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Using Concepts of Shoot Growth and Architecture to Understand and Predict Responses of Peach Trees to Pruning

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Abstract

One definition of horticulture is the art of cultivating garden plants and pruning is a horticultural practice that is traditionally approached as more of an art than a science. This is largely because of the complexity of tree growth and development and a lack of general understanding and appreciation about the processes involved in governing shoot and tree growth and development. However recent tree architectural studies have provided systematic analyses of the shoot growth and statistical and dynamic simulation models have been developed that predict tree development and responses to pruning based on scientific concepts. These concepts include apical dominance (and its subcomponents; correlative inhibition, apical control and shoot epinasty); prolepsis and syllepsis; preformation and neoformation; epicormic shoot formation and plastochron (leaf emergence rates). In this paper we will discuss how many of these concepts can be combined with hidden semi-Markov chain models of shoot bud fates and a simulation model of source-sink interactions in peach trees (L-PEACH) to understand and predict natural development of peach trees and their responses to pruning. The results of these modeling efforts help explain the architectural and physiological basis of several common, empirically-based pruning systems used in California. These concepts also provide an understanding of the limitations of relying primarily on the use of pruning to control size of trees growing on commonly used invigorating rootstocks. This research demonstrates how computer simulation modeling can be used to test and analyze interactions between environmental factors and management practices in determining patterns of tree growth and development.

INTRODUCTION

The objective of the L-PEACH model is to simultaneously simulate the 3-dimensional architecture, carbon partitioning and physiology of growing peach trees (Allen et al., 2005, Lopez et al., 2008). While developing a systematic approach to context-specific modeling of carbon assimilation and partitioning within the framework of a growing tree represented substantial challenges (Allen et al., 2007, Prusinkiewicz et al., 2007),

development of a systematic approach for simulating the architectural growth of a peach tree and it's responses to pruning was also a significant challenge (Smith et al., 2008, Lopez et al., 2009). The development of the architectural sub-model required a systematic assessment of "rules" that control and/or influence the growth of individual shoots based on their origin, location and time of development as well as a way to systematically characterize various shoot types. The primary purpose of this paper is to describe and illustrate these "rules" and demonstrate how they can be used to understand and predict natural tree growth in addition to responses to pruning.

GENERAL "RULES" FOR UNDERSTANDING BRANCH GROWTH

Timing of branch development and kinds of branch growth

Based on published literature we consider that branches (shoots) can be produced from meristems or buds at three times during development: from lateral meristems without a period of dormancy, giving birth to **sylleptic** branches; from buds after a period of dormancy, producing **proleptic** branches (Wilson, 2000; Costes et al., 2006); or from preventitious buds on older branches, producing **epicormic** branches (water shoots) (Wilson and Kelty, 1994; Fink, 1983). Furthermore, these branches are characteristically made up of two different kinds of growth; preformed (organs of this kind of growth are preformed in a bud that goes through a resting stage) or neoformed (shoot organs formed directly from apical growth) (Wilson and Kelty, 1994; Fournier et al., 1998; Costes et al., 2006). Sylleptic shoots and epicormic shoots are composed only of neoformed growth whereas proleptic shoots can consist of only preformed growth or both preformed and neoformed growth (mixed shoots) (Wilson and Kelty, 1994; Costes et al., 2006).

Shoot growth dynamics

Normally the extension growth of most shoots occurs after budbreak in the spring. However the length of time that each shoot grows varies according to its type. The plastochron is the length of time that occurs between the initiations of successive leaves on a shoot. For practical purposes it is approximated by measuring the time between the appearance of two successive leaves on a shoot or the phyllochron (Bell, 2008; Seleznyova and Greer, 2001). It can vary some with temperature but data from our lab and others (Kervella et al 1995) indicate that it is generally 2-3 days for peach . Thus spurs and short extension shoots with less than 11 nodes generally complete their growth within 30 days after budbreak. Medium and long shoots are made up of both preformed and neoformed growth and characteristically have less that 34 nodes and thus stop putting on new leaves by approximately 60-100 days after budbreak. However, epicormic shoots are entirely neoformed, can have approximately 70 nodes and can continue adding new nodes until weather conditions become unsatisfactory for growth in the fall (DeJong and Doyle 1985). It is important to realize that the proleptic shoots that are primarily responsible for developing the crop in mature trees generally stop growing within 100 days after bud-break and that the epicormic shoots are the primary shoots responsible for what many consider "excessive" growth of peach trees.

Apical dominance

Sylleptic shoot growth and shoot extension growth can be strongly influenced by hormonal control as exhibited by phenomena related to apical dominance. However, as noted by Wilson (2000) there is confusion about the concept of apical dominance as it relates to perennial species. Apical dominance, also referred to as correlative inhibition

(Hillman, 1984; Cline, 1997), is generally defined as the control exerted by the shoot apex over the outgrowth of lateral buds. Its meaning is clear in annual plants but there is confusion about the term in perennial plants because, in addition to suppression of lateral shoot growth in the same season there is often control of the length growth of basal lateral proleptic shoots by the apical and distal lateral shoots that grow out on the same parent shoot during the subsequent season (Fig. 1). This later phenomena has been termed apical control (Wilson, 2000). Furthermore, there is a third factor that appears to be related to apical dominance and that is shoot epinasty (Wilson, 1970). This is the tendency for the angle of the upper, more vigorously growing apical shoots on the same parent to have a narrower branch angle than the lower shoots (Fig. 1). Experiments have shown that the wider branch angle of the lower shoots is related to the same factors that cause apical control as it relates to branch length (Wilson, 2000). All three of these phenomena (correlative inhibition, apical control and shoot epinasty) contribute to what is often described as acrotony (Bell, 2008) and appear to be related to auxin transport down the shoot from the apical growing meristems to those lower down the shoot (Wilson, 2000). Therefore we have chosen to use the term correlative inhibition to refer to the suppression of lateral shoot growth by the growing shoot apex during the first season of growth and to consider all three of these phenomena (correlative inhibition, apical control and shoot epinasty) as separate but collective manifestations of the general phenomenon of apical dominance.

Characterization of shoot branching

The potential growth of an axillary shoot is characterized by its position on a branch which leads to a predictable shoot branching structure (Costes et al., 2006). The branching structure of different categories of shoots have been coded as bivariate sequences of axillay productions along the shoots and modeled by hidden semi-Markov chains (Fournier et al 1998; Costes et al., 2006). These bivariate statistical models facilitate a systematic analysis and characterization of the patterns of lateral bud fates along individual shoots and these patterns have been shown to be fairly consistent for specific shoot categories of a given peach cultivar (Fournier et al., 1998). In these bivariate models, the first variable represents the fate of the central bud, while the second variable represents the fate of the lateral buds associated with the central bud. Data that was previously available for peach was only from unpruned trees but we have recently also obtained data for pruned peach trees. For this analysis shoots of five length categories; spurs, short shoots, medium shoots, long shoots and water shoots (epicormic shoots) were analyzed separately (Fig. 2, example data only for long shoots). Four sets of parameters were estimated for each shoot type: initial probabilities that determine the first zone at the base of the shoots, transition probabilities to model the succession ofzones along the shoot, occupancy distributions representing the length of each zone, and two observation distributions representing the fate of the central bud and the fate of the lateral buds within each zone, respectively.

Spurs consist of only preformed growth with up to eleven preformed nodes (Gordon et al 2006). Short, medium and long shoots are mostly mixed shoots consisting of both preformed and neoformed growth with eight to about thirty-three nodes. These shoots generally exhibit fairly strong correlative inhibition and thus produce few, if any, sylleptic shoots. Water shoots are entirely neoformed because the preventitious buds from which they originate have no preformed nodes. They also exhibit very little

correlative inhibition and thus produce many sylleptic shoots. Wherever sylleptic shoots are present there are generally few flower buds produced on the parent shoots and in most cultivars sylleptic shoots produce few flower buds. The main axis of water shoots can have as many as ninety nodes.

The nodes along a shoot are characterized by the bud fates that occur at the node. The example of hidden semi-Markov chain analysis of long shoots from pruned trees (Fig. 2) shows that shoots have zones or bud fate states that are fairly consistently characterized as containing nodes with specific types of buds. Blind nodes produce no lateral proleptic buds or sylleptic shoots, and are located primarily at the basal and distal ends of the shoots. Many nodes produce a lateral proleptic central vegetative bud and this bud can have either zero, one or two flower buds associated with it. These nodes occupy the middle part of the shoots, with fewer flowers being associated with nodes toward the distal end. Some nodes, usually toward the apex of the shoot, produce a solitary lateral flower bud. Some nodes may produce a lateral sylleptic shoot (these are characteristic of water shoots). In addition to proleptic buds or sylleptic shoots there are one or two preventitious buds at each node that maintain the potential to form an epicormic shoot in response to catastrophic injury (or pruning).

Tree reactions to pruning

Based on the concept of reiteration (Barthélémy et al. 1991) and data from Gordon and DeJong (2007) epicormic shoots in peach are primarily generated from preventitious buds in response to branch breakage, severe bending of large limbs (generally below horizontal) and severe pruning. For practical horticultural purposes epicormic shoot growth can be considered to be almost exclusively stimulated by severe pruning of large branches (older than one-year-old) or strong water shoots in which sylleptic shoots have previously grown and used up the preformed lateral buds in close proximity to the pruning cut. If shoots of any of the other categories are headed they are replaced by a shoot(s) of the same category arising from lateral buds in close proximity to the cut. If no pruning cut occurs on a given shoot, new proleptic shoots arising near the apex of a shoot are generally either the same or one category smaller than the parent shoot and lateral proleptic shoots are progressively smaller further down the shoot because of apical control effects. The reiteration response to heavy pruning is natural and is the primary reason why pruning cannot be relied upon exclusively to control peach tree size when trees are grown in highly fertile soils without size-controlling rootstocks.

APPLICATION OF RULES FOR UNDERSTANDING GROWTH RESPONSES TO PRUNING PRACTICES

In California, as well as in many other peach production areas, most peach trees are propagated by bud-grafting scion cultivars onto newly sprouted rootstocks in late spring. The buds used for this are excised from new shoots produced the same spring and thus they are not fully developed proleptic buds. Therefore the shoot that results from the bud-grafting is totally neoformed and behaves like an epicormic or water shoot with low correlative inhibition. This shoot produces many syleptic branches and has an extended period of growth into the fall resulting in a tree that is 1.5 2.0 m tall after one season in the nursery (Fig 3a).

When these trees are removed from the nursery and planted in a production orchard they are generally headed to a height of 0.5 □0.7 m above the soil Fig. 3a). This heading cut stimulates a reiteration response and several shoots are initiated below the pruning cut. These new shoots originate from preventitious buds and thus are epicormic, entirely neoformed, and grow late into the season. The classic □open vase□ training system used on California (Micke et al., 1980) involves selecting three or four of these vigorous water shoots at the end of the next year to establish main scaffolds and heading them again so they are ~0.5 to 0.8 m in length. (The □perpendicular V system□ involves selecting two of these vigorous water shoots and heading them again as described in the □open vase□ system (Fig. 3b)). The heading cuts on the selected scaffold branches again stimulate a reiteration response and production of new water sprouts (Fig. 3b). With the vase system the same type of pruning is repeated for another year to establish a set of two tertiary scaffolds on the top of each secondary scaffold. At the end of the third year this classic open vase tree has a strong structure however the watersprouts produced as a result of the previous year□s heading cuts are so tall that the grower is compelled to prune them fairly hard again because without pruning they will begin to bend over with crop and/or the tree is taller than is optimal for management. In vigorous growing conditions this results in a non-productive cycle of pruning and excessive growth responses.

CONCLUSION

Pruning practices such as the stimulation of excessive growth by hard pruning of peach trees during tree training has been empirically practiced for many years. However the developmental and physiological reasons for these responses have been fairly obscure. We believe that the exercise of developing a simulation model of physiology and architectural growth of peach trees has encouraged the development of a systematic analysis of peach shoot growth and development that has clarified both the natural habit of peach shoot growth and tree architecture as well as responses to common pruning practices used in commercial peach orchards. The challenge is now to use this increased understanding to develop more physiologically and horticulturally efficient pruning practices for peach trees. While the stimulation of epicormic shoot growth through pruning is helpful for rapidly establishing the tree canopy it is also a primary factor that leads to □excessive□ vegetative growth in commercial peach production. Thus new strategies targeted at controlling excessive vigor of peach trees need to be primarily directed toward reducing water shoot (epicormic) growth in mature trees.

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Figures:

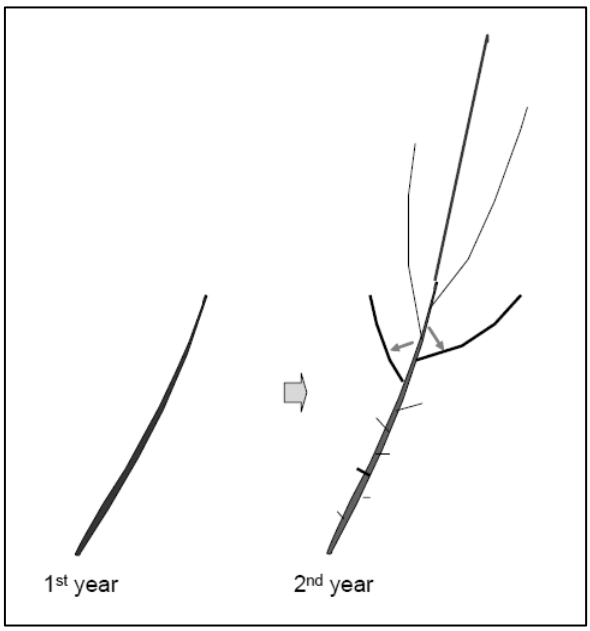

Fig. 1. Diagram of the three manifestations of apical dominance. The first year shoot has no lateral bud breaks (sylleptic shoots) and thus exhibits complete correlative inhibition. This pattern is repeated on the new shoots in the second year. The terminal and distal lateral shoots in the second year are the longest and have relatively narrow branching angles while lateral shoots lower down are progressively shorter and have wider branch angles; thus exhibiting apical control and shoot epinasty, respectively.

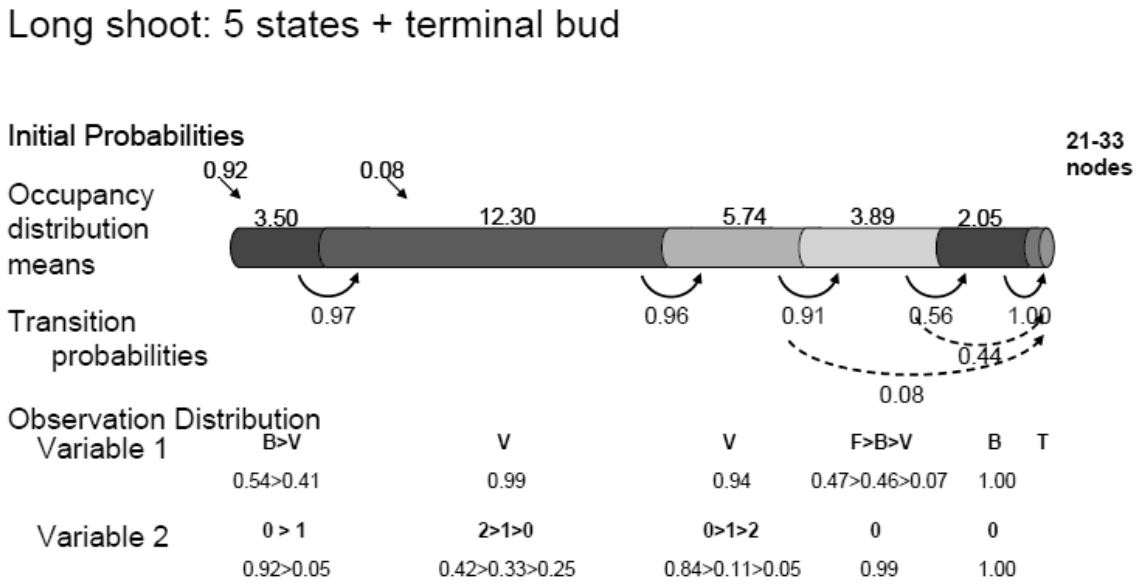

Figure 2. An example of the results of hidden semi-Markov chain statistical analysis of 40 long proleptic shoots on a pruned Summer Fire nectarine tree. The analysis indicates that shoots containing 21-33 nodes fairly consistently exhibited five successive zones (states) before the terminal (T) vegetative bud (last state). There was a high probability to start in the first state (0.92) and then the transitions between the next three states were very predictable (see transition probabilities). However the 5th state was skipped in 44% of the shoots. Central buds in the first state were either blind or vegetative (variable 1 indicates the probability of the fate of central axillary buds, including Blind (B), Vegetative (V) or Floral (F)). The first state rarely had floral buds lateral to a central bud (variable 2 indicates the fate of lateral buds associated to the central bud; 0, 1, or 2 flower buds). Nodes in the longer second state almost all had central axillary vegetative buds (variable 1) with 2 (42%), 1 (33%) or 0 (25%) floral buds (variable 2) associated with them. This was followed by a state that characteristically had central axillary vegetative buds and with associated floral buds only 16% of the time. The fourth state was characterized by nodes that were either blind or had central axillary floral buds. The 5th zone, when it occurred, only had blind nodes.

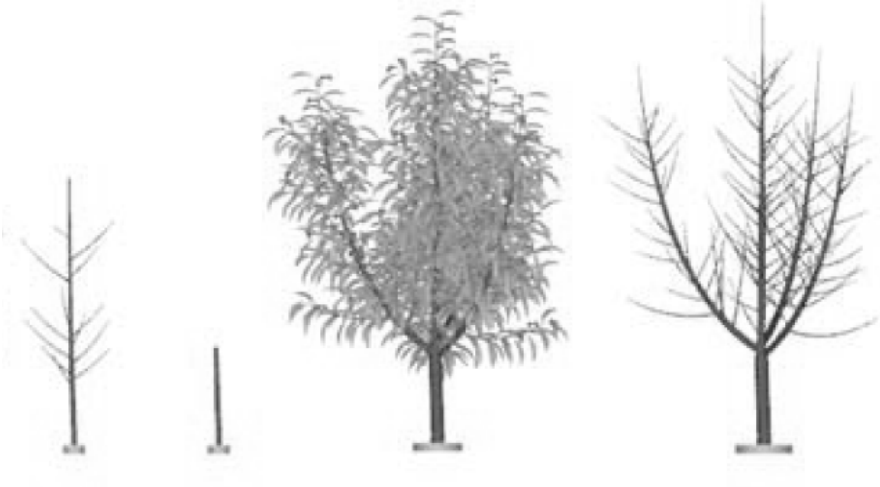

Fig. 3a. An example of output from the L-Peach model demonstrating how hard pruning is used to stimulate reiterative (water shoot) growth to develop the canopy in peach trees. The first figure represents a tree grown in the nursery. At the time of planting it is severely headed to a single trunk. This results in strong epicormic shoot growth the subsequent growing season.

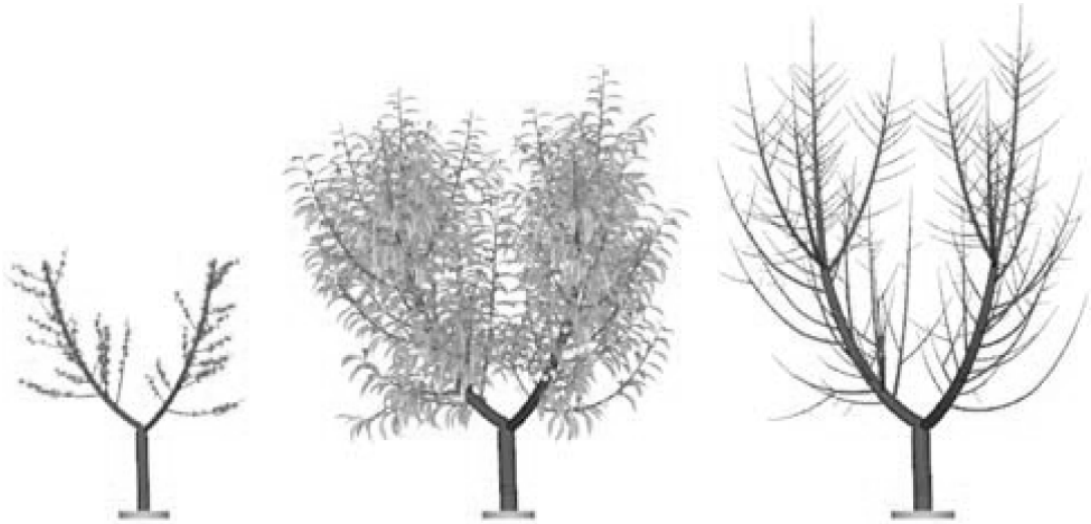

Fig. 3b. During the dormant season after the first year in the field, 2, 3 or 4 primary scaffolds (depending on the training system) are selected and usually headed to again stimulate strong reiterative growth to continue development of the major scafflolds. In this figure the tree was trained to a perpendicular V system by selecting 2 water shoots. Cropping primarily occurs on proleptic shoots that are produced after the scaffolds are established.