Using Hidden Semi-Markov Chains to Compare the Shoot Structure of Three Different Almond Cultivars

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Abstract

Shoot structure, resulting from lateral branching and flowering patterns, determines final tree form, fruit bearing habit, and cropping potential. The genetic make-up of different cultivars controls vegetative and reproductive growth, but few structural studies have been done to systematically describe almond shoot structure. A specific class of Markovian models, referred to as hidden semi-Markov chains (HSMC), has been proposed to identify and characterize branching and flowering patterns in fruit trees. This type of model is particularly appropriate when the shoot structure is organized as a succession of homogeneous branching zones and captures the variable character of the observed patterns. This study reports the first almond HSMC analysis of shoot structure based on data collected from epicormic shoots and five length categories of proleptic shoots in three almond cultivars with distinctly different tree architecture. 'Nonpareil' is the most important cultivar grown in California and has a relatively spreading tree habit. 'Aldrich' is a newer cultivar with an upright growth habit, and 'Winters' has a spreading habit with a high tendency for sylleptic branching on proleptic shoots. Shoots of these three cultivars were analyzed to determine different zones that could be classified according to lateral bud fates and the number of flower buds at each node. This modeling technique showed that almond shoot structures are highly organized and predictable. Substantial differences were found in the structure of the proleptic shoots of similar length, among the cultivars, but fewer differences were found among epicormic shoots. For long shoots, 'Aldrich' had the highest probability of flower buds and 'Winters' had the greatest lateral branching distributed along shoots. 'Nonpareil' had similar branching probabilities as 'Aldrich' and its probability of flower buds was similar to 'Winters'. It is anticipated that these HSMC will be useful for identifying desirable shoot structures for cultivar improvement and will help to explain the differences in tree architecture and cropping potential among cultivars.

INTRODUCTION

In California, different almond cultivars develop diverse tree architectures. Since almond trees are minimally pruned to maximize yield, these diverse architectures among cultivars are mainly due to their genetic make-up rather than pruning practices (Gradziel et al., 2002). Tree architecture and resulting cropping potential are determined, among other factors, by the branching habit and flowering of shoots (Sarvisé and Socias i Company, 2005). To compare almond selections and cultivars, the quantity of lateral branching and floral buds on a shoot is usually expressed as the density of these traits (Bernad and Socias i Company, 1998; Kodad and Socias i Company, 2008). Statistical methods ranging from exploratory analysis to Markovian models have been used to provide a systematic analysis of the shoot structures, resulting from branching and flowering distribution along the shoots of apple (Costes and Guédon, 1997, 2002), peach

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(Fournier et al., 1998), and apricot (Costes and Guédon, 1996). These methods have been proposed for conducting structural and probabilistic analyses of the branching and flowering data which are structured along the shoots and have variable patterns. The identification of shoot patterns is the first step toward characterizing tree architecture and cropping potential (Guédon et al., 2001).

Flowering, and therefore fruit set, is usually linked to the branching process (Costes et al., 2006). The degree of lateral branching has been used to qualitatively classify almond species and cultivars (Gradziel et al., 2002). Some almond cultivars of commercial interest have been described as having an intermediate branching habit. For example, 'Nonpareil' is a large, upright-to-spreading tree which has limited lateral shoot development on current season's shoots (Gradziel et al., 2002); 'Aldrich' is an upright, tall tree that mainly produces on short spurs; and 'Winters' has an open tree architecture that produces on lateral spur-type shoots (Gradziel et al., 2007).

In addition, there are different types of shoots within a canopy, depending on the meristems or buds that produced them. Sylleptic shoots elongate from lateral meristems immediately after their differentiation, proleptic shoots originate from lateral or terminal meristems after a period of dormancy, and epicormic shoots arise from preventitious buds formed before the previous growing season (Wilson and Kelty, 1994; Wilson, 2000; Costes et al., 2006). Furthermore, sylleptic shoots and epicormic shoots are formed of one type of growth (neoformed), and proleptic shoots can develop from one (preformed) or two (preformed and neoformed) types of growth (Wilson and Kelty, 1994; Costes et al., 2006).

Branching and flowering patterns, produced by the different types of growth on different cultivars, can be quantitatively evaluated using Markovian models to describe their prominent structures. This study's main objectives were to identify the lateral branching and flowering patterns of three almond cultivars which develop different tree architectures, and to determine whether these structures change according to the size of the shoots and the type of buds that produce them.

MATERIALS AND METHODS

The study was conducted in a 3-year-old almond orchard located in Sutter County, California, that had three almond cultivars with different tree architectures ('Nonpareil', 'Aldrich', and 'Winters'). Five categories of 1-year-old proleptic shoots in the tree canopies were described. These were: long shoots (more than 1 m); medium-long shoots (between 60 and 100 cm); medium shoots (between 20 and 60 cm); medium-short shoots (between 5 and 20 cm); and short shoots (less than 5 cm). Before bloom in 2009, 40 shoots of each category were tagged; one of each shoot category in each quadrant of 10 trees. In addition, 40 epicormic shoots (4 in each of ten trees) were also tagged. They were mainly located in the center of the tree canopies.

The structure of every shoot was evaluated by recording two variables at every node: the fate of the lateral meristems and the number of lateral flower buds. Data were collected from the base to the tip of the shoot, in the same way as the shoot developed. For the meristem fate evaluation, each node was placed into one of the following categories: blind, central floral bud, central vegetative bud, or sylleptic shoot. For the number of flower buds per node, the axillary flower buds, as well as the number of flower buds growing on the sylleptic shoots, were recorded.

The two variables were coded and arranged as a bivariate discrete sequence that represented the observations at each node along the shoots. The bud fate variable was coded using increasing numbers from 0 to 3, to indicate the increment of growth activity from one observation to another (i.e., 0: blind; 1: floral bud; 2: vegetative bud; 3: sylleptic shoot). In the sequences, the terminal bud was coded as 4. The second variable that represented the number of flower buds per node was coded from 0 to 3. The numbers 0, 1, or 2 flower buds were the more common numbers per node. Three or more flower buds per node were less common; therefore, when 3 or more flowers were observed at a node, they were coded as 3.

The sequences were analyzed using V-Plants software, the successor of AMAPmod (Godin et al., 1997). The data were interpreted according to three points of view, described by Costes and Guédon (1997) and Guédon et al. (2001). Intensity represented the empirical distribution of the different observations at each node rank. From the intensity distributions of bud fate and number of flower buds, it was possible to identify zones along the shoots with different frequencies of observations between zones. These types of sequences have been modeled in other species as hidden semi-Markov chains (Costes and Guédon, 1996, 2002; Fournier et al., 1998). In these models, the number and succession of branching zones were represented by a Markov chain. The sub-model combining the Markov chain with the distributions of the length of each zone, in number of nodes, was a semi-Markov chain. Each branching zone was not characterized by a single possible observation, but by a specific distribution of observations. Thus, the complete models, incorporating these observation distributions, were hidden semi-Markov chains. A hidden semi-Markov chain is defined by four subsets of parameters: (i) initial probabilities that determined the first zone at the base of the shoot; (ii) transition probabilities that described the succession of zones along the shoot; (iii) occupancy distributions that represented the length of each zone in number of nodes; (iv) two observation distributions in each zone, that described the fate of the central bud and the number of flower buds per node (Renton et al., 2006).

The initial models were based on these empirical distributions, in determining the number of zones in the shoots, the direction of the sequences described, and the presence of a given observation in each zone. The V-Plants software estimated the parameters of the theoretical models, using an iterative algorithm which maximized the likelihood of the observed sequences, starting with the hypotheses established in the initial model. Theoretical distributions were plotted along with the empirical distributions to evaluate estimated models (Guédon et al., 2001) (Fig. 1).

Comparison of the number of states, the occupancy distributions and observation distributions were made among the estimated models of the shoots of different sizes and bud origin for three almond cultivars.

RESULTS AND DISCUSSION

The estimated models showed that there were substantial differences in the structure of proleptic shoots of similar length, among the cultivars, but the epicormic shoots had a more similar structure. Differences were observable in the type and distributions of lateral productions, and in the number of flower buds along the shoots. Specific results are presented here for long and medium proleptic shoots, as well as for epicormic shoots.

The shoot structures for two of the cultivars ('Nonpareil' and 'Aldrich') could be described very well using the HSMC analysis methods (Fig. 1). Defining the structure of the 'Winters' cultivar was more difficult (Fig. 2). Long shoots of 'Nonpareil' could be described with a six-state hidden semi-Markov chain (Figs. 1a and 3). The last state always corresponded to the terminal bud of the shoots. This model was highly structured since the succession of states was almost deterministic and most of the observation distributions were concentrated in one value (Fig. 3). This was similar to the results obtained in apple, suggesting that the fate of the lateral buds depended on the location along the shoots, and this location was related with the growth and environmental factors influencing the developing process of the shoots (Costes and Guédon, 2002). A similar model with six zones located in the same positions was observed along the long shoots in 'Aldrich'. This indicated that the same developmental processes were expressed, while shoots were developing. In both cultivars, there was an association between vegetative buds and 1 or 2 flower buds, and between sylleptic shoots and 3 or more flower buds. Differences in structure between these two cultivars were primarily the length of the zones and the probabilities of the different productions (Fig. 1). For example, 'Nonpareil' had a higher probability of blind nodes after growing sylleptic shoots, while 'Aldrich' had higher probabilities of flower buds per node. 'Winters' had quite different shoot structures

than the other two cultivars, and the HSMC analysis was not able to capture the structure of the long (Fig. 2) or medium-long (data not shown) proleptic shoots. Alternative models that incorporate explanatory variables may be more appropriate in these cases, but this analysis has not been completed. The intensity plots (Fig. 2) indicated that 'Winters' had the greatest probabilities of having lateral branching distributed along shoots and, therefore, expressed very little correlative inhibition (lateral bud dormancy while the apical meristem was growing (Hillman, 1984)). 'Winters' also had the lowest probabilities of producing flower buds along the shoot. Sylleptic shoots, located in the first half of the proleptic shoots, had a higher probability of having 3 or more flower buds per node, similar to what Founier et al. (1998) reported for peach. However, sylleptic shoots in the second half of the shoots had lower probabilities of flowering.

Shorter proleptic shoots had fewer differentiated zones, with reduced lateral branching and fewer lateral flower buds. Vegetative central bud zones became shorter or were not present in the shoots, while the central flower bud zone became larger. Medium proleptic shoots had no lateral branching in 'Nonpareil' and 'Aldrich'; however, there was a small probability of lateral branching (0.09) in 'Winters' (Fig. 4). In addition, lateral flower buds were produced more frequently in the basal part of the medium shoots, while single vegetative buds occurred toward the apical part. The differences in the lateral production of shoots with different length have been related to the growth rate, while the shoots developed (Fournier et al., 1998), but it is clear that the genetic make-up of the cultivars had a strong influence on the expression of lateral productions.

Epicormic shoots had highly structured patterns with more similarities among cultivars than those observed in proleptic shoots (Fig. 5). They had a basal blind zone followed by a single vegetative central bud zone. The third zone corresponded to central vegetative buds with lateral flower buds. In this zone, 'Winters' was the only cultivar that developed a few sylleptic shoots (probability 0.14) and also had the lowest probability of having flower buds (0.30) in 54% of the shoots. The last zone had central flower buds and blind nodes. The similar structures of this type of shoot, among the cultivars, may be more determined by the type of growth (only neoformed) and probably by the rapid growth rate during shoot development, than by the genetic make-up of the cultivars.

CONCLUSIONS

Hidden semi-Markov chains were useful for describing differences in the branching habit and flowering patterns of the three almond cultivars that were analyzed. The only exception was for the structure of long and medium-long proleptic shoots in 'Winters', which were not adequately described using hidden semi-Markov chains. The high transition probabilities between zones of the shoots and the observation distributions, mostly concentrated on a single observation within a zone, confirmed the highly structured nature of branching and flowering in almond. Greater differences were found in the structure of the proleptic shoots of similar length, among the cultivars, but fewer differences were found among epicormic shoots. Within a cultivar, shorter proleptic shoots had fewer differentiated zones with reduced lateral branching and fewer axillary flowers buds, and a proportionally larger central flower bud zone.

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Figures

(a)

(b)

Observed blind node ——+—— ; theoretical blind node —— ✕ ——
Observed flower bud ····✳···· ; theoretical flower bud — · ⊟ · —
Observed vegetative bud — ■ — ; theoretical vegetative bud ——⊖——
Observed sylleptic shoot — ● — ; theoretical sylleptic shoot ·····⌃·····
Observed terminal bud — · ▲ · — ; theoretical terminal bud — · ▽ · —

Observed no flower buds ——+—— ; theoretical no flower buds —— ✕ ——
Observed 1 flower bud ····✳···· ; theoretical 1 flower bud — · ⊟ · —
Observed 2 flower buds — ■ — ; theoretical 2 flower buds ——⊖——
Observed 3 or more flower buds — ● — ;theoretical 3 or more flower buds ··⌃··
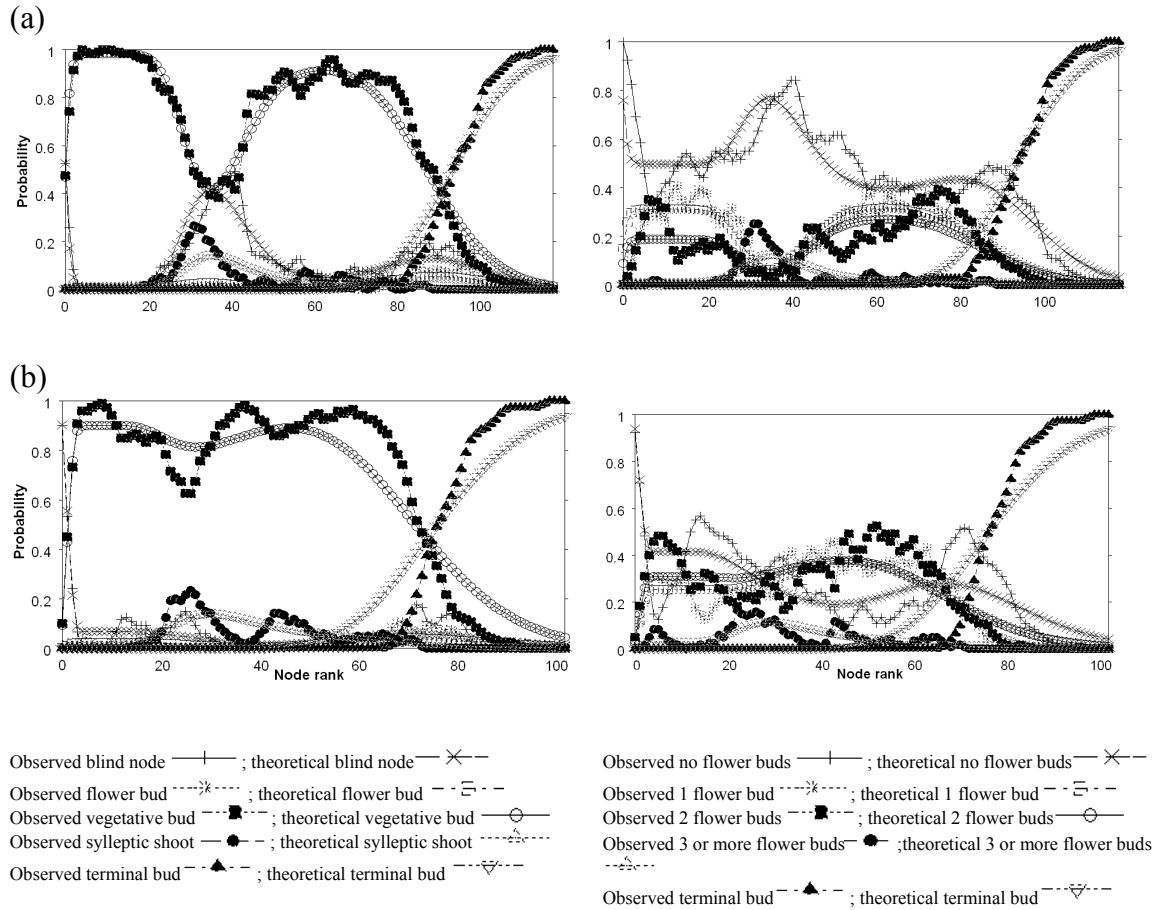Observed terminal bud — · ▲ · — ; theoretical terminal bud — · ▽ · —

Fig. 1. Empirical distributions extracted from the observed sequences along with the theoretical distributions, calculated from the estimated model, for the fate of the lateral bud (left) and the number of flower buds per node (right), along long proleptic shoots for two almond cultivars: 'Nonpareil' (a) and 'Aldrich' (b).

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Observed blind node ——+—— ; Observed flower bud ——✕——
Observed vegetative bud ····✳···· ; Observed sylleptic shoot — · ☐ · —
Observed terminal bud —·■·—

Observed no flower buds ——+—— ; Observed 1 flower bud ——✕——
Observed 2 flower buds ····✳···· ; Observed 3 or more flower buds — · ☐ · —
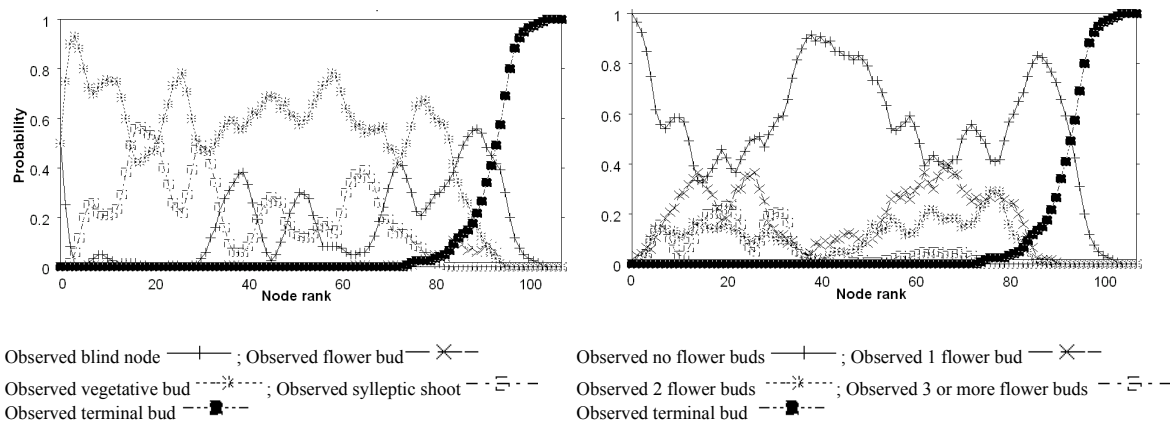Observed terminal bud —·■·—

Fig. 2. Empirical distributions extracted from the observed sequences of the fate of the lateral bud (left) and the number of flower buds per node (right), along long proleptic shoots in 'Winters'.
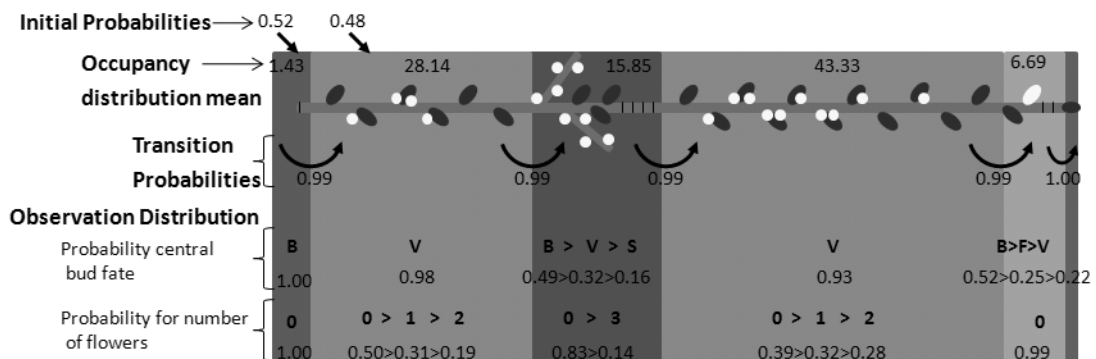

Fig. 3. Schematic representation of the hidden semi-Markov chain for the long proleptic shoots of 'Nonpareil', with the four sets of estimated parameters. The mean length of the different zones of the shoots is represented by each segment. The observations for the central bud fate are: Blind node (B), Floral central bud (F), Vegetative bud (V), or Sylleptic shoot (S). The observations for number of flower buds per node were: no flower bud (0), 1 flower bud (1), 2 flower buds (2), and 3 or more flower buds (3).
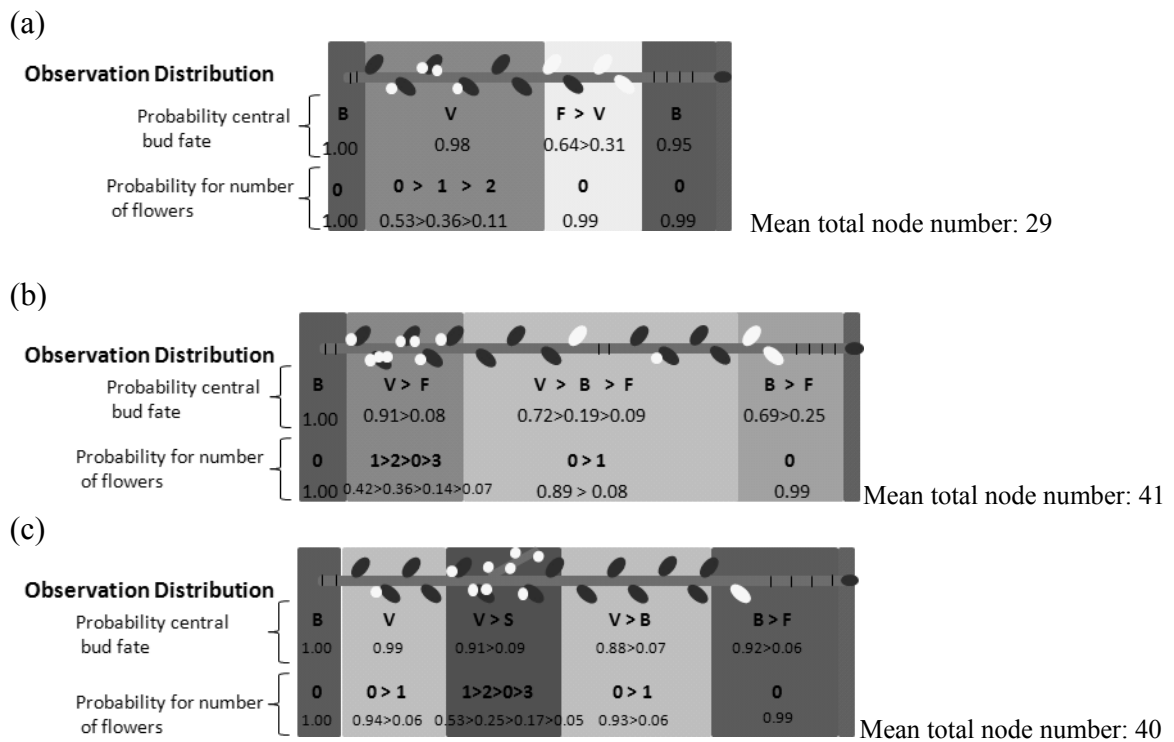
(a)

Observation Distribution

Probability central bud fate

B	V	F > V	B
1.00	0.98	0.64>0.31	0.95

Probability for number of flowers

0	0 > 1 > 2	0	0
1.00	0.53>0.36>0.11	0.99	0.99

Mean total node number: 29

(b)

Observation Distribution

Probability central bud fate

B	V > F	V > B > F	B > F
1.00	0.91>0.08	0.72>0.19>0.09	0.69>0.25

Probability for number of flowers

0	1>2>0>3	0 > 1	0
1.00	0.42>0.36>0.14>0.07	0.89 > 0.08	0.99

Mean total node number: 41

(c)

Observation Distribution

Probability central bud fate

B	V	V > S	V > B	B > F
1.00	0.99	0.91>0.09	0.88>0.07	0.92>0.06

Probability for number of flowers

0	0 > 1	1>2>0>3	0 > 1	0
1.00	0.94>0.06	0.53>0.25>0.17>0.05	0.93>0.06	0.99

Mean total node number: 40

Fig. 4. Schematic representation of the estimated model, for the medium proleptic shoots of 'Nonpareil' (a), 'Aldrich' (b), and 'Winters' (c), with the main values of the observation distributions for the central bud fate and the number of flower bud per node variables.
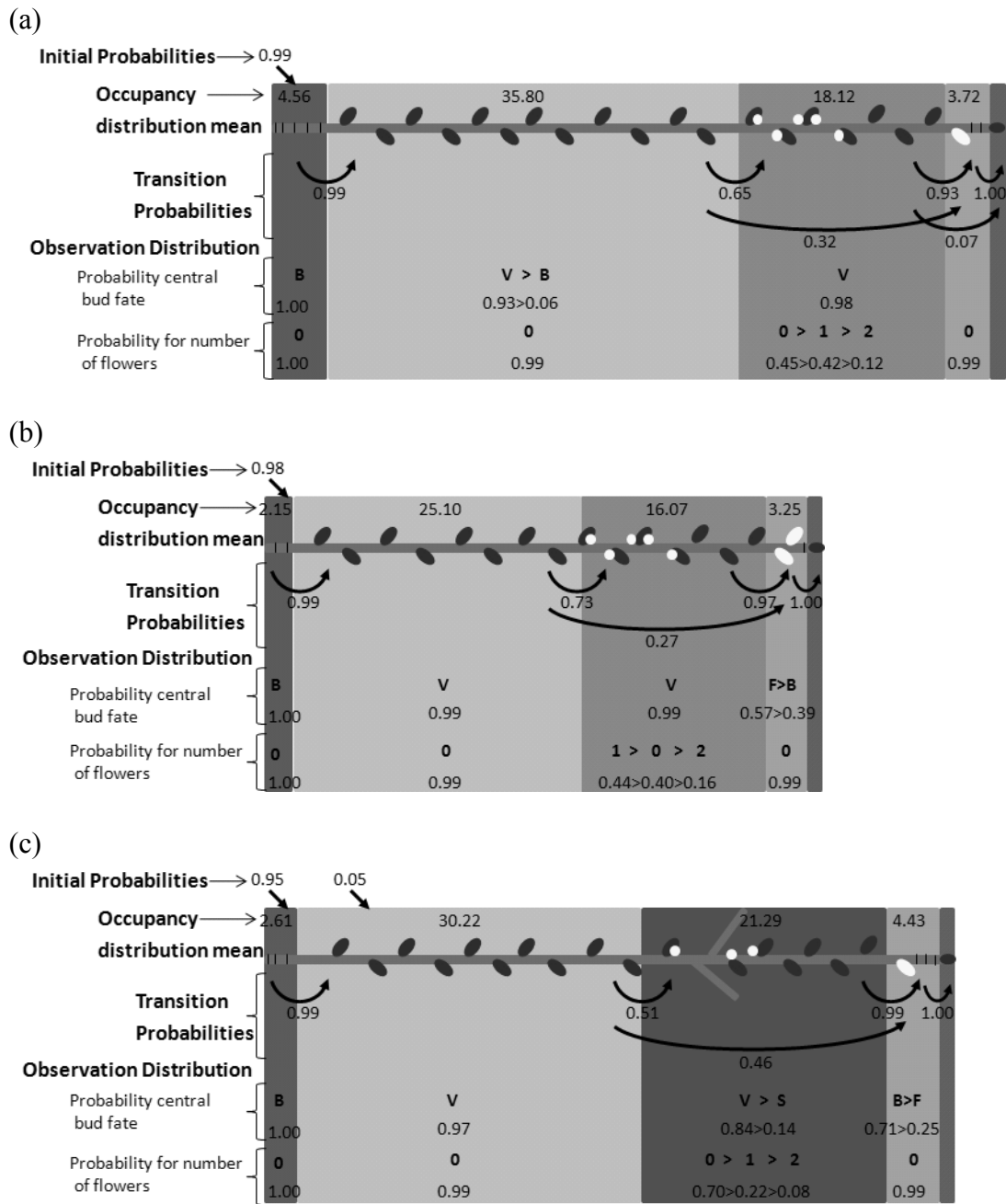
Fig. 5. Schematic representation of the estimated model for the epicormic shoots of 'Nonpareil' (a), 'Aldrich' (b), and 'Winters' (c), with the main values of the observation distributions for the central bud fate and the number of flower bud per node variables.