualitative, generally represents the nature of the axillary production and is expressed in the form of shoot classes. Other variables can be considered, notably the number of associated flowers. The sequences are, thus, usually composed of several variables at each rank.

2.2. data analysis

At this stage the sequences can be written bottom up or top down. Choosing the direction of the description is important and must precede any processing of data as it represents an a priori as to the possible dependence of the successive nodes of the phenomenon under study. Indeed, the dependence of the observed events for any given rank will be analyzed relative to the observed events for preceding ranks, and only in the chosen direction. Therefore, if the shoots under study are subject to immediate development, that is to say they develop along with the growth of the bearer shoot, indexing is carried out in the direction of the growth, from the base up. Likewise, floral differentiation and flowering progress from the base towards, which dictates the GU descriptive direction. In contrast, when the shoots under study develop after a resting period and have acropetal distribution, indexing is carried out from the point at which growth stops, that is to say downwards.

To characterize and compare different types of cultivar behaviour, it is necessary to dispose of a method of comparing the individuals amongst themselves so as to analyze dissimilarities both within the group of individuals and between groups. In the following we present, first of all, the method of comparing sequences, then the exploratory analysis carried out on sequence samples and, finally, the building of parametric models.

2.2.1. sequence comparison

Comparison of two sequences, the first of which being called the reference sequence

[1] The term "axillary production" is used to name the axillary structure borne by a metamer whatever the branching level or the form (vegetative or flower) it is going to have in the future.

[2] Set of leaves, nodes, subjacent internodes and axillary buds [1].

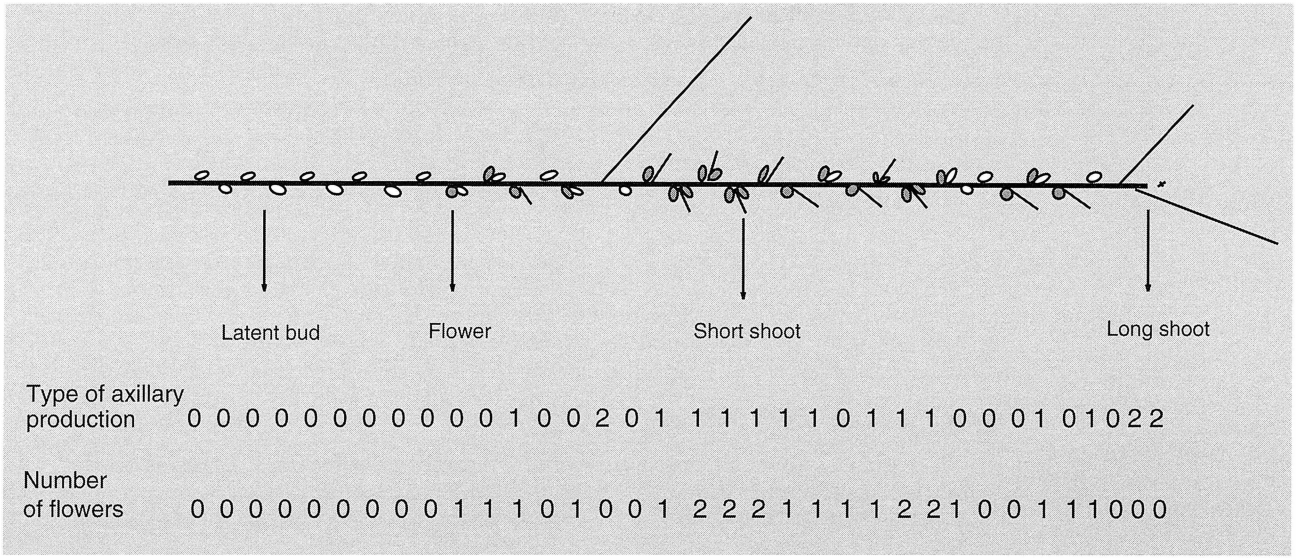

Figure 1.
Observation of a peach tree growth unit and transcription in the form of a sequence. The nature of the axillary is given by the symbol:
0 for a latent bud;
1 for a short shoot;
2 for a long shoot.
The number of associated flowers is indicated in a second variable. The sequence to be analyzed is formed by these two variables at every rank.

and the second the test sequence, relies upon the calculation of the dissimilarity between these two sequences [4]. Determining this dissimilarity is carried out by counting the costs involved in transforming the latter sequence, the test sequence, to match the reference sequence (*figure 2*). Through local comparison of the two sequences, the test sequence is "transformed" according to three elementary operations:

– substitution (represented by the letter s), meaning to replace one sequence element by another,

– match (represented by the letter m), whenever the elements are identical,

– insertion / deletion (represented by the letters i and d), to add or suppress an element so as to, on the one hand, take the difference in the number of nodes in the two sequences into account, and, on the other hand, to align homologous zones in the two sequences.

At each elementary operation is attributed a cost which expresses the distance between the two elements compared (the cost is nil when the elements are identical). Hence, when speaking about axillary production, the cost of substituting a short shoot for a latent bud will be intuitively lower than substituting a long shoot for the same bud. By repeating the same procedure for all ranks and by adding the local costs, the total cost of transforming the test sequence into the reference sequence is obtained. An optimisation procedure makes it possible to choose the sequence of operations which represents the lowest cost. This minimum cost is taken as the distance between the two compared sequences.

Using the sequence samples, it is therefore possible to compare all the sequences two at a time, while identifying several groups. It thus becomes possible to calculate the average distance between sequences inside each group (intra-class distance), which expresses the homogeneity of the group, as well as the average distance between the sequences of a given group and those of other groups (inter-class

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0 0 0 0 _ 0 1 0 1 1 1 2 _ 1 0 2 1 1 1 0 1 1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0
m m m m d m m m i s m m d m m m i i s m m m s m m m i i m m m m m m m m m m m m
0 0 0 0 2 0 1 0 _ 0 1 2 0 1 0 2 _ _ 0 0 1 1 2 0 0 0 _ _ 0 0 0 0 0 0 0 0 0 0 0 0
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Figure 2.
Extract from the comparison of two sequences: on the top is the reference sequence, the middle line represents the elementary transformation operations (m, match; d, delete; i, insertion; s, substitution) and at the bottom is the test sequence.

distance). The ratio between these two distances makes it possible to evaluate the behavioural separation between the trees of each group.

2.2.2. exploratory analysis of sequence samples

Given the complexity of the discrete sequence samples, using appropriate exploratory tools to study them in depth and from different points of view (*figure 3*) proved necessary. It is a question of descriptive techniques, of extracting characteristics and making graphic displays. Three types of characteristics are extracted, corresponding to three ways of grouping and counting the events in the sequences [2, 4].

An initial point of view, called "intensity", consists in adding up the values according to the rank of the node and displaying the relative frequency of each of the values. If the nature of axillary production is of interest, this point of view expresses the relative frequency of short shoots, long shoots and buds which remained latent according to the rank of bearer shoot (*figure 3a*).

The second point of view, called "interval", describes the number of successive nodes making up a sole event (series) or, on the contrary, separating two identical events (recurrence time). This point of view expresses the scattered or aggregated distribution of the observed events (*figure 3b*).

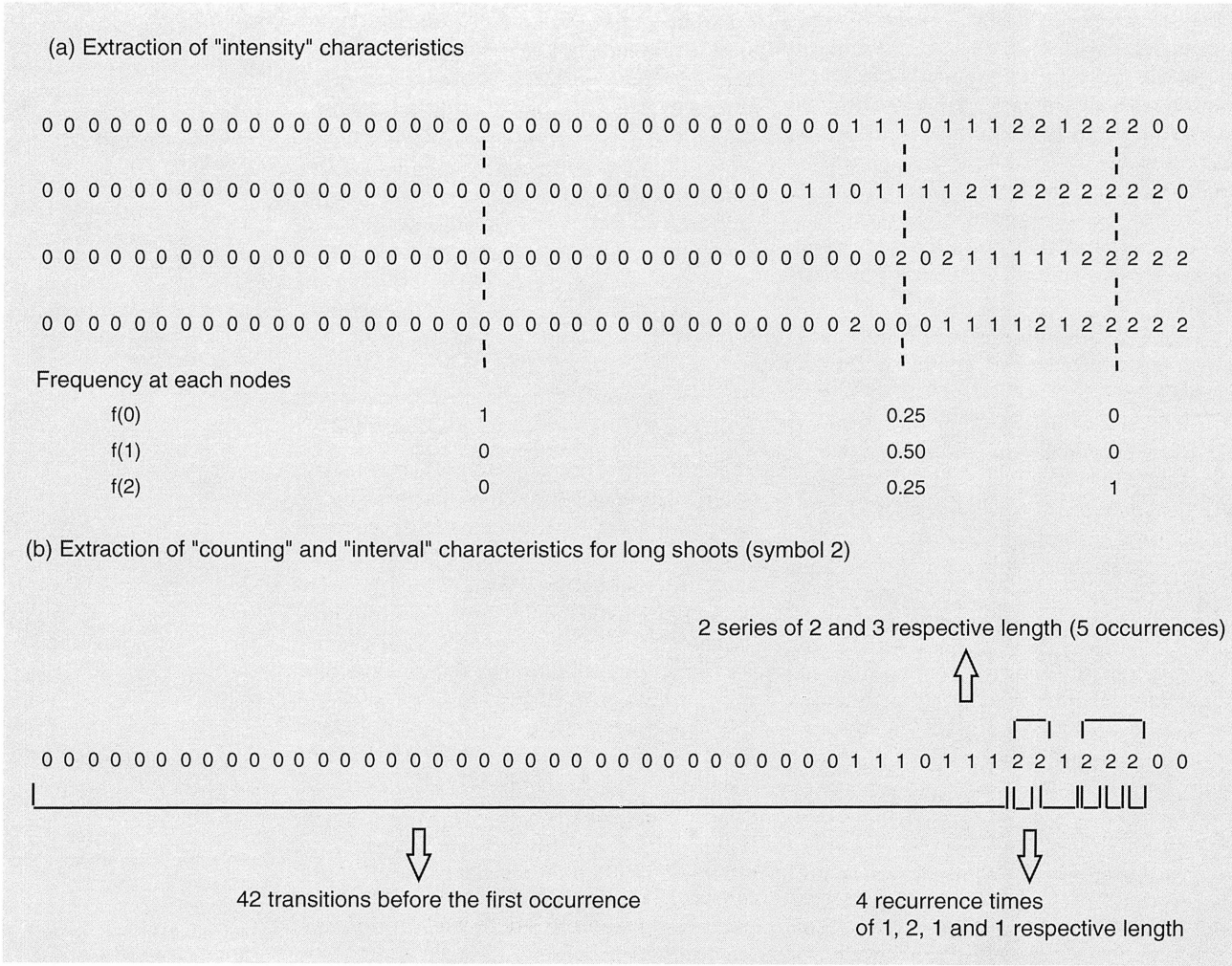


Figure 3.
Exploratory analysis of a sequence sample built using a variable representing the nature of axillary shoot.

In the case of short axillary shoots, the "interval" point of view corresponds to the number of successive nodes supporting a short shoot and the number of transitions between successive nodes separating two short shoots. This point of view also makes it possible to access the first occurrence of an event in the sequence.

The third point of view, called "counting", corresponds to both the total number and the number of series of each event in the sequence (*figure 3b*). Staying with the long axillary shoots example, this point of view gives the total number of long axillary shoots on the bearer GU. The number of series for each type of shoot completes the "interval" point of view on the more or less diffuse aspect of branching.

These three points of view make it possible to display the axillary production organization for the observed sequences. Indeed, for the same number of shoots of a given type, differing structures are brought to light through intensity, interval and the various counting plots [3]. Exploratory analysis thus makes it possible to formulate hypotheses on the observed organization; these hypotheses in turn make it possible to build parametric models.

2.2.3. model assisted analysis

Models which account for discrete data organized in the form of sequences for which successive variable dependence is taken into account belong to the family of Markov processes [11]. The goal of such modelling is to bring zones of homogeneous behaviour to light, if any, and to characterize their lengths and succession. Building such a model comprises three steps. The first step, called the specification, consists in choosing the class of model on the basis of the exploratory analysis results. The second step, the estimation, concerns in part the estimation of the model parameters. The third step, referred to as the evaluation, consists in comparing the theoretical characteristics calculated on the basis of the model parameters with those extracted from the data according to the intensity, interval and counting points of view. This final step makes it possible to disclose any inadequacy of the model and to reformulate the initial hypotheses.

In the two examples described here after, the models chosen to represent the branching zones are hidden semi-Markov chains. The highlighted zones stand out due to particular axillary production combinations, that is to say they are characterized by the proportions of each type of axillary production they contain. Therefore, zones in which short shoots are dominant will be spoken of, or zones where the majority of nodes bear two flowers. The length of a zone corresponds to the number of successive nodes it covers. This length follows a distribution expressed by a probability distribution called the occupancy distribution.

The succession of zones along the bearer GUs is expressed by the transitions from zone to zone to which probabilities are attached. If the zones are found repeatedly, that is to say if they are recurrent along the bearer GU, the transitions make it possible to come back to zones which have already been encountered. In contrast, whenever the zones are in succession along the bearer GU, the probability of transition towards the zones already covered is nil, thus making it impossible to go back.

3. applications

3.1. behavioural homogeneity and separability: example of branching for different varieties of apple trees

The trees used in this study belonged to 7 varieties with contrastive growth and fruiting habits: 'Wijcik' (type I, spurs and compact), 'Belrène' and 'Reinette Blanche du Canada' (type II), 'Imperial Gala', 'Elstar' and 'Fuji' (type III), and 'Granny Smith' (type IV) [12, 13]. After bench-grafting on M7 rootstock, the trees were planted in blocks of 20 trees per variety with a spacing of 6 m × 4.5 m at the Melgueil Inra experimentation centre, near Montpellier, France. The first year of growth, 1991, was particularly vigorous: there was no slowing and an abundance of lateral shoots was

produced. The second year of growth, axillary shoots distributed according to an acropetal gradient appeared on the 1991 GU.

At the end of this second year of growth, the nature of the axillary productions was described. Each bearer node on the first GUs of the trunks was attributed a symbol according to the following classification: 0, bud which remained latent; 1, short shoot, no more than 5 cm in length; 2, long shoot, all twigs no more than 20 cm in length were grouped into this class, along with shoots exceeding 20 cm in length; 3, axillary shoot of which the first GU was floral; 4, axillary shoot subject to immediate development, no distinction was made between short and long shoots because they had been treated in an earlier study [2].

Each block of 20 trees constituted a sample of 20 sequences with a sole qualitative variable representing the axillary production type. The sequences were analyzed from the top down so as to favour analysis of their differed branching. The homogeneity and separability of the samples required a pairwise comparison of the sequences, taking into account the given variety to which they belonged (*table I*). It thus became apparent that the 'Reinette Blanche', the 'Granny Smith' and the 'Belrène' had the most homogenous behaviour. 'Reinette' and 'Belrène' have relatively pronounced separability from the other varieties, 'Granny Smith' somewhat less. By contrast, 'Wijcik' was the variety which showed the highest level of separability, in spite of its low level of behavioural homogeneity. The behaviour of the samples of the 'Fuji' and 'Elstar' varieties had a low level of homogeneity while showing slight separability.

The modelling method used on these samples was already described in previous publication papers [4, 5].

Table I.
Distances between seven apple tree varieties, assessed from homogeneity and separability of the samples.

a) Pairwise comparison of the sequences.

Variety	Belrène	Elstar	Fuji	Imperial Gala	Granny Smith	Reinette[1]	Wijcik
Belrène	0.196	0.293	0.269	0.262	0.262	0.269	0.431
Elstar	0.293	0.246	0.258	0.237	0.235	0.272	0.424
Fuji	0.269	0.258	0.225	0.247	0.251	0.245	0.388
Imperial Gala	0.262	0.237	0.247	0.205	0.222	0.252	0.424
Granny Smith	0.262	0.235	0.251	0.222	0.187	0.262	0.429
Reinette[1]	0.269	0.272	0.245	0.252	0.262	0.184	0.383
Wijcik	0.431	0.424	0.388	0.424	0.429	0.383	0.225

b) Intra-class and mean inter-class distances.

Variety	Distance		Ratio [Intra-class/inter-class]
	Intra-class	Inter-class	
Belrène	0.196	0.299	0.656
Elstar	0.246	0.287	0.857
Fuji	0.225	0.277	0.812
Imperial Gala	0.205	0.276	0.743
Granny Smith	0.187	0.278	0.670
Reinette[1]	0.184	0.281	0.655
Wijcik	0.225	0.414	0.544

[1] Reinette Blanche du Canada.

3.2. model assisted analysis: example of flowering distribution on various fruiting shoots of cv. Robin peach tree

The trees under study belonged to the cv. Robin variety of white peaches, grafted onto GF 305 and planted at the Melgueil Inra experimentation centre in 1987. In spring 1992, 200 vegetative buds were identified and their vegetative development was observed. At the end of growth, the shoots were classified according to length; only shoots with a sole GU and a length of between 25 and 75 cm were retained for the study. These shoots were then divided into three classes: "brindles", "mixed shoots" and "vigorous mixed shoots".

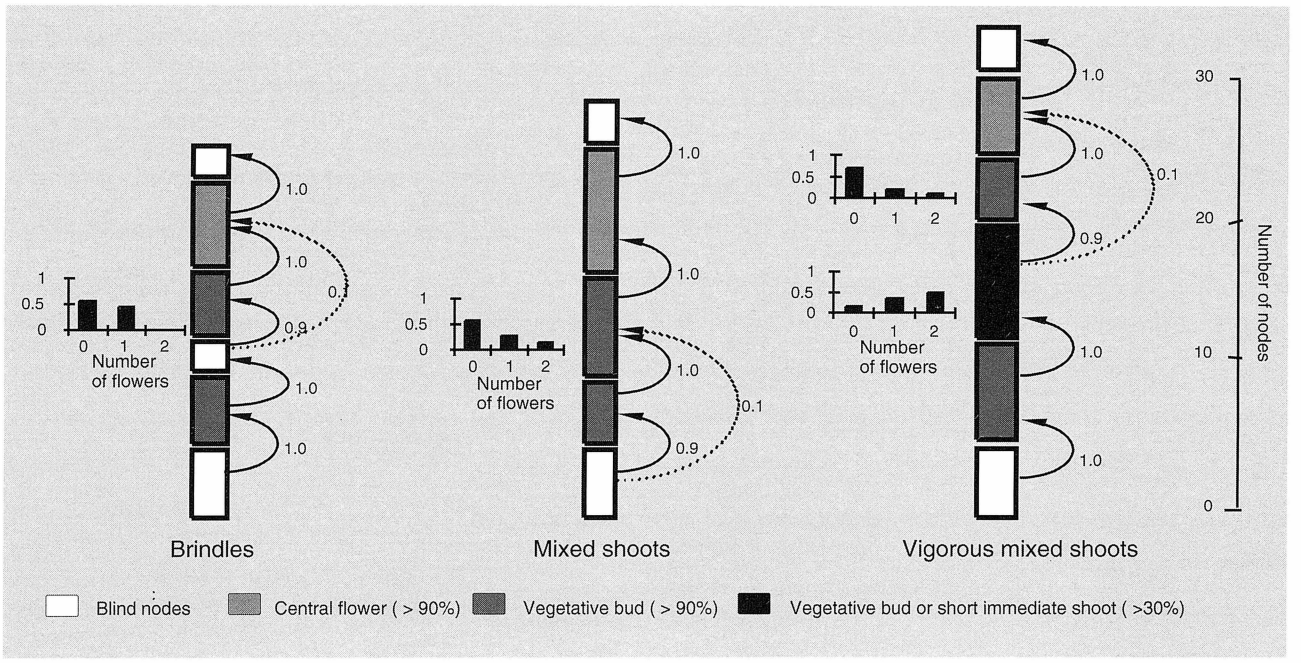
The following year, after an initial cycle of growth, the entire set of shoots was described at node level using two variables (*figure 1*): the first variable corresponded to the vegetative or floral nature of the axillary bud; the second variable indicated the number of associated flowers.

The exploratory analysis brought to light various zones characterized by the predominance of specific types of axillary production [7]. These zones appear only once along the shoot, which led us to build a model composed of transient zones. After choosing the number of zones and estimating the parameters of the model, the validity of the model was checked while fitting the characteristic distributions calculated using the parameters of the model to their empirical equivalents extracted from the data. This approach, applied to the various types of peach tree shoots, made it possible to compare their structures, specifically as concerns the abundance and position of flowering.

For the different types of shoots, *figure 4* shows the organization in successive zones, the lengths of which are depicted proportionally, according to the average number of nodes they covered. The frequencies of the various values for the two variables are also given. Some zones were found which were common to more than one shoot type; others were found only on specific shoot types.

Basal zones, corresponding to pre-formed sections [14–17], and the most distal zones were common to three of the shoot types. The transitions between preformed sections and neo-formed sections were visible only on the brindles. The floriferous section

Figure 4.
Schematic representation of axillary production distribution along three types of peach tree shoots. The length of each zone is proportional to its number of nodes. The transition probability between the different zones is indicated by the arrows. The differing motifs show the most probable values for the axillary bud. The bar graphs display the distribution of the number of lateral flowers for the floriferous zones.



can be broken down into three zones, of which two were common to all shoots. The first, found at the most distal zone, was characterized by the presence of a central flower in more than 90% of the nodes. This section was longer in mixed shoots. The second common zone was characterized by vegetative buds, of which less than 50% were associated with one or more lateral flowers. The length of this zone increased with the length of the shoot [7].

In vigorous mixed shoots, an additional zone was expressed at the beginning of the floriferous section. This zone was characterized by frequent lateral flowers (85% of the nodes), more than a third being borne on short, immediate shoots. The vigorous mixed shoots thus presented the longest floriferous section, as 2/3 of its length was made up of the additional lateral floriferous zone (*figure 4*). Génard et Bruchou [18] have shown that fruit produced on this type shoot is of superior quality; it would also seem that these vigorous mixed shoots present a better distribution of flowering which, moreover, is expressed through a better initial stage in fruit formation [19] and a better fruit distribution on the floriferous section in general. Finally, even though these shoots require more thinning out, fruit will be better spaced and have a better exposition.

4. conclusion

The developed approach takes into account successive axillary production along growth units. It makes it possible to analyze behavioural variability of different shoot types within tree canopies (peach tree example [7]), of various cultivars (apple tree example [2, 3]), or issuing from different cultural practices [20]. At present, the main limit to this approach is found in the need to privilege a specific direction in the description of the sequence. In fact, in certain cases dependency seems to be expressed at the top and at the base of the growth unit at the same time [7].

When applied to the branching of young scions, this approach makes it possible to characterize the zones where the nodes bear long shoots as well as the ratio between shoots resulting from immediate or delayed development. It thus becomes possible to evaluate the growth and branching potential of scions as of the nursery. Knowing this potential for newly-created varieties makes it possible to specify what interventions are necessary to train the plants. Indeed, over the past few years, French nurserymen have relied upon the use of long axillary shoots from the young scion in preparing "ready to produce" or "preformed" plants. This early training of the plant facilitates orchard establishment during the first years of growth and makes more rapid fructification possible.

Moreover, in peach trees the study of axillary flowering distribution brought the production potential of different shoot types to light. It shows shoot structuring in successive zones, the number of floriferous zones increasing with the vigour of the shoots. On the most vigorous shoots, the flowers, which are more numerous, are no longer in a central position but rather in lateral association with vegetative buds or short immediate shoots. Here the notion of "vigour" thus becomes the equivalent of the occurrence of zones characterized by heavy flowering associated with vegetative development.

Finally, the phenomenon of repetition studied in the present work at growth unit level has also been described at axis level and at branching system level in the case of reiteration [21]. Expressed at all levels of organization, repetition phenomenons are thus involved in the development of overall tree architecture [22, 23]. For this reason, a study of how to apply this method to more complex levels of organization capable of accounting for the structure of the entire plant is already underway for fruit species.

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Análisis y modelización de la distribución de las ramas axilares y de las floraciones en los árboles frutales.

Resumen — Introducción. Para caracterizar el comportamiento de varias variedades de árboles frutales a partir de caracteres morfológicos, se comparó la distribución de las producciones axilares a lo largo de las ramas. Se estudiaron las ramas vegetativas distribuidas a lo largo de los troncos y de las asociaciones de yemas vegetativas y florales en las ramas de un año de edad. **Aspectos metodológicos**. Las unidades de crecimiento se representan por secuencias cuyo índex es el rango del nudo. El tipo de producción axilar y otras variables cualitativas o cuantitativas se examinan a cada nudo sucesivo. Se propone el cálculo de una distancia entre secuencias permitiendo analizar la variabilidad de las secuencias inclusive de una misma muestra. Por otro lado, teniendo como base un análisis exploratorio de las secuencias observadas, la construcción de modelos permite sintetizar y caracterizar la organización interna de las unidades de crecimiento. **Aplicaciones**. Se estudiaron la homogeneidad y la separabilidad del comportamiento de ramificación de siete variedades de manzano a partir de la comparación de las secuencias dos por dos, teniendo en cuenta su pertenencia a una variedad dada. Constan los resultados de esta comparación. Por otro lado, la distribución de las floraciones en diferentes tipos de ramos de melocotonero se analiza mediante utilización de modelos. **Conclusión**. Aplicada a la ramificación de jóvenes púas, el presente paso presentado permite caracterizar las zonas donde los nudos llevan ramas largas y la proporción entre ramas de desarrollo inmediato y diferido. Resulta entonces posible evaluar, a partir del vivero, el potencial de crecimiento y de ramificación de las púas y pues aclarar las intervenciones que se necesitan para una formación de las plantas favorable para el establecimiento del vergel y para una puesta en fruta más rápida. © Éditions scientifiques et médicales Elsevier SAS

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