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Long proleptic and sylleptic shoots in peach (*Prunus persica* L. Batsch) trees have similar, predetermined, maximum numbers of nodes and bud fate patterns

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- **Background and Aims** In peach (*Prunus persica*) trees, three types of shoots can be distinguished depending on the time of their appearance: sylleptic, proleptic and epicormic. On proleptic shoots, an average of ten phytomers are preformed in dormant buds prior to shoot growth after bud-break, whereas all phytomers are considered neoformed in sylleptic and epicormic shoots. However, casual observations indicated that proleptic and sylleptic shoots appear quite similar in number of phytomers and structure in spite of their different origins. The goal of this research was to test the hypothesis that both proleptic and sylleptic shoots exhibit similar growth characteristics by analysing their node numbers and bud fate patterns. If their growth characteristics are similar, it would indicate that the structure of both types of shoots is primarily under genetic rather than environmental control.
- **Methods** The number of phytomers and bud fate patterns of proleptic and sylleptic shoots of four peach cultivars grown in the same location (Winters, California) were analysed and characterized using hidden semi-Markov models. Field data were collected during winter 2016, just prior to floral bud-break.
- **Key Results** Sylleptic shoots tended to have slightly fewer phytomers than proleptic shoots of the same cultivars. The bud fate patterns along proleptic and sylleptic shoots were remarkably similar for all the cultivars, although proleptic shoots started growing earlier (at least 1 month) in the spring than sylleptic shoots.
- **Conclusions** This study provides strong evidence for the semi-deterministic nature of both proleptic and sylleptic shoots across four peach cultivars in terms of number of phytomers and bud fate patterns along shoots. It is apparent that the overall structure of shoots with similar numbers of phytomers was under similar genetic control for the two shoot types. Understanding shoot structural characteristics can aid in phenotypic characterization of vegetative growth of trees and in providing a foundation for vegetative management of fruit trees in horticultural settings.

Key words: Branching pattern, buds, growth cessation, hidden semi-Markov model, neoformation, phytomers, preformation, shoot growth, tree architecture.

INTRODUCTION

Tree architecture is the result of the arrangement of several types of shoot. In peach (*Prunus persica*) trees, three types of shoots can be distinguished depending on the time of their appearance: sylleptic shoots, which are produced from axillary meristems along shoots without a period of dormancy while the terminal part of the parent shoot is still growing (Wilson, 2000; DeJong *et al.*, 2012); proleptic shoots, which are produced from axillary buds after a period of dormancy (Wilson, 2000; Costes *et al.*, 2006); and epicormic shoots, which are produced from dormant preventitious meristems on branches that are usually >2 years old (Fink, 1983; DeJong *et al.*, 2012; Negrón *et al.*, 2015). The preventitious meristems remain latent under the bark until limb breakage, severe limb bending or a severe pruning action occurs distal to the preventitious meristem (Wilson, 2000; Costes *et al.*, 2006; Gordon *et al.*, 2006b; DeJong *et al.*, 2012).

In addition to the above classification, sections of peach shoots can also be categorized according to two organogenesis processes: preformation and neoformation. Preformed sections of proleptic shoots are present within buds during the dormant stage. The growth of shoots less than ten nodes long is solely the consequence of internode elongation during shoot extension growth (Gordon *et al.*, 2006a). However, in long shoots, neoformed sections, with new phytomers, are created as the shoot grows until a terminal vegetative bud is set (Wilson and Kelty, 1994; Costes *et al.*, 2006; Gordon *et al.*, 2006a). Epicormic shoots are considered entirely neoformed because they are initiated from preventitious meristems and continuously add new phytomers until weather conditions or day length become unfavourable for growth conditions late in the season (usually ~180 d after full bloom) (Wareing, 1956; DeJong and Doyle, 1985; DeJong, 2018). Consequently, long epicormic shoots can have between 70 and 90 phytomers in peach trees (DeJong and

Doyle, 1985; DeJong, 2018). Long proleptic shoots can be composed of both preformed and neofomed growth. It is assumed that the additional phytomers appearing after bud-break are neofomed and their appearance is subject to the environmental and growth conditions of the current season (Gordon *et al.*, 2006a). Long proleptic shoots have been reported to be usually limited to <40 phytomers and cessation of growth occurs <100 d after bud-break, even though the environmental conditions and day length are not limiting for epicormic shoot growth (DeJong *et al.*, 2012). In mature producing trees, proleptic shoots are the primary shoots responsible for bearing fruit, while epicormic shoots often produce excessive growth and are removed during pruning (DeJong *et al.*, 2012; DeJong, 2018).

DeJong (2018) suggested that proleptic shoot growth in peach trees is predetermined because growth ceases by mid- to late June, when there are no clear apparent environmental cues that stimulate the cessation of growth. Day length and patterns of daily temperature are usually consistent during that period. There is a paucity of information about the number of phytomers or general characteristics of sylleptic shoots. However, sylleptic shoots grow under different weather conditions later in the spring or summer than proleptic shoots (Davidson *et al.*, 2017) and they must be totally neofomed since the axillary meristems that produce them do not exist prior to the initiation of growth in the meristem that gives rise to the epicormic shoot. Since sylleptic shoots are produced from axillary meristems on neofomed sections of either epicormic or proleptic shoots, it seems logical that sylleptic shoots would not be limited to numbers of phytomers similar to those of proleptic shoots but might instead follow biological rules similar to those followed by epicormic shoots. However, casual observations of shoots growing in the field indicate that sylleptic shoots on epicormic shoots also rarely exceed 40 phytomers in length (T. M. DeJong, personal observation). Thus, we hypothesized that the growth constraints on sylleptic shoots may be similar to those on proleptic shoots. This would indicate that proleptic and sylleptic shoots of peach trees may have similar growth constraints, resulting in similar, predetermined maximum phytomer numbers.

The determination of the total number of phytomers and more detailed analysis of the organization of the axillary bud fates along shoots using Markovian models has been useful for characterizing shoot structure in numerous fruit tree species (Costes and Guédon, 1996, 2002; Costes *et al.*, 1999; Guédon *et al.*, 2001; Negrón *et al.*, 2013, 2014; Renton *et al.*, 2006). In addition to analysing similarities in shoot length (phytomer number) of proleptic and sylleptic shoots, four peach cultivars with differing times of fruit maturity grown in the same experimental orchard were studied to compare their shoot architectural characteristics by developing Markovian bud fate models.

The primary goal of this research was to test the hypothesis that proleptic and sylleptic shoots of peach trees are under similar developmental constraints regarding maximum number of phytomers and to determine whether the two types of shoot have similar axillary bud fate patterns. If both the maximum shoot phytomer numbers and bud fate patterning along the shoots are similar for proleptic shoots that grow in early spring and sylleptic shoots that grow in late spring or summer, it would indicate that both proleptic and sylleptic shoots on field-grown peach trees are more under genetic control than responsive to environmental signals prevailing at the time of growth. A better understanding of

the biological processes underlying shoot growth, growth cessation and development of trees in general, and in peach trees specifically, can provide a better understanding of the development and growth of the structure of trees, as well as providing a scientific basis for management practices such as pruning.

The specific objectives of this study were to: (1) compare the number of phytomers on long proleptic and sylleptic shoots for a given cultivar; (2) analyse the axillary bud fate patterns of the proleptic and sylleptic peach shoots; and (3) compare these traits in four peach cultivars to test for the consistency of these biological traits among cultivars.

MATERIALS AND METHODS

Plant material

The experiment was performed in 2016 in an experimental peach (*Prunus persica*) orchard located at the UC Wolfskill Experimental Orchards in Winters (38°30' N, 121°58' W), CA, USA. Four peach cultivars, 'Lorrie May' (early maturing, June), 'Flavorcrest' (early maturing, June), 'Elegant Lady' (mid-season maturing, July) and 'O'Henry' (mid-late maturing, August), were selected for the study. 'Lorrie May' trees were grafted on Controller™ 9 rootstock (DeJong *et al.*, 2011) in 2006 and planted in the orchard in 2007. 'Elegant Lady' and 'O'Henry' trees were grafted on 'Lovell' rootstock in 2007 and planted in the orchard in 2008. The 'Flavorcrest' trees were on 'Lovell' rootstock and planted in the orchard in 1986. Controller™ 9 rootstock produces trees that are generally less vigorous than trees on the standard peach rootstocks but in previous trials there were no noticeable differences in terms of tree structure or architecture other than tree vigour. There are generally more differences in tree architecture among scion cultivars than among the same scions on different rootstocks (Weibel *et al.*, 2003). All trees were trained to a perpendicular V training system (DeJong *et al.*, 1994) with north-south row orientation. The distances between trees and rows were 1.8 and 5.2 m, respectively. The trees were maintained according to standard orchard management practices for the area with irrigation scheduled weekly to supply ample water to match orchard evapotranspiration over the growing season and ~60 kg ha⁻¹ of nitrogen fertilizer was applied early in the growing season. Trees from one row located in the middle of each 0.4-ha cultivar block were selected for the study. Trees were pruned in all the winters from the year of planting to maintain their training system, but trees selected for the study were not pruned during the winter of 2015–16 to retain epicormic shoots and their sylleptic shoots for the study. In early February 2016, 40 of the longest proleptic shoots and 20 epicormic shoots were selected and tagged from ten trees of each cultivar for subsequent morphological description. The longest sylleptic shoots (three shoots per epicormic shoot) were selected and tagged on each vigorous epicormic shoot.

Shoot architecture

The sequence of axillary bud fates along each shoot was recorded from the base to the tip using two variables (Costes *et al.*, 2006; Negrón *et al.*, 2015). The first variable indicated the fate of the central bud according to the following categories: blind node (no bud present), floral bud, vegetative

bud and sylleptic shoot. The second variable indicated the number of floral buds that were axillary to the central vegetative bud (referred to as the number of associated floral buds in the following). The number of associated floral buds ranged from zero to two. From this quantification, the numbers of phytomers and bud fates on each shoot were recorded, and the bud fate frequency was calculated.

Analysis of the impact of cultivar and shoot type on phytomer number per shoot, axillary bud proportion and associated floral buds

All the statistical analyses were performed using the R software (R Core Team, 2017) (R version 3.2.4 Revised). The effect of cultivar and shoot type (proleptic or sylleptic) on the number of phytomers per shoot and the number of central and associated floral buds were tested by two-way ANOVA with interaction after checking the normality of residuals with a Shapiro–Wilk test. The analysis was followed by Tukey’s honest significant difference test for pairwise comparison considering all the shoot type and cultivar combinations. The effect of each shoot and cultivar combination on proportions of central bud fates and proportions of buds with associated floral buds was assessed with a χ^2 test (Siegel and Castellan, 1988; Sharpe, 2015). The analysis was followed by a *post hoc* test considering all the shoot type and cultivar combinations using the *chisq.post.hoc* function of the *fifer* package of R software.

Organization of bud fates along shoots

To determine the sequence of bud fates along shoots, hidden semi-Markov models (HSMMs) were built for all shoot types and cultivars (Costes and Guédon, 1997, 2002; Renton *et al.*, 2006), using the V-Plants software (release 0.9) of the OpenAlea platform (Pradal *et al.*, 2008). Shoot structure information was represented in these models with the estimation of the following parameter subsets: (1) initial probabilities for delineating the first zone at the base of the shoot; (2) transition probabilities determining the succession of zones along the shoot; (3) occupancy distributions representing the length of each zone (in number of phytomers); and (4) observation distributions representing the mixture of observations in each zone for the two observed variables (central bud fate and number of associated floral buds) (Costes and Guédon, 1997, 2002; Renton *et al.*, 2006). To select the number of zones, i.e. the number of states of the HSMMs, the following four criteria were used, as proposed by Guédon *et al.* (2007).

- (1) Almost deterministic succession of states, i.e. in most cases states cannot be skipped, and when they can be skipped it is always with a rather small probability.
- (2) Small relative dispersions of state occupancy (i.e. zone length) distributions, evaluated by the ratio of the standard deviation to the mean (i.e. the coefficient of variation), which is expected to be <1.
- (3) Small overlap between observation distributions for consecutive states. To assess the contrasting definition of zones, the overlap between observation distributions for consecutive states was computed as $\sum_x \min \{b_i(x), b_{i+1}(x)\}$, where

$b_i(x)$ is the probability of observing category x (i.e. either a central bud fate or a given number of associated floral buds depending on the observed variable) in state i . This similarity measure takes values between 0 (no overlap) and 1 (full overlap).

- (4) Low ambiguity of the segmentation in successive zones. To assess this criterion, the posterior probabilities of the optimal segmentations (i.e. weight of the optimal segmentation among all the possible segmentations of a given observed sequence) were examined and were expected to be high with respect to the number of possible segmentations.

Complementary to the comparison of parameters and characteristics of HSMMs (i.e. zone length and composition), using the zone lengths extracted from the optimal segmentation we also analysed the correlations (1) between the length of each zone and (2) between zone lengths and the total length of the sequence. Clustering was also applied to develop a global view of the dissimilarities between the axillary bud fate patterns of the proleptic and sylleptic shoots of the four cultivars. For this, we applied the approach proposed in Guédon *et al.* (2003). We first computed the matrix of pairwise dissimilarities between HSMMs using a probabilistic dissimilarity measure (Kullback–Leibler divergence). We then clustered the HSMMs using a hierarchical clustering approach applied to the matrix of pairwise dissimilarities.

RESULTS

Number of phytomers

There was a significant cultivar effect on the number of phytomers per shoot (Table 1). Similarly, there was a significant shoot type effect that was mainly associated with fewer phytomers on

TABLE 1. Mean numbers of phytomers, associated standard deviations, coefficients of variation (i.e. ratio of the standard deviation to the mean) and maximum numbers of phytomers for proleptic and sylleptic shoots on mature trees of four peach cultivars

Shoot type	Cultivar	Mean \pm s.d.	Coefficient of variation	Maximum number of phytomers
Proleptic	‘Lorrie May’	32.5 \pm 5.82 ^{abc}	0.17	44
	‘Flavorcrest’	33.7 \pm 7.19 ^{ab}	0.21	46
	‘Elegant Lady’	35.1 \pm 5.45 ^a	0.15	44
	‘O’Henry’	28.6 \pm 6.94 ^{de}	0.23	44
Sylleptic	‘Lorrie May’	27.9 \pm 4.73 ^e	0.16	39
	‘Flavorcrest’	31.6 \pm 5.74 ^{bcd}	0.18	44
	‘Elegant Lady’	29.8 \pm 4.68 ^{ode}	0.15	41
	‘O’Henry’	23.0 \pm 3.74 ^f	0.16	33
Shoot type effect		***		
Cultivar effect		***		
Shoot type \times cultivar effect		ns		

Shoot type and cultivar effects were assessed by a two-way ANOVA with interaction. This analysis was followed by a *post hoc* Tukey’s honest significant difference test considering the complete dataset.

Values with different superscript letters are significantly different ($P < 0.05$).

*** $P < 0.001$; ns, not significant.

sylleptic compared with proleptic shoots for all cultivars. There were no significant interactions between cultivar and shoot type on the mean number of phytomers (Table 1). Based on the *post hoc* analysis, the number of phytomers in proleptic shoots was similar among cultivars, except for ‘O’Henry’, having fewer phytomers than the other cultivars (Table 1). ‘O’Henry’ also had the lowest mean number of phytomers on sylleptic shoots. The maximum number of phytomers on sylleptic shoots was less than on proleptic shoots of the same cultivar and ‘Flavorcrest’ had the highest maximum number of phytomers both for sylleptic and proleptic shoots (Table 1).

Bud fates along shoots and floral bud number

The analysis of the composition of phytomers and bud frequencies revealed the existence of the following axillary bud fates for both proleptic and sylleptic shoots: blind nodes (with latent buds); nodes with a central vegetative bud with no associated floral buds; nodes with a central vegetative bud with one or two associated floral buds; and nodes with only a central floral bud (Table 2). Three associated floral buds with a central vegetative bud occurred in some phytomers on sylleptic shoots but at a very low frequency (0.37 % of total buds).

There was a significant shoot type effect for the number of central floral buds and the number of associated floral buds; all proleptic shoots had higher numbers of floral buds than sylleptic shoots (Table 3). There was a cultivar effect on the number of associated floral buds, with ‘O’Henry’ having the fewest associated floral buds in both shoot types (Table 3). There was a significant effect of the shoot type × cultivar interaction on the number of associated floral buds. This interaction effect was due to a larger decrease in the number of associated floral buds between proleptic and sylleptic shoots in ‘Lorrie May’ (–39 %), ‘O’Henry’ (–59 %) and ‘Flavorcrest’ (–31 %) compared with ‘Elegant Lady’ (–12 %).

Analysis of the estimated HSMMs

Models with different numbers of states, including an absorbing state (terminal bud), were compared in order to find an optimal number of zones for shoot segmentation. Six-state

HSMMs were clearly over-parameterized, with far more transition-skipping states compared with the selected five-state HSMMs, whereas the four-state HSMMs were roughly nested within the five-state HSMMs, with similar states 0 and 1 and a merging of states 2 and 3 with respect to the corresponding five-state HSMMs (data not shown).

The same zones were identified using the five-state HSMMs for all proleptic and sylleptic shoots. The zones were defined as follows: zone 1, basal zone dominated by blind nodes or a central vegetative bud without associated floral buds (~93 % for both bud fates); zone 2, central vegetative bud zone dominated by nodes with a central vegetative bud (~92 %) with zero, one or two associated floral buds; zone 3, central floral bud zone, composed of a mixture of nodes with a central floral, latent or vegetative bud with few or no associated floral buds; zone 4, distal zone, composed mainly of blind nodes (~0.85 %) and occasionally a floral bud (Fig. 1). Regarding overlaps between observation distributions for consecutive zones, the central bud fate appeared more indicative than the number of associated floral buds, which was not discriminant for the last two zones (Supplementary Data Table S1). However, the number of associated floral buds was more discriminant for ‘Lorrie May’ and ‘Flavorcrest’, which had more associated floral buds in zone 2, than for ‘Elegant Lady’ and ‘O’Henry’. Nevertheless, there was some heterogeneity in the zone separation, ranging from ‘O’Henry’ proleptic shoots, where consecutive zones were clearly separated by the central bud fates, to ‘Flavorcrest’ sylleptic shoots, where consecutive zones were less markedly separated. As a consequence, the segmentation in successive zones was more certain for ‘O’Henry’ proleptic shoots than for ‘Flavorcrest’ sylleptic shoots (Supplementary Data Table S2).

Very similar zones were identified between the two types of shoots for all cultivars. However, there were some differences in bud compositions for some cultivars in specific zones. The main differences were associated with a higher proportion of central vegetative buds in zone 1 in ‘Lorrie May’ and ‘Flavorcrest’ and in zone 3 in ‘Flavorcrest’ (Fig. 1) for sylleptics compared with proleptics.

For all cultivars and shoot types the coefficients of variation of each zone length were far less than 1 for all the estimated distributions (Table 1), indicating a relatively small dispersion of zone length distributions. While the same bud fate zones were present in the majority of shoots analysed

TABLE 2. Means and standard deviations for relative frequencies of nodes (% of total node number) with different types of buds per shoot type and cultivar

Shoot	Cultivar	Blind nodes	Vegetative without associated floral buds	Vegetative with associated floral buds	Central floral bud
Proleptic	‘Lorrie May’ ^d	27.9 ± 9.60	22.6 ± 9.79	33.8 ± 9.50	15.8 ± 6.95
	‘Flavorcrest’ ^e	29.4 ± 10.09	29.8 ± 12.27	24.1 ± 9.62	16.7 ± 6.65
	‘Elegant Lady’ ^b	31.5 ± 10.14	33.6 ± 12.80	22.3 ± 8.93	12.7 ± 5.91
	‘O’Henry’ ^c	28.8 ± 11.16	38.7 ± 16.33	15.8 ± 10.54	16.6 ± 7.78
Sylleptic	‘Lorrie May’ ^a	28.4 ± 10.97	32.9 ± 13.92	23.8 ± 12.49	14.8 ± 9.40
	‘Flavorcrest’ ^b	29.6 ± 10.23	34.9 ± 12.28	21.2 ± 12.18	14.3 ± 8.22
	‘Elegant Lady’ ^{ac}	32.2 ± 9.65	36.1 ± 9.79	16.9 ± 10.31	14.3 ± 8.78
	‘O’Henry’ ^f	33.7 ± 10.13	39.4 ± 14.43	8.1 ± 9.44	18.7 ± 8.80

Significances of differences between bud proportion among shoot types and cultivars were assessed with the χ^2 test ($P < 0.001$). This analysis was followed by a *post hoc* test ($P < 0.05$) for pairwise comparison and the significant differences between shoot type–cultivar combinations are represented by different superscript letters.

TABLE 3. Means and standard deviations for number of central floral buds and number of associated floral buds comparing four cultivars per shoot type

Shoot	Cultivar	Central floral buds	Number of associated floral buds
Proleptic	'Lorrie May'	5.0 ± 2.25 ^{ab}	17.2 ± 5.74 ^a
	'Flavorcrest'	5.7 ± 2.71 ^a	12.0 ± 5.53 ^b
	'Elegant Lady'	4.3 ± 1.94 ^{ab}	11.5 ± 5.45 ^b
	'O'Henry'	4.6 ± 2.04 ^{ab}	6.9 ± 5.59 ^d
Sylleptic	'Lorrie May'	4.0 ± 2.44 ^b	10.4 ± 6.51 ^{bc}
	'Flavorcrest'	4.5 ± 2.51 ^{ab}	10.5 ± 7.41 ^{bc}
	'Elegant Lady'	4.1 ± 2.51 ^b	7.9 ± 5.71 ^{cd}
	'O'Henry'	4.3 ± 2.17 ^{ab}	2.8 ± 3.80 ^e
Shoot type effect	**	***	
Cultivar effect	ns	***	
Shoot type × cultivar effect	ns	*	

Shoot type and cultivar effects were assessed by a two-way ANOVA with interaction. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant. This analysis was followed by Tukey's honest significant difference *post hoc* test ($P < 0.05$) for pairwise comparison and statistical differences between shoot type–cultivar combination are represented by different superscript letters.

across all cultivars, there were substantial differences in the mean lengths of the individual zones, especially among cultivars (Fig. 1). The length of zone 1 was the most consistent and shortest (2.5 nodes on average) among cultivars and shoot types. Zone 2, dominated by having central vegetative buds (with or without associated floral buds), was the longest zone (14.1 nodes on average) among all cultivars and shoot types. The mean length of zone 3, which characteristically had central floral buds at most nodes, was quite consistent between shoots of the same cultivar, but differed among cultivars and its mean length tended to vary inversely with the mean lengths of zone 4 within a cultivar (Fig. 1). Among the different cultivars and shoot types, zone 3 was shortest in 'O'Henry' (<4.5 nodes) whereas 'Flavorcrest' proleptics shoots had the longest zone 3 (11.9 nodes).

The transition probabilities between consecutive zones had a value of 1 for most of the shoot type–cultivar combinations, indicating a distinct succession of zones. Zone 4 was skipped in a few 'Flavorcrest', 'Elegant Lady' and 'O'Henry' proleptic shoots (probability between 0.02 and 0.2). Zones 2 and 3 were occasionally skipped in some 'Lorrie May' and 'Flavorcrest' shoots (probabilities between 0.02 and 0.08), but overall the numbers of shoots with zone skips was very low (Fig. 1).

Scaling of zones as a function of the total shoot length

Negative correlations between the lengths of each zone were observed between zones 2 and 3 for four types of shoot ('Lorrie May', 'Flavorcrest', 'Elegant Lady' sylleptic shoots and 'Elegant Lady' proleptic), and between zones 1 and 2 for only two shoot types ('Flavorcrest' and 'O'Henry' sylleptic) (Supplementary Data Table S3). Regarding the correlations between zone lengths and the total shoot length (Table 4), shoot length variations were mainly associated with variations in the lengths of zones 2 and 4. The only exception was the proleptic shoots of 'Flavorcrest', in which the total shoot length was

correlated with the length of zone 3. This latter correlation was likely a result of the longer length of zone 3 for these shoots compared with the other shoots (Fig. 1).

Similarities and differences in the bud fate patterns among shoot types and cultivars

Similarities and differences among the axillary bud fate patterns for the different shoot types and cultivars were analysed by hierarchical clustering based on Kullback–Leibler divergences between the estimated HSMMs (Fig. 2). Differences between HSMMs highlighted by the cluster analysis combine differences in zone lengths and within-zone axillary bud fates with more subtle effects due to potential mixing between consecutive zones ('Elegant Lady' had similar proleptic and sylleptic HSMMs; differences only concerned some zone lengths, while for the other cultivars the differences between proleptic and sylleptic HSMMs combined differences in zone length and within-zone axillary bud fates; Table 1, Figs 1 and 2). The clusters obtained reflected differences in the number of phytomers (Table 1) and consequently in zone lengths and within-zone axillary bud fates among the shoots (Fig. 1). 'Lorrie May' and 'O'Henry' sylleptic shoots had the fewest phytomers and were characterized by the shortest 2nd zones compared with the other shoot and cultivar combinations (Table 1, Fig. 1). 'Flavorcrest' proleptic and sylleptic and 'Lorrie May' proleptic shoots were close on the dendrogram and had similar numbers of phytomers (Table 1, Fig. 2). These shoots were also characterized by a high number of associated floral buds in zone 2 compared with 'Elegant Lady' proleptic, 'Elegant Lady' sylleptic and 'O'Henry' proleptic shoots (Fig. 1). These differences were consistent with the observed number of associated floral buds (Table 3).

In this clustering the cultivar effect was marked for 'Flavorcrest' and 'Elegant Lady', for which proleptic and sylleptic shoots were particularly similar (Fig. 2). The case of 'Elegant Lady' is rather specific since the axillary bud fates were very similar for all the zones between proleptic and sylleptic shoots and the differences mainly concerned the shorter central vegetative bud and distal zones for sylleptic shoots compared with proleptic shoots. For 'Flavorcrest' there were differences in axillary bud fates, particularly in the basal and central floral bud zones, and differences in zone length between successive central floral bud and distal zones (but there was compensation because of mixing between these two successive zones). Proleptic and sylleptic shoots were more strongly differentiated for 'Lorrie May' and 'O'Henry' due to the differences in phytomer number (Table 1). 'Lorrie May' proleptic and sylleptic shoots were also differentiated by central bud fates in the basal zone and to a lesser extent in the distal zone, as well as differences in zone lengths of the central vegetative bud and distal zones. There was a higher proportion of vegetative buds in the basal zone in sylleptic shoots (0.61) than in proleptic shoots (0.01) (Fig. 1). For 'O'Henry' the main differences among shoot types were in the length of the central vegetative bud and distal zones, where proleptic shoots were longer than sylleptic shoots. The ranking of cultivars in terms of the number of floral buds (differences were mainly in zone 2) was 'Flavorcrest' and 'Lorie May' > 'Elegant Lady' > 'O'Henry'.

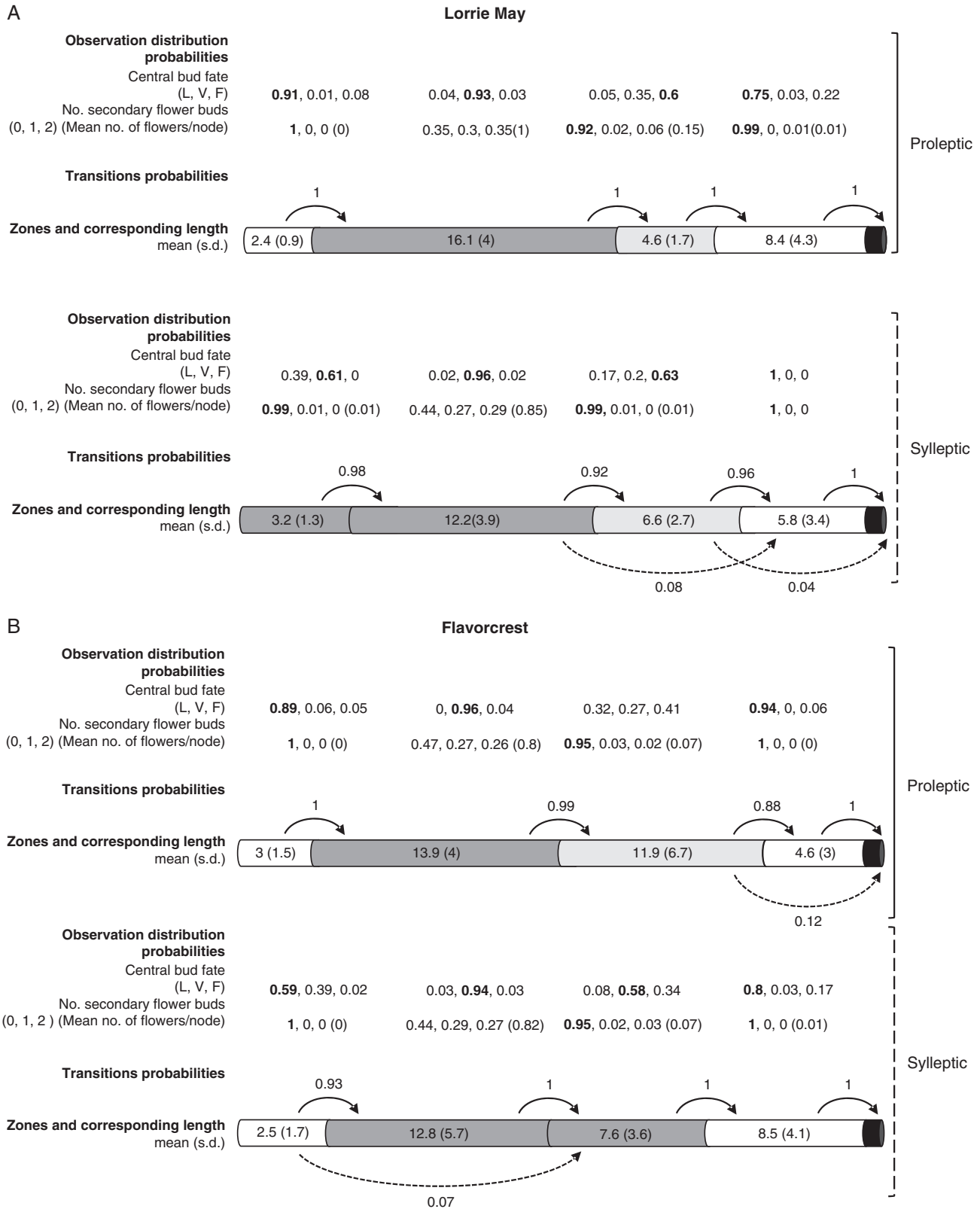


FIG. 1. Schematic representations of the HSMs for proleptic and sylleptic shoots of four peach cultivars. Relative proportions of central bud fates [latent (blind), vegetative and floral (L, V, F)] and numbers of flowers per node are shown above each bar. Shading of bars represents differences in most probable bud fates in each zone. Arrows represent the transition probabilities (>0.04) between zones with their respective probabilities. Mean zone lengths (number of nodes per zone) and standard deviations are identified inside each zone shade.

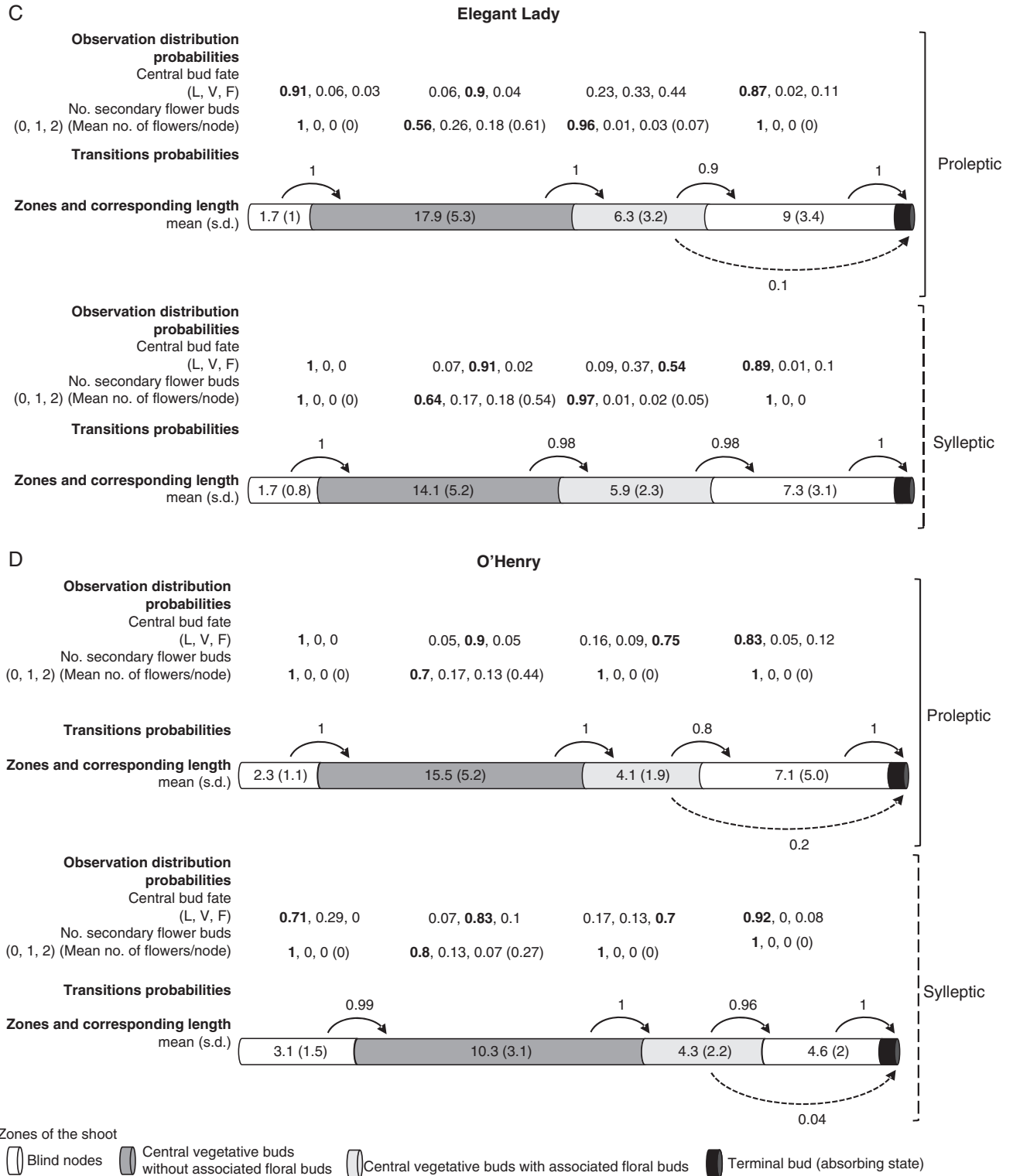


FIG. 1. Continued

DISCUSSION

Contrary to expectations, in this study the number of nodes in sylleptic peach shoots tended to be fewer than in proleptic shoots. This was unexpected because the sylleptic shoots observed in

this study were borne on vigorous epicormic shoots, which can grow throughout the growing season and reach as many as 80 nodes (Davidson *et al.*, 2017). This research indicates that proleptic and sylleptic shoots for a given peach cultivar were under

TABLE 4. Correlation between zone lengths extracted from the optimal segmentation of the observed sequences using the estimated HSMs and the observed sequence length for the proleptic and sylleptic shoots of the four cultivars. Correlation coefficients (and ns for non-significant correlation coefficients at $\alpha = 0.05$) which were between the limits indicated in the last column

Cultivar, shoot type	Zone 1	Zone 2	Zone 3	Zone 4	Limit
'Lorrie May', proleptic	ns	0.66	ns	0.71	± 0.30
'Lorrie May', sylleptic	ns	0.6	ns	0.54	± 0.25
'Flavorcrest', proleptic	ns	ns	0.74	0.4	± 0.30
'Flavorcrest', sylleptic	-0.30	0.68	ns	0.34	± 0.25
'Elegant Lady', proleptic	ns	0.57	ns	0.58	± 0.30
'Elegant Lady', sylleptic	0.37	0.69	ns	0.36	± 0.25
'O'Henry', proleptic	ns	0.68	ns	0.65	± 0.29
'O'Henry', sylleptic	ns	0.65	0.38	0.4	± 0.25

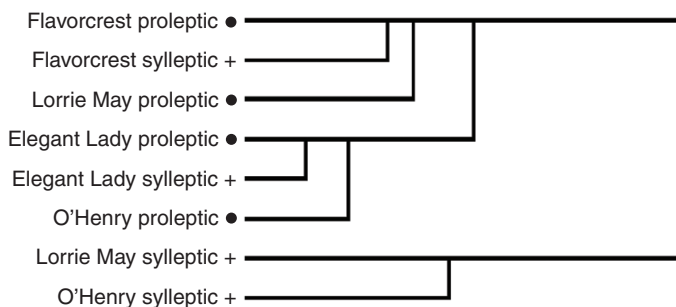


Fig. 2. Dendrogram of the hierarchical clustering of the branching and associated flowering patterns on the basis of Kullback–Leibler divergences between estimated HSMs.

similar constraints with regard to the numbers of phytomers per shoot and had similar axillary bud fate patterns along the shoots. Considered together, the small overlap between observation distributions for consecutive zones, particularly for central bud fate, the relatively high probabilities of the optimal segmentation, and the overparameterization of the six-state HSMs clearly indicated that the five-state HSMs we selected were relevant for modelling the observed bud fate patterns on both shoot types in this study. The general bud fate patterns described in this research were very similar to patterns previously reported for peach trees. Terminal buds were always vegetative and located at the end of the shoot. Axillary buds could abort (resulting in a 'blind' node), be vegetative with zero to two associated lateral floral buds or be floral (López *et al.*, 2008). Axillary buds, depending on their fates, were organized on the shoot following a succession of several zones as reported by Fournier *et al.* (1998). Peach bud fate patterns were well described using bivariate HSMs for different shoot types to determine the succession of zones and the proportion of axillary production fates in the zones, as reported by Costes *et al.* (2006) and Smith *et al.* (2008). Furthermore, while there were minor specific differences, the general bud fate patterns were markedly similar among the four cultivars studied. Thus, this study supported the notion of endogenous control in determining the maximum length and architecture of both proleptic and sylleptic shoots of peach trees.

Number of phytomers and growth cessation of shoots

The maximum number of phytomers in the long sylleptic shoots analysed in this study never exceeded 44 over a sample

of 240 shoots in four different cultivars. This number is similar to the maximum number of phytomers previously reported for sylleptic shoots of very young trees of 'Flavortop' and 'Redwing' peach trees (Costes *et al.*, 1993). This value was also similar to the maximum number of phytomers on the 160 proleptic shoots (46 phytomers) examined in this study. These maximum phytomer numbers were less than the number of phytomers observed on epicormic peach shoots in other studies (between 70 and 100) (DeJong and Doyle, 1985; Gordon *et al.*, 2006a; Davidson *et al.*, 2017).

Even though there were statistically significant differences between the mean numbers of phytomers on sylleptic and proleptic shoots of three cultivars ('Lorrie May', 'Elegant Lady' and 'O'Henry') and between the same shoot types of the four cultivars, the mean numbers of phytomers per shoot among shoot types and cultivars were quite similar with respect to the range of the number of phytomers that can be observed within a peach tree (Table 1). This may have been partially due to the fact that all trees received similar amounts of irrigation water and nutrients. However, the mean numbers of phytomers per shoot for the long proleptic shoots tagged in this study were also very similar to the numbers reported previously for 'Robin' peach trees grown in France (Costes *et al.*, 1999) and for 'Summer Fire' nectarine trees grown near Fresno, CA, USA (DeJong *et al.*, 2012). The fact that the mean numbers of phytomers on sylleptic shoots were less than on proleptic shoots is interesting since sylleptic shoots are entirely neofomed while proleptic shoots are partially preformed (Gordon *et al.*, 2006a), and thus the apical meristem of proleptic shoots might be more likely to be 'preprogrammed' while still in an overwintering proleptic bud.

Based on the numbers of phytomers for both shoot types, their maximum number appeared to be limited in a similar way, i.e. the maximum phytomer number of these shoots appeared to be determined by some internal mechanism or genetics rather than being subject to environmental cues. In California, the timing of the cessation of the longest proleptic peach shoots occurs from mid- to late June (DeJong and Doyle, 1985; Davidson *et al.*, 2017). At that time of year day length is still increasing and daily changes in day length are very minor. In addition, the mean daily temperature patterns in California are relatively similar from late May to late July in most years. Although reductions in photoperiod have been linked to the cessation of shoot growth during late summer or autumn in many tree species, Wareing (1956) concluded that in woody species where 'extension growth ceases in June or July before there has been any appreciable reduction in natural length of day and that ...

cessation of extension growth at this time cannot be due to the fact that day length conditions have become limiting and it seems probable that the duration of extension growth is here controlled endogenously’.

Growth cessation of all proleptic shoots was likely not coordinated and actually most proleptic shoots probably stopped growing much earlier than the longest shoots chosen for this study. Thus, the timing of the cessation of growth of most proleptic shoots was likely subject to endogenous signals (resource availability and/or growth regulators). With an average maximum phytomer number of around 35 phytomers and a leaf appearance rate of between 2 and 4 d (Davidson *et al.*, 2015), proleptic shoots were probably entirely formed between 88 and 132 d after full bloom (May to late June) in spite of the apparent absence of environmental factors that could cause the cessation of growth. No proleptic shoots grew past a limited number of phytomers and thus virtually all stopped growing by the end of June, when conditions were still satisfactory for growth of epicormic shoots, which could grow for another 2–3 months (DeJong *et al.*, 1987; Davidson *et al.*, 2017). This supports the assertion of Wareing (1956) and indicates that there was some internal programming that limited their phytomer number. The current research extends the concept proposed by DeJong (2018), that the maximum length of proleptic shoots of peach trees appears to be deterministic (predetermined), and this also appears to pertain to sylleptic shoots borne on epicormic shoots.

Proleptic buds have ~10 preformed phytomers prior to bud-break in the spring (Gordon *et al.*, 2006a), and subsequent successive phytomers appear to be neofomed after bud-break until the cessation of growth. Sylleptic and epicormic shoots are entirely neofomed (Wilson and Kelty, 1994) and epicormic shoots do not stop growing until environmental conditions become unfavourable (DeJong and Doyle, 1985). It has been reported that peach trees have a high capacity for neofomation (Gordon *et al.*, 2006a), which implies a high plasticity for adaptation to current environmental conditions of the season (Puntieri *et al.*, 2002), but this appears to be mainly the case for epicormic shoots. Since both epicormic and sylleptic shoots are neofomed while the maximum phytomer numbers of both proleptic and sylleptic shoots appear to be endogenously limited, the extended growth of epicormic shoots over the growing season does not appear to be necessarily associated with neofomation.

One internal mechanism proposed for explaining determinacy in plants is ‘node counting’ (Sachs, 1999). However, this mechanism has been mostly referred to in studies of annual plants where a floral apex is formed after shoots develop specific numbers of phytomers. But Sachs (1999) also suggested that node or phytomer counting is a mechanism that ‘enables a plant to be divided into sectors whose developmental state is determined separately’. Along similar lines, de Reffye *et al.* (1991) statistically modelled the cessation of growth of the neofomed portion of proleptic shoots of cherry and apricot as a function of meristem ‘ageing’ or meristem ‘fatigue’. This concept of shoot node or phytomer number being under the control of mechanisms within the shoot also supports the notion of viewing plants or peach trees as populations of semi-independent organs (White, 1979; DeJong, 1999).

The number of phytomers of individual proleptic shoots is generally considered to be at least partially governed by apical control: the inhibition of lateral branch growth by distal shoots on the same axis (Wilson, 2000). Apical control has been reported to be mediated by hormones, particularly auxin and cytokinins (Cline, 2000; Wilson, 2000). There is little doubt that apical control is likely the phenomenon that affects the length of many of the shorter proleptic shoots of a peach tree; however, this study focused on the longest proleptic shoots and the mean number of phytomers on these shoots was almost similar for all four cultivars. Furthermore, the numbers of phytomers of sylleptic shoots on epicormic shoots was similar or smaller than on proleptic shoots, but apical control is thought to not pertain to sylleptic shoots on epicormic shoots (Wilson, 2000). Field observations indicated that multiple sylleptic shoots produced in the central section of very long epicormic branches all had similar numbers of phytomers and the length (number of phytomers) of sylleptics on these epicormic branches did not systematically increase or decrease from the tip or the base of the branches (data not shown). Thus, apical control does not appear to be the mechanism involved in limiting the number of phytomers on the shoots examined in the study.

Axillary bud fate patterns along proleptic and sylleptic shoots

The second aspect of this study concerned the organization of buds along the shoots using Markovian models. The most striking aspects of the HSMM analysis of axillary bud fates along the shoots analysed were the similar patterns between proleptic and sylleptic shoots of the same cultivars and between shoots of different cultivars (Fig. 1).

Within the common axillary bud fate patterns, the cluster analysis based on the dissimilarities between HSMMs highlighted some quantitative differences. An unexpected result was that the shoot type effect did not dominate the cultivar effect, as illustrated by the closeness between ‘Elegant Lady’ and ‘Flavorcrest’ proleptic and sylleptic HSMMs, respectively. The combination of the differences in zone length (sylleptic shoots were shorter than proleptic shoots for each cultivar except ‘Flavorcrest’) and in within-zone axillary bud fates led to different results for the two other cultivars, ‘Lorrie May’ and ‘O’Henry’.

While it has been shown that the general characteristics of shoot architecture are related to the genetic background of the plant that is studied, there are still many questions about how the specific bud fates at nodes along shoots are determined (Costes *et al.*, 2014). The factors that trigger the development of floral buds at axillary positions along shoots have been of particular interest and have been studied at several levels of organization (Kervella *et al.*, 1995; Hsu *et al.*, 2011; Costes *et al.*, 2014). While these factors were not specifically studied in this research, the striking similarities in bud fate patterns among the various shoots in this study are pertinent to this topic. They seem to indicate that, while substantial plasticity was exhibited among shoots, the general patterns on both proleptic and sylleptic shoots were quite consistent. Thus, they were likely dependent on an internal control rather than on conditions during the period of development of their corresponding phytomers (Fig. 1).

The proleptic shoots examined in this study, by definition, began their growth during spring vegetative bud-break in March and completed it by the end of June of the 2015 growing season. Previous research (T. M. DeJong, unpubl. res.) has indicated that sylleptic shoots do not appear on epicormic shoots until eight to ten phytomers have been formed at the base of the shoots. Since the phyllochron (time between appearance of successive leaves) for epicormic peach shoots early in the growing season is ~3 d (Davidson *et al.*, 2017), the initiation of the first sylleptic shoots likely did not occur until at least 1 month after vegetative bud-break of proleptic shoots. In addition, the sylleptic shoots that were studied included some that arose from mid-shoot nodes on epicormic shoots as well as those arising from more proximal nodes. Thus, the sylleptic shoots that were evaluated began growing from axillary meristems on epicormic shoots at least 1 month later than the proleptic shoots. It follows that the growth conditions when most sylleptic shoots were growing were likely quite different from those when the corresponding phytomers of proleptic shoots were being formed; nevertheless, the structures of the two shoot types were quite similar. This indicates that the bud fate patterns along proleptic and sylleptic shoots were likely more greatly influenced by endogenous factors than environmental factors.

Cultivar differences in floral bud production

While the same bud fate zones were identified in the majority of shoots analysed across all cultivars, the most substantial differences in mean lengths of the individual zones occurred in zone 2 (the longest zone dominated by central vegetative buds, with or without associated floral buds). The mean length of zone 3, which had central floral buds at most nodes, was quite consistent between shoots of the same cultivar, but differed among cultivars and its mean length tended to vary inversely with the mean lengths of zone 4 within a cultivar (Fig. 1). This implies that variability in the factors that trigger floral bud formation at a node may be dominant factors in determining the plasticity in bud fate patterns that were identified by HSM analysis.

At the study site, fruits of the earliest-maturing cultivars ('Lorrie May' and 'Flavorcrest') ripen in mid- to late June, followed by 'Elegant Lady' in mid-July and 'O'Henry' in mid-August. Even though there were similar bud fate patterns among both shoot types of all four cultivars, it is interesting to note that the amount of floral bud production tended to decline on cultivars with later times of fruit maturation (Table 2, Fig. 1) and the decline in flower production was mostly with flowers associated with central vegetative buds (Table 3). The decline in floral bud production corresponding to time of fruit maturation tends to support the notion that the stimulation of floral buds is affected by resource/carbohydrate status of the plant associated with periods of overlap between fruit growth and flower bud initiation (Bernier *et al.*, 1993). Rapid fruit growth during the later stages of fruit development is known to be a major sink for carbohydrates (Grossman and DeJong, 1994, 1995; López *et al.*, 2008). Since floral bud development in peach begins in late July and August (Tufts and Morrow, 1925; Johnson *et al.*, 1992), the overlap with fruit growth could be detrimental to floral bud production. Thus, the period of major fruit growth

in the later-maturing cultivars corresponded more closely with the timing of floral development, and this may have had a negative effect on the number of floral buds produced. Furthermore, the greater reduction in numbers of flower buds associated with central vegetative buds may indicate that development of floral buds formed lateral to the central vegetative buds may be more susceptible to competition for carbohydrates than central flower buds formed farther up the shoot.

It is also possible that the tendency for more floral buds associated with central vegetative buds in the 'Lorrie May' trees may have been related to the fact that they were on the less vigorous Controller™ 9 rootstock. Previous research with size-controlling rootstocks has shown that shoots on less vigorous trees can produce more flowers, presumably because of less internal canopy shading (R. S. Johnson, UC Davis, Davis, CA, USA unpubl. data).

Relevance of this study to other tree species

Markovian models have been used previously for providing an understanding of shoot architecture for several fruit species, such as apple (*Malus × domestica*) (Costes and Guédon, 1997, 2002; Costes *et al.*, 1999; Renton *et al.*, 2006), peach (Fournier *et al.*, 1998; Smith *et al.*, 2008), almond (*Prunus dulcis*) (Negrón *et al.*, 2013, 2014, 2015) and apricot (*Prunus armeniaca*) (Costes and Guédon, 1996). However, there has been a lack of clarity about how much bud fate patterns are genetically controlled as opposed to environmentally determined. The close similarities in bud fate patterns among peach cultivars was likely a result of the relatively narrow range of diversity in the germplasm base of most peach cultivars developed in the USA (Scorza *et al.*, 1985; Gradziel, 2002; Font i Forcada *et al.*, 2012). In addition, the pollen of most peach cultivars is self-compatible and their flowers tend to be self-pollinating (Gradziel *et al.*, 1993). The high similarity in bud fate patterns among peach cultivars observed in the study is in stark contrast to comparisons of bud fate patterns of three Californian almond cultivars (Negrón *et al.*, 2013) and six apple cultivars (Costes and Guédon, 2002). Bud fate patterns of these species were much more variable, corresponding with the fact that almond and apple pollen tends to be self-incompatible, and thus they are generally out-crossing species (Simmonds, 1976). The contrast between the differences in bud fate patterns of peach, almond and apple cultivars highlights the potential utility of using HSM shoot bud fate patterns for phenotypic analysis of the vegetative characteristics of fruit trees. In recent years there has been tremendous progress in analysing the genomic make-up of many plant species, but a bottleneck in utilizing these advances has been a lack of phenotypic data that can be linked with genomic data. This problem is particularly acute in assessing the vegetative characteristics of trees, partly because of a lack of understanding of the functional units of tree architecture. Based on this study, it is apparent that growth of proleptic and sylleptic shoots of peach trees is partially deterministic, and by extension this is likely the case for many tree species, even though it may not have been as apparent as with peach because of the greater structural diversity among genotypes of other tree species.

In conclusion, as with all biological systems, substantial plasticity was exhibited in the bud fate patterns of the studied shoots,

but this study provided evidence for the deterministic nature of both proleptic and sylleptic shoots across four peach cultivars in terms of mean maximum shoot length and overall bud fate patterns along shoots. While there is still a lot to be learned about the factors that caused differences among shoot types and shoots of different cultivars, it was apparent that the overall structure (bud fate patterns) of shoots of similar length was endogenously controlled and that this control appeared to be similar for both proleptic and sylleptic shoots. The understanding of shoot structural characteristics derived from this study can aid in phenotypic characterization of the vegetative growth of trees, as well as providing a foundation for vegetative management, such as pruning of fruit trees, in horticultural settings.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Table S1: overlap between observation distributions for consecutive zones for the two observed variables for the proleptic and sylleptic shoots of the four cultivars. Table S2: uncertainty concerning the segmentation of the shoots into successive zones: minimum posterior probability of the optimal segmentation, proportions of individuals whose posterior probability of the optimal segmentation is above given thresholds, and number of possible segmentations for the proleptic and sylleptic shoots of the four cultivars. Table S3: correlation coefficients between the lengths of the four zones extracted from the optimal segmentation of the observed sequences using the estimated HSMMs.

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