Provided for non-commercial research and education use. Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Scientia Horticulturae 121 (2009) 495-500

Contents lists available at ScienceDirect



Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti



Contributions of short- and long-shoots to yield of 'Kerman' pistachio (*Pistacia vera* L.)

Timothy M. Spann^{a,*}, Robert H. Beede^b, Theodore M. DeJong^a

^a Plant Sciences Department, Mail Stop 2, University of California, Davis, CA 95616, USA ^b University of California Cooperative Extension, 680 North Campus Drive, Suite A, Hanford, CA 93230, USA

ARTICLE INFO

Article history: Received 17 November 2008 Received in revised form 6 February 2009 Accepted 28 February 2009

Keywords: Alternate bearing Yield components Inflorescence bud abscission Rootstock

ABSTRACT

The canopy of a mature 'Kerman' pistachio (*Pistacia vera* L.) tree is composed of two types of shoots: short-shoots composed entirely of preformed nodes, and long-shoots composed of both preformed and neoformed nodes. Since the production of these two types of shoots is known to be related to rootstock and rootstock influences yield of pistachio the relationship of these two types of shoots to yield was investigated during two cropping years. Individual short-shoots produced significantly less yield and had fewer fruit clusters per shoot compared with long-shoots, but collectively produced 55–60% of the total yield. Long-shoots positively affected yield components in one year, but had no effect in the other year. Whether the differences in the one year were due to canopy position and light interception or differences in the carbohydrate allocation within the two types of shoots could not be determined from the current data. Long-shoots initiated more inflorescence buds, although inflorescence bud formation was restricted to the preformed growth and only the 3–4 earliest neoformed nodes. However, when expressed as a percentage, long-shoots retained a lower percentage of initiated inflorescence buds, compared with short-shoots. Regardless of shoot type, less than half of the retained inflorescence buds produced mature fruit clusters. Thus, inflorescence bud retention, a previously hypothesized mechanism of pistachio alternate bearing, may not be the primary limiting factor to yield in pistachio.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

The marketed pistachio nut, the fruit of Pistacia vera L., is comprised of a shell (endocarp) and kernel (seed), with a fleshy hull (mesocarp) which is removed during processing. Endocarp dehiscence, or shell splitting (split nuts), occurs naturally in approximately 65% of commercially harvested pistachios in California, and this feature is important in the marketing of pistachio nuts. The percentage of nuts that do not dehisce (non-split nuts) corresponds to a lower grade of nuts that are not as marketable and do not command as high a price. Pistachio dehiscence is a physical phenomenon resulting from outward pressure from the developing kernel on the shell (Nevo et al., 1974; Polito and Pinney, 1999). This is supported by reports of larger kernel sizes for split nuts compared with non-split nuts (Nevo et al., 1974; Crane and Iwakiri, 1982; Crane et al., 1982; Polito and Pinney, 1999). Therefore, it is logical that factors that affect kernel size, whether positively or negatively, will also alter the percentage of split nuts.

A common problem to pistachio production worldwide is alternate bearing, the production of a heavy crop one year followed by a light crop the next year (Crane and Iwakiri, 1981), which varies in severity depending on the cultivars grown (Crane and Nelson, 1971; Esmailpour, 2005). A large body of work indicates that the alternate bearing phenomenon in pistachio is related to carbohydrate supply and demand, and this has led to speculation as to whether shoot growth alternates with cropping cycle as well. In general, it has been reported that heavy fruiting suppresses vegetative growth in fruit trees (Murneek, 1924), and several studies in pistachio have reported suppressed vegetative growth (i.e. shorter shoots) during on-years (Weinbaum et al., 1994; Brown et al., 1995; Rosecrance et al., 1996; Picchioni et al., 1997). However, a number of studies have also reported that vegetative growth is enhanced (i.e. longer shoots) during the on-year (Crane and Nelson, 1972; Crane and Al-Shalan, 1977; Nzima et al., 1997), suggesting the potential for competition between vegetative and reproductive growth. If competition exists between vegetative (shoot) and reproductive (nut) growth this could have negative effects on shell splitting.

Detailed studies of pistachio vegetative growth have shown that the majority (*ca.* 90%) of the shoots in mature pistachio canopies are preformed short-shoots that finish growing by mid-to late May under California conditions (Spann et al., 2007). Thus,

^{*} Corresponding author. Present address: Horticultural Sciences Department, Citrus Research and Education Center, University of Florida, 700 Experiment Station Road, Lake Alfred, FL, 33850, USA. Tel.: +1 863 956 1151; fax: +1 863 956 4631. *E-mail address:* spann@ufl.edu (T.M. Spann).

^{0304-4238/\$ –} see front matter \circledcirc 2009 Elsevier B.V. All rights reserved. doi:10.1016/j.scienta.2009.02.029

T.M. Spann et al. / Scientia Horticulturae 121 (2009) 495-500



Fig. 1. 'Kerman' pistachio nut development at approximately final nut set (25 DAB, A.), completion of shell expansion (50 DAB, B.), completion of shell hardening/lignification (80 DAB, C.), onset of kernel development (100 DAB, D.), mid-point of kernel development (115 DAB, E.), and completion of kernel development/start of final maturation (135 DAB, F.). Vertical bar = 1 cm.

the majority of shoot growth does not have the potential to compete with the kernel development stage of fruit growth that begins in early July [about 80–90 days after bloom (DAB), Fig. 1]. Any potential competition between short-shoot growth and nut growth would occur during the shell expansion stage of nut development 30–60 DAB (late April through late May), and may actually enhance shell splitting by reducing shell enlargement. However, about 10% of the total shoots in the canopy of normally pruned 'Kerman' pistachio trees on vigorous rootstocks in California are long-shoots produced as a result of neoformed growth (Spann et al., 2007). These shoots continue growing much later into the season than their short counterparts and, thus, could directly compete with the kernel development stage of nut growth and reduce shell splitting.

The mechanism for alternate bearing in pistachio appears to be unique to the genus Pistacia. In most alternate bearing tree crops flower bud initiation is inhibited when a crop is present (Davis, 1957; Monselise and Goldschmidt, 1982). However, in pistachio flower buds are produced in abundance each year, regardless of crop load, but they abscise in large numbers at the onset of kernel development (early July in California, Fig. 1) when large crops are present (Crane and Iwakiri, 1981). Therefore, alternate bearing in pistachio is a function of low flower bud retention as opposed to lack of initiation. The percentage of flower buds retained at the end of a season represents the maximum yield potential for a tree the following season. Recent data indicate a strong correlation between carbohydrate reserve depletion and inflorescence bud abscission (Spann et al., 2008). Long-shoots, because of their greater number of nodes, may have the potential to initiate more flower buds; however, their continued growth and carbohydrate demand may lead to greater inflorescence bud abscission.

We hypothesized that nut clusters harvested from long-shoots would have higher total yields and higher percentages of split nuts compared to short-shoot clusters because of the locally higher carbohydrate supply from the greater leaf area of the long-shoots. Thus, we also hypothesized that the greater yield of long-shoots would lead to lower inflorescence bud retention on long- compared to short-shoots. Therefore, the objectives of this study were to (1) determine if long-shoots are more productive than short-shoots, and if the proportions of split, non-split and blank nuts varied by shoot type, (2) determine the relationship between shoot type and inflorescence bud initiation and retention (i.e. yield potential), and (3) determine the relative importance of short- and long-shoots to total yield of mature pistachio trees growing on different rootstocks.

2. Materials and methods

2.1. Plant material

All experiments were conducted in a rootstock trial block located at the University of California, Kearney Agricultural Center, Parlier, CA, USA ($36^{\circ} 36'' 42'$ N lat., $119^{\circ} 32'' 02'$ W long.). The block

was planted in 1989 and consisted of 90 trees on each of four rootstocks, planted as a randomized complete block design (one tree of each rootstock per block), budded with the cultivar 'Kerman.' The planting and irrigation design are described fully by Ferguson et al. (1998) and Spann et al. (2007). Prior to the beginning of these experiments in 2002, all trees had been grown according to standard commercial practices (Ferguson et al., 2005). The current research only used trees on three of the four rootstocks originally planted: *Pistacia atlantica* Desf. (Atl), *P. integerrima* Stew. selection 'Pioneer Gold I' (PGI), and *P. atlantica* \times *P. integerrima* selection 'UC Berkeley 1' (UCB). 'Kerman' trees in California grown on these three rootstocks are least vigorous on Atl and most vigorous on UCB and PGI, as indicated by the number of longshoots produced on each rootstock (Spann et al., 2007).

2.2. Components of yield

To study the effects of shoot type (short or long) on the components of yield, three trees on the UCB rootstock were hand harvested at full nut maturity in 2003 and 2004. Trees on UCB were selected because of this rootstock's vigor and propensity to produce long-shoots (Spann et al., 2007). The same three trees were harvested each year. Based on historical averages, 2003 was predicted to be an off-year and 2004 an on-year; although, alternate bearing in this block had not been severe. The nuts from each stem were removed and placed in separate paper bags. The length, number of nodes, and type of shoot (short or long, but not whether the shoots were of terminal or lateral origin) was recorded for the current season growth distal to the nut clusters on each bearing stem; additionally the number of clusters per stem was recorded in 2004. The nuts from each stem were hand hulled the day of harvest. The hulled nuts were then sorted into split, nonsplit and blank nuts before drying.

2.3. Whole tree cluster data

To determine the source of yield differences among the three rootstocks, three trees on each rootstock with average crop loads for trees on that rootstock were hand harvested at full nut maturity in 2005. Prior to the full tree harvest, a 50 cluster sample was collected from each tree. Sampled clusters were collected from the uppermost portion of the canopy, regardless of shoot type (long vs. short) or origin (terminal vs. lateral), on each tree so as to avoid possible variation due to canopy shading effects. The remaining clusters on each tree were then removed and counted to determine the total number of clusters per tree. The nuts were separated from the rachis structure for one tree to determine the ratio of rachis tissue to nuts on a fresh weight basis; this factor was applied to the total fresh weight of each remaining tree to calculate total nut fresh weight per tree. Each of the 50 clusters sampled from each tree were hand sorted into split, non-split and blank nuts and the fresh weight of each component was recorded.

T.M. Spann et al./Scientia Horticulturae 121 (2009) 495-500

Table 1

Total dry yield and cluster data per shoot for short- and long-shoots of mature 'Kerman' pistachio (*Pistacia vera*) trees on UCB rootstock (*P. integerrima* × *P. atlantica* selection 'UC Berkeley 1') in two consecutive years.

Shoot type	No. fruit bearing shoots per tree ^a	Total yield per tree (kg)	Yield per shoot (g)	Clusters per shoot	Nuts per cluster
2003					
Short	226.3 ± 89.5	$\textbf{8.90} \pm \textbf{4.3}$	$\textbf{39.3} \pm \textbf{34.4}$	ND ^b	ND
Long	$\textbf{72.0} \pm \textbf{35.6}$	6.12 ± 5.6	85.0 ± 65.7	ND	ND
LSD $(P = 0.05)$	154.3	11.33	6.4		
2004					
Short	259.0 ± 68.0	$\textbf{7.87} \pm \textbf{2.2}$	$\textbf{30.4} \pm \textbf{27.7}$	$\textbf{2.3}\pm\textbf{1.4}$	12.7 ± 6.3
Long	55.3 ± 3.1	$\textbf{3.90} \pm \textbf{0.6}$	$\textbf{70.4} \pm \textbf{56.0}$	3.2 ± 2.1	18.5 ± 8.0
LSD(P = 0.05)	109.1	3.69	5.6	0.3	11.0

 $^a\,$ Values are means $\pm\,$ sd.

^b ND: no data; these data were not collected during the 2003 harvest.

Table 2

Components of yield for data presented in Table 1 from mature 'Kerman' pistachio (*Pistacia vera*) trees on UCB rootstock (*P. integerrima* \times *P. atlantica* selection 'UC Berkeley 1') as affected by the type of vegetative shoot distal to the fruit clusters in two consecutive years.

Shoot type	Yield components (%) ^a			
	Split nuts ^b	Non-split nuts	Blank nuts	
2003				
Short	44.2 ± 2.4	$\textbf{33.3} \pm \textbf{2.0}$	18.8 ± 1.5	
Long	49.2 ± 2.2	$\textbf{33.7} \pm \textbf{1.9}$	17.1 ± 1.3	
LSD ($P = 0.05$)	3.1	2.6	2.3	
2004				
Short	42.6 ± 2.4	$\textbf{32.0} \pm \textbf{2.3}$	$\textbf{25.4} \pm \textbf{2.0}$	
Long	58.2 ± 1.6	$\textbf{20.6} \pm \textbf{1.3}$	21.2 ± 1.3	
LSD (<i>P</i> = 0.05)	3.6	3.5	3.2	

^a Values are means \pm sD.

^b Split nuts: nuts with a fully mature kernel and naturally dehisced shell; Nonsplit nuts: nuts with a fully mature kernel and a non-dehisced shell; Blank nuts: nuts with no kernel development and a non-dehisced shell.

2.4. Inflorescence bud retention in "off" year trees

Shortly after bloom in 2003 several trees on each rootstock that had produced a crop in 2002, had all inflorescences removed by hand to produce completely "off" trees. At the end of 2003, three of these "off" trees (one per rootstock) adjacent to one another were selected and the number of inflorescence buds initiated and retained were counted for 30 short- and 30 long-shoots on each tree. Shoots were selected from full sun positions in the upper portion of the canopy to eliminate possible variation due to canopy position or shading. The percentage of buds retained was calculated by dividing the number of buds retained by the total number of buds initiated on each shoot.

2.5. Statistical analysis

Analyses of variance were performed using the general linear models procedure of SAS (SAS Institute Inc., Cary, NC, USA). For comparison of yield and inflorescence data among shoot types the shoot was considered the experimental unit, and means were separated by least significant difference. For comparison of yield and cluster data among rootstocks the tree was considered the experimental unit and means were separated by Duncan's multiple range test.

3. Results

3.1. Components of yield and total yield by shoot type

In both 2003 and 2004, there were significantly more fruitful short-shoots than long-shoots per tree and short-shoots collectively produced a greater portion (although not significantly so) of the total tree yield (Table 1). However, individual long-shoots produced significantly higher yield on a dry weight basis compared with individual short-shoots (Table 1). This difference was reflected in an average of one more fruit cluster per shoot on long-shoots compared with short-shoots (Table 1). The average number of nuts per cluster was not significantly different, although, there was a trend toward fewer nuts per cluster on short-shoots.

The percentage of split nuts was significantly greater for longcompared with short-shoots in 2004 (Table 2). This increase was coincident with a significant decrease in the percentage of nonsplit and blank nuts on long shoots. Although not significant, there was a similar pattern of greater split nuts and fewer non-split and blank nuts in 2003 for long-shoots compared with short ones.

3.2. Whole tree cluster data

The number of clusters per tree was significantly less for trees on Atl rootstock compared with those on PGI or UCB (Table 3). However, the number of nuts per cluster as well as the average cluster fresh weight, calculated from both the 50 cluster sample and whole tree data, were similar across rootstocks.

3.3. Inflorescence bud retention

The absolute number of inflorescence buds retained was significantly greater for long-shoots compared with short-shoots for trees on all rootstocks (Table 4), reflecting the greater number

Table 3

Total number of nut bearing clusters per tree, number of nuts per cluster, and average cluster weight for mature 'Kerman' pistachio trees grown on three rootstocks.

Rootstock ^a	No. of clusters per tree	No. of nuts per cluster ^b	Sampled cluster fresh weight $(g)^{b}$	Whole tree cluster fresh weight (g) ^c
Atl	$482\pm103.2b^d$	19.7 ± 0.7	57.3 ± 5.5	44.8 ± 14.8
PGI	$1105\pm106.2ab$	18.4 ± 0.9	52.4 ± 1.9	44.7 ± 1.0
UCB	$1608\pm537.9a$	16.5 ± 2.9	53.9 ± 11.3	41.5 ± 7.3

^a Atl: *Pistacia atlantica*; PGI: *P. integerrima* selection 'Pioneer Gold I'; UCB: *P. integerrima* × *P. atlantica* selection 'UC Berkeley 1.'

 $^{b}\,$ Values are means $\pm\,$ sp calculated from a 50 cluster sub-sample per tree, three trees per rootstock.

^c Values are means \pm s_D calculated from whole tree cluster counts and yield, three trees per rootstock.

^d Different letters indicate significant differences within a column by Duncan's multiple range test, *P*: 0.05; no letters indicate no significant differences within a column.

T.M. Spann et al./Scientia Horticulturae 121 (2009) 495-500

498

Table 4

Inflorescence bud set and retention data for 30 short- and 30 long-shoots from mature 'Kerman' pistachio trees on three rootstocks sampled from full-sun positions in the canopy at the end of an artificially induced off-bearing year (2003).

Shoot type	Rootstock ^a	Rootstock ^a			
	Atl	PGI	UCB		
Total inflorescence bu	d set (mean \pm sD)				
Short	$\textbf{8.4}\pm\textbf{1.1}$	$\textbf{8.2}\pm\textbf{0.8}$	9.3 ± 1.2		
Long	12.8 ± 3.5	11.7 ± 3.2	13.2 ± 3.0		
LSD $(P = 0.05)$	1.4	1.2	1.2		
No. of inflorescence buds retained (mean \pm sD)					
Short	$\textbf{6.5} \pm \textbf{1.3}$	5.3 ± 1.3	6.6 ± 1.6		
Long	$\textbf{8.0}\pm\textbf{3.5}$	$\textbf{6.8} \pm \textbf{3.3}$	8.6 ± 3.1		
LSD (<i>P</i> = 0.05)	1.4	1.3	1.3		

^a Atl: *Pistacia atlantica*; PGI: *P. integerrima* selection 'Pioneer Gold I'; UCB: *P. integerrima* \times *P. atlantica* selection 'UC Berkeley 1.'

of buds set on long shoots, but long-shoots retained a significantly lower proportion of inflorescence buds compared with shortshoots across all rootstocks. The greatest difference in the percentage of buds retained by long-shoots compared with short-shoots was for trees on Atl rootstock, 62.5% vs. 77.4%, respectively. Trees on PGI and UCB had a smaller difference between short- and long-shoots, approximately 9% and 7% difference, respectively.

4. Discussion

Historically, pistachio trees grown on PGI and UCB rootstocks in California produce significantly higher yields than trees on Atl (Ferguson et al., 2005). This difference has generally been attributed to the larger size of trees grown on UCB and PGI rootstocks and, thus, more fruit clusters per tree, as opposed to more nuts per cluster (Ferguson et al., 2005). The data presented here support the attribution of yield differences to more fruit clusters per tree and not to differences in cluster size among rootstocks (Table 3). However, our previous research has shown that trees on PGI and UCB rootstocks also produce more shoots with neoformed growth (i.e. long-shoots) than do trees on Atl (Spann et al., 2007). Therefore, we thought that it was beneficial to examine yield differences between the short- (preformed) and long-shoots (composed of preformed and neoformed growth) within a canopy to determine the contribution of each shoot type to yield and, thus, further elucidate the source of yield differences among rootstocks.

It should be noted that long-shoots are generally restricted to the upper well-exposed portion of the canopy in pistachio (Spann et al., 2007), whereas short-shoots occur throughout the canopy, from full-sun to heavy shade environments. Thus, at the whole tree level, short-shoots on average likely had a lower average light exposure than long-shoots. Whole tree harvest data of trees on UCB rootstocks over two years showed that long-shoots produced significantly higher yields than short-shoots and actually accounted for approximately 20-30% of the bearing shoot population in the canopy (Table 1), in spite of their accounting for only 10% of the total shoot population (Spann et al., 2007). These higher yields were associated with significantly more clusters per shoot as well as a trend toward more nuts per cluster. However, when the number of nuts per cluster of long-shoots (Table 1) is compared with the full-sun sample taken across shoottypes for UCB trees (Table 3) the number of nuts per cluster are similar (18.5 and 16.5, respectively). This suggests that the difference in the number of nuts per cluster between short- and long-shoots may be more related to canopy position and light exposure than shoot type per se.

A lower average light environment (i.e. canopy position) for short-shoots compared with long-shoots may have been related to the observed variation in both the number of nuts per cluster and the number of clusters per shoot compared with long-shoots when the whole canopy is considered. Specific leaf weight (SLW, leaf mass per unit area) has been shown to be a correlated with light exposure and canopy position across many species (Lewandowska and Jarvis, 1977; Gulmon and Chu, 1981; Jurik, 1986; Klein et al., 1991a; Reich and Walters, 1994; Rosati et al., 2001). Generally, the greater the cumulative light exposure (daily light integral) the greater the SLW, and SLW has been shown to be correlated with photosynthetic capacity (DeJong and Doyle, 1985). Furthermore, SLW and canopy light exposure have been positively correlated with yield in walnuts, peach and apple (Ryugo et al., 1980; Tustin et al., 1988; Klein et al., 1991b; Myers, 1993), as well as with flowering and fruit set in walnut and apple (Tustin et al., 1988; Klein et al., 1991b). The SLW of full-sun exposed leaves was found to be almost twice that of shaded leaves in pistachio across rootstocks (data not shown). Thus, it can be hypothesized that the better yield associated with long-shoots is a canopy position effect, related to carbohydrate production and availability, and not necessarily the number of nodes on the shoots. That is to say, shortand long-shoots from similar light environments would have similar yields, if the hypothesis is correct.

We had hypothesized that nut clusters harvested from longshoots would have higher percentages of split nuts compared to short-shoots because of the locally higher carbohydrate supply from the greater leaf area of the long-shoots. However, components of yield were similar for short- and long-shoots in 2003, but long-shoots produced significantly more split nuts compared with short-shoots in 2004. Shell splitting is a physical phenomenon in pistachio (Nevo et al., 1974; Polito and Pinney, 1999), and split nuts typically have a greater kernel dry weight than non-split nuts (Nevo et al., 1974; Crane and Iwakiri, 1982; Crane et al., 1982; Polito and Pinney, 1999). This indicates that shell splitting may be dependent on carbohydrate production and availability. Since most long-shoots are found in the top of the canopy where light interception is greatest it is logical that there would be greater carbohydrate availability to drive kernel development and consequently shell splitting on these shoots. Therefore, the greater percent of split nuts on long-shoots in 2004 may be due to greater shoot leaf area and thus carbohydrate production as we hypothesized.

This possibility, however, raises the question, why did the nuts from long-shoots not have a greater split percentage compared with short-shoots in 2003? One hypothesis is that 2003 was an "off" year and thus carbohydrate availability was relatively high for all shoots, thereby limiting the beneficial effect of the longshoots. However, the three trees harvested did not significantly alternate bear in the two years studied, averaging 12.64 kg per tree (dry hulled weight) in 2003 and 15.54 kg per tree in 2004. Another hypothesis is that high temperatures during kernel development in 2003 reduced net photosynthesis and offset the benefits of the greater leaf area on the long-shoots. Weather data for 2003 indicate that there were approximately 50 more daylight hours above 30 °C during the first half of the kernel development period compared with the same growth phase in 2004 (CIMIS, 2008). Additionally, under typical growing conditions in the central valley of California, pistachio net photosynthesis declines at temperatures above \sim 30 °C (Spann, unpublished data), most likely due to increased respiration at higher temperatures (Amthor, 1989; Grossman and DeJong, 1994). The high temperatures experienced in 2003 likely decreased net photosynthesis and may have offset the benefits associated with the greater leaf area and canopy position of long-shoots in that year. These hypotheses, total tree yield and temperature, are not necessarily mutually exclusive and may be one reason why 'Kerman' pistachio does not follow a strict alternate bearing pattern in the California Central Valley as do other cultivars in other parts of the world.

Because inflorescence bud abortion has been positively correlated with crop load (Crane and Nelson, 1971; Crane and Nelson, 1972; Wolpert and Ferguson, 1990) it has been viewed as the cause of alternate bearing in pistachio (Ferguson et al., 2005). Thus, bud retention is generally thought of as a good indicator of yield potential the next season. We hypothesized that long-shoots would have lower inflorescence bud retention compared to shortshoots due to the competition between vegetative growth and inflorescence bud retention on the long-shoots. Given the greater number of nodes on long-shoots the absolute number of buds initiated was significantly higher compared with short-shoots (Table 4). However, long-shoots of pistachio typically have as many as 25 nodes (Spann et al., 2007), but only set an average of four inflorescence buds more than short-shoots in the present study (Table 4). Thus, the majority of the neoformed nodes on longshoots did not initiate inflorescence buds. It has been reported that floral bud initiation for the next year's crop begins very soon after new growth emerges in late March and early April (Hormaza and Polito, 1996); therefore, many of the neoformed nodes were likely produced after floral initiation had taken place. Thus, only the earliest 3-4 neoformed nodes were produced early enough in the season to initiate inflorescence buds, and the majority of inflorescence buds on long-shoots were initiated on the preformed portion of the shoot.

Ultimately, long-shoots retained only ~1.5 more inflorescence buds than short-shoots; thus, retaining a lower proportion of set inflorescence buds compared with short-shoots from a similar light environment across rootstocks (Table 4). Therefore, the ongoing production of neoformed growth on the long-shoots appears to have negatively affected percent bud retention as we hypothesized, but because there were more buds initiated the absolute bud retention was higher on long-shoots. Crane and Nelson (1972) and Crane et al. (1973) suggested that assimilate depletion was responsible for bud abscission in pistachio. Similarly, a number of reports indicate that factors reducing vegetative competition (Leopold and Lam, 1960; Cooper, 1964) or increasing assimilate supply (Cooper and Hurd, 1968) reduce inflorescence abortion in tomato. Thus, it could be hypothesized that the continued neoformed growth of long-shoots reduced assimilate availability and relative bud retention.

Regardless of shoot type, the average number of clusters per shoot for whole trees in 2004 (Table 1) was less than half the number of inflorescence buds retained on shoots at the end of 2003 (Table 4). It is possible that this difference was because many of the short-shoots bearing fruit were from relatively low light positions in the canopy whereas the sampled shoots were from well exposed positions. However, if we limit our analysis to long-shoots, which are known to be restricted to well exposed positions (Spann et al., 2007), the same difference exists [8.6 buds retained (Table 4, UCB rootstock) vs. 3.2 clusters per shoot (Table 1)]. That is to say, not all of the inflorescence buds retained at the end of a season produce mature clusters the following season. It is unknown at what point between the onset of dormancy and harvest the inflorescences were lost. They could have abscised as buds during the dormant season indicating that there may be a second phase of bud abscission during dormancy, or they may have been retained until bloom and abscised as immature inflorescences. This suggests that inflorescence bud abscission during the growing season as described by Crane and Nelson (1972) may not be the sole cause of alternate bearing or limitation to yield in 'Kerman' pistachio. Typically, "off" trees retain 75% of set inflorescence buds whereas "on" trees retain <20% (Crane and Nelson, 1972; Porlingis, 1974; Wolpert and Ferguson, 1990) when measured during the dormant season. The current "off" year data indicate that 70% of set inflorescence buds were retained, but only 35% eventually developed into a cluster which was present at harvest on shortshoots (calculated from Table 1 clusters/shoot and Table 4 inflorescence buds set, both short- and long-shoots on UCB rootstock). If a similar phenomenon occurs in an "on" year, only approximately 10% of initiated buds would develop into mature clusters. The actual number of inflorescence buds retained which bloom and set fruit the following season should be investigated under natural crop loads and for other cultivars and under other environmental conditions.

Although significant differences were observed in total yield per shoot, the number of fruit clusters per shoot, yield components and inflorescence bud retention between short- and long-shoots, it could not be determined whether these differences were related to canopy position and light exposure or to carbohydrate allocation changes associated with these two types of shoots. It is very likely that both of these sets of factors played a role in creating the observed differences. Based on comparison of data from selected exposed shoots and whole canopy means, less than half of the inflorescence buds retained on a shoot produced a fruit cluster, indicating a potential second period of bud abscission between the onset of dormancy and nut set. This second phase of bud abscission may be a potential area of study for further understanding alternate bearing in pistachio. However, it appears that there may not be any single factor responsible for alternate bearing, and that the phenomenon is a complex response to a number of physiological and environmental factors.

References

- Amthor, J.S., 1989. Respiration and crop productivity. Springer-Verlag, New York, p. 215.
- Brown, P.H., Weinbaum, S.A., Picchioni, G.A., 1995. Alternate bearing influences annual nutrient consumption and the total nutrient content of mature pistachio trees. Trees 9, 158–164.
- California Irrigation Management Information System (CIMIS). 2008. http:// www.cimis.water.ca.gov. Accessed on 17 November 2008.
- Cooper, A.J., 1964. A study of development of the first inflorescence of glasshouse tomatoes. J. Hortic. Sci. 47, 231–241.
- Cooper, A.J., Hurd, R.G., 1968. The influence of cultural actors on arrested development of the first inflorescence of glasshouse tomatoes. J. Hortic. Sci. 43, 243–248.
- Crane, J.C., Al-Shalan, I., 1977. Carbohydrate and nitrogen levels in pistachio branches as related to shoot extension and yield. J. Am. Soc. Hortic. Sci. 102, 396–399.
- Crane, J.C., Al-Shalan, I., Carlson, R.M., 1973. Abscission of pistachio inflorescence buds as affected by leaf area and number of nuts. J. Am. Soc. Hortic. Sci. 98, 591–592.
- Crane, J.C., Iwakiri, B.T., 1981. Morphology and reproduction of pistachio. Hort. Rev. 3, 376–393.
- Crane, J.C., Iwakiri, B.T., 1982. Shell dehiscence in pistachio. HortScience 17, 797–798.
- Crane, J.C., Iwakiri, B.T., Lin, T.-S., 1982. Effects of ethephon on shell dehiscence and flower bud abscission in pistachio. HortScience 17, 383–384.
- Crane, J.C., Nelson, M.M., 1971. The unusual mechanism of alternate bearing in the pistachio. HortScience 6, 489–490.
- Crane, J.C., Nelson, M.M., 1972. Effects of crop load, girdling, and auxin application on alternate bearing of the pistachio. J. Am. Soc. Hortic. Sci. 97, 337–339.
- Davis, L.D., 1957. Flowering and alternate bearing. Proc. Am. Soc. Hortic. Sci. 70, 545–556.
- DeJong, T.M., Doyle, J.F., 1985. Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). Plant Cell Environ. 8, 701–706.
- Esmailpour, A., 2005. Evaluation of alternate bearing intensity in Iranian pistachio cultivars. Proc. XIII GREMPA 63, 29–32.
- Ferguson, L., Beede, R., Buchner, R., Kallsen, C., Freeman, M., Reyes, H.C., Metheney, P., Kafkas, S. 1998. California pistachio rootstock trials: Final report, 1989–1997. Cal. Pist. Ind. Annu. Rep. Crop Year 1997–98, 60–63.
- Ferguson, L., Beede, R.H., Freeman, M.W., Haviland, D.R., Holtz, B.A., Kallsen, C.E., 2005. Pistachio Production Manual, 4th ed. Fruit and Nut Research and Information Center, University of California, Davis, California. Grossman, Y.L., DeJong, T.M., 1994. Carbohydrate requirements for dark respiration
- Grossman, Y.L., DeJong, T.M., 1994. Carbohydrate requirements for dark respiration by peach vegetative organs. Tree Physiol. 14, 37–48.
- Gulmon, S.L., Chu, C.C., 1981. The effects of light and nitrogen on photosynthesis, leaf characteristics and dry matter allocation in the Chaparral shrub *Diplacus aurantiacus*. Oecologia 56, 341–347.

Author's personal copy

T.M. Spann et al. / Scientia Horticulturae 121 (2009) 495-500

- Hormaza, J.I., Polito, V.S., 1996. Pistillate and staminate flower development in dioecious *Pistacia vera* (Anacardiaceae). Am. J. Bot. 83, 759–766.
- Jurik, T.W., 1986. Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. Am. J. Bot. 73, 1083–1092.
- Klein, I., DeJong, T.M., Weinbaum, S.A., Muraoka, T.T., 1991a. Specific leaf weight and nitrogen allocation responses to light exposure within walnut trees. HortScience 26, 183–185.
- Klein, I., DeJong, T.M., Weinbaum, S.A., Muraoka, T.T., 1991b. Relationship between fruiting, specific leaf weight, and subsequent spur productivity in walnut. J. Am. Soc. Hortic. Sci. 116, 426–429.
- Leopold, A.C., Lam, S.L., 1960. A leaf factor influencing tomato earliness. Proc. Am. Soc. Hortic. Sci. 76, 543–547.
 Lewandowska, M., Jarvis, P.G., 1977. Changes in chlorophyll and carotenoid content,
- Lewandowska, M., Jarvis, P.G., 1977. Changes in chlorophyll and carotenoid content, specific leaf area and dry weight fraction in sitka spruce, in response to shading and season. New Phytol. 79, 247–256.
- Monselise, S.P., Goldschmidt, E.E., 1982. Alternate bearing in fruit trees. Hortic. Rev. 4, 128-173.
- Murneek, A.E., 1924. The effects of fruit on vegetative growth in plants. Proc. Am. Soc. Hortic. Sci. 21, 274–276.
- Myers, S.C., 1993. Preharvest watersprout removal influences canopy light relations, fruit quality, and flower bud formation of 'Redskin' peach trees. J. Am. Soc. Hortic. Sci. 118, 442–445.
- Nevo, A., Werker, E., Ben-Sasson, R., 1974. The problem of indehiscence of pistachio (*Pistacia vera* L.) fruit. Israel J. Bot. 23, 1–13. Nzima, M., Martin, G., Nishijima, C., 1997. Leaf development, dry matter accumula-
- Nzima, M., Martin, G., Nishijima, C., 1997. Leaf development, dry matter accumulation, and distribution within branches of alternate bearing 'Kerman' pistachio trees. J. Am. Soc. Hortic. Sci. 122, 31–37.
- Picchioni, G.A., Brown, P.H., Weinbaum, S.A., Muraoka, T.T., 1997. Macronutrient allocation to leaves and fruit of mature, alternate-bearing pistachio trees: magnitude and seasonal patterns at the whole-canopy level. J. Am. Soc. Hortic. Sci. 122, 267–274.

- Polito, V.S., Pinney, K., 1999. Endocarp dehiscence in pistachio (*Pistacia vera* L.). Int. J. Plant Sci. 160, 827–835.
- Porlingis, I.C., 1974. Flower bud abscission in pistachio (*Pistacia vera* L.) as related to fruit development and other factors. J. Am. Soc. Hortic. Sci. 99, 121–125.
- Reich, P.B., Walters, M.B., 1994. Photosynthesis-nitrogen relations in Amazonian tree species II. Variation in nitrogen vis-a-vis specific leaf area influences massand area-based expressions. Oecologia 97, 73–81.
- Rosati, A., Badeck, F.W., DeJong, T.M., 2001. Estimating canopy light interception and absorption using leaf mass per unit area in *Solanum melongena*. Annal. Bot. 88, 101–109.
- Rosecrance, R.C., Weinbaum, S.A., Brown, P.H., 1996. Assessment of nitrogen, phosphorous, and potassium uptake capacity and root growth in mature alternate-bearing pistachio (*Pistacia vera*) trees. Tree Physiol. 16, 949–956.
- Ryugo, K., Marangoni, B., Ramos, D.E., 1980. Light intensity and fruiting effects on carbohydrate contents, spur development, and return bloom of 'Hartley' walnut. J. Am. Soc. Hortic. Sci. 105, 223–227.
- Spann, T.M., Beede, R.H., DeJong, T.M., 2008. Seasonal carbohydrate storage and mobilization in bearing and non-bearing pistachio (*Pistacia vera*) trees. Tree Physiol. 28, 207–213.
- Spann, T.M., Beede, R.H., DeJong, T.M., 2007. Preformation in vegetative buds of pistachio (*Pistacia vera*): relationship to shoot morphology, crown architecture and rootstock vigor. Tree Physiol. 27, 1189–1196.
- Tustin, D.S., Hirst, P.M., Warrington, I.J., 1988. Influence of orientation and position of fruiting laterals on canopy light penetration, yield, and fruit quality of 'Granny Smith' apple. J. Am. Soc. Hortic. Sci. 113, 693–699.
- Weinbaum, S.A., Picchioni, G.A., Muraoka, T.T., Ferguson, L., Brown, P.H., 1994. Fertilizer nitrogen and boron uptake, storage, and allocation vary during the alternate-bearing cycle in pistachio trees. J. Am. Soc. Hortic. Sci. 119, 24–31.
- Wolpert, J.A., Ferguson, L., 1990. Inflorescence bud retention in 'Kerman' pistachio: effects of defruiting date and branch size. HortScience 25, 919–921.