

Partial Defoliation Can Decrease Average Leaf Size but Has Little Effect on Orange Tree Growth, Fruit Yield and Juice Quality

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Abstract. The effects of 2 consecutive years of annual defoliation during the harvest season on fruit size, yield, juice quality, leaf size and number were examined in trees of the midseason cultivar ‘Hamlin’ and the late-season cultivar ‘Valencia’ orange [*Citrus sinensis* (L.) Osb.]. In ‘Hamlin’, removal of up to 50% of the leaves in late November had no effect on fruit yield, fruit number, fruit size, soluble solids yield, juice °Brix, and °Brix to acid ratio of juice the following year. In ‘Valencia’, removal of 50% of the leaves in late March decreased fruit yield and soluble solids yield but did not affect Brix or the Brix to acid ratio of the juice. Leaf size of new flush was reduced by removal of 50% of the leaves in both cultivars but there was little effect on total canopy size. There were no measured effects of removing 25% of leaves from tree canopies. Thus, canopy growth, fruit yield, fruit quality, and leaf size were not negatively impacted when annual defoliations did not exceed 25% of the total canopy leaf area in ‘Valencia’ and ‘Hamlin’ orange trees for two consecutive years. Overall, fruit weight increased linearly with increasing ratio of leaf area to fruit number, suggesting that fruit enlargement can be limited by leaf area.

‘Hamlin’ and ‘Valencia’ are the two most important processing orange [*Citrus sinensis* (L.) Osb.] cultivars grown in Florida. Fruit from the midseason cultivar ‘Hamlin’ usually mature from November through January, whereas fruit from the late-season cultivar ‘Valencia’ usually mature after bloom in late March through June. Thus, ‘Hamlin’ fruit are harvested before bloom in the spring, whereas ‘Valencia’ orange fruit are harvested after bloom when fruit are at least one year of age and while young fruit are developing for next year’s crop (Yuan et al., 2001). Due to increasing labor costs, the use of mechanical technologies to harvest Florida processing oranges is steadily increasing. Successful mechanical harvesting of orange fruit is enhanced by the use of abscission agents that reduce fruit detachment force and increase the efficiency of fruit removal during mechanical harvesting (Burns, 2002; Burns et al., 2005). However, most abscission agents not only loosen fruit but also cause leaf abscission (Burns

et al., 2003b). The use of abscission agents as a one-time application during harvest could result in defoliation of as much as 20% (Burns et al., 2003a, 2003b; Pozo et al., 2004a, 2004b) annually for the life of the tree. Little is known about effects of defoliation of mature citrus trees during harvest, and no data are available on effects of annual defoliation on tree growth or fruit yield.

Most studies addressing effect of leaf removal on fruit growth and yield have been done in a single year using branches or young trees (Ferree and Palmer, 1982; Fishler et al., 1983; Roe et al., 1997; Yuan and Greene, 2000b). Limiting leaf photosynthates can reduce vegetative growth and fruit development in citrus (Goldschmidt, 1999). Partial removal of leaves from small trees or girdled branches caused extensive fruit abscission in dwarf Satsuma mandarin (Mehouachi et al., 1995), apple (Ferree and Palmer, 1982; Yuan and Greene, 2000b), and litchi trees (Roe et al., 1997; Yuan and Huang, 1988). Partial defoliation of citrus seedlings, however, can increase photosynthetic rates of remaining leaves in proportion to the number of vegetative buds that are allowed to regrow (Syvertsen, 1994). Canopy shading or application of photosynthetic inhibitors shortly after bloom reduced carbohydrate available to developing fruitlets and increased early fruit abscission of orange (Moss, 1976), litchi (Yuan and Huang, 1988), peach (Byers et al., 1985), and apple trees (Byers et al., 1985, 1990; Yuan and Greene, 2000a). In addition, fruit weight from girdled branches at harvest decreased with decreasing leaf area per fruit in various fruit crops (Fishler et al., 1983; Roe et al., 1997;

Yuan and Greene, 2000b). Nevertheless, many reports have confirmed that trees can increase leaf photosynthetic rates in response to crop requirements for photosynthates (Hansen, 1970; Iglesias et al., 2002; Lenz, 1978; Roe et al., 1997; Syvertsen et al., 2003). Wunsche et al. (2000) found that leaf photosynthesis or whole canopy gas exchange per unit leaf area was positively related to crop load in apple. Furthermore, moderate defoliation may improve light penetration and distribution within the canopy, thereby improving whole-tree CO₂ assimilation. Understanding the critical level of defoliation at which fruit yield and quality are decreased will define conditions for the safe and effective use of fruit abscission compounds or other plant growth regulators during the harvest season of oranges.

The objectives of this work were to determine the effect of different levels of defoliation during two consecutive harvest seasons on fruit yield, and quality in mature ‘Hamlin’ and ‘Valencia’ orange trees. Our goal was to define the critical level of defoliation that would begin to limit fruit yield and/or quality.

Materials and Methods

Plant materials. We selected uniform blocks of 11-year-old ‘Hamlin’ orange trees on ‘Carrizo’ citrange [*Citrus sinensis* (L.) Osb. × *Poncirus trifoliata* (L.) Raf.] rootstock and 13-year-old ‘Valencia’ orange trees grafted on rough lemon (*Citrus jambhiri* Lush) rootstock located at the Citrus Research and Education Center (CREC), Lake Alfred, Fla., for these experiments. ‘Hamlin’ orange trees were planted at 4.5 × 6.0 m spacing, and averaged 2.5 m in canopy height and 2.6 m in canopy diameter in late November 2001, and 2.7 m in height and 2.7 m in diameter at the end of the experiment in 2004. ‘Valencia’ orange trees were planted at a spacing of 4.5 × 6.3 m with an average of 3.2 m in height and 3.3 m in diameter in late March 2002, and 3.2 m in height and 3.4 m in diameter at the end of the experiment in 2004. Trees were not hedged or topped during the course of these experiments. The soil type was an excessively drained Candler sand with low organic matter content. Trees were well-irrigated and fertilized and received normal horticultural care.

The experiment was initiated within the normal harvest season: late November 2001 for ‘Hamlin’ oranges and late March 2002 for ‘Valencia’ oranges. Defoliation treatments were performed annually in late November on ‘Hamlin’ and in March on ‘Valencia’, and repeated on the same trees until November 2003 for ‘Hamlin’ and March 2004 for ‘Valencia’. Additional annual defoliations were planned, but experiments were halted due to defoliation and fruit removal of test trees caused by three hurricanes over a 6-week period in August and September 2004. Sixteen ‘Hamlin’ and ‘Valencia’ orange trees were grouped based on canopy size into four randomized complete blocks of four trees each. One tree from each block was manually defoliated by systematically removing 12.5% (one in eight leaves), 25% (one in four leaves), or 50% (one in two leaves) of the total leaves. Thus, by removing leaves on branches beginning from

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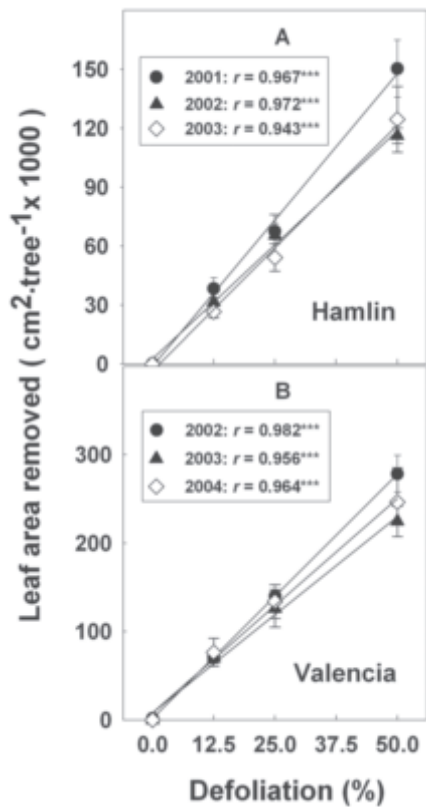


Fig. 1. Relationships between defoliation levels and removed leaf area per tree in 'Hamlin' (A) and 'Valencia' (B) oranges during 3 years. ***Significant or significant adjusted r^2 values at $P \leq 0.001$. Data are means \pm SE ($n = 4$).

the trunk and working toward the outer canopy, a random assortment of mature and immature leaves was removed from each tree. The fourth tree in each block had no leaves removed and served as a control. Thus, the experiment was a randomized complete block design with four defoliation treatments (0%, 12.5%, 25%, and 50% leaf removal) and four replications.

Fruit and leaf measurements. Immediately before defoliation treatments each year, mature fruit were harvested to determine yield and fruit characteristics. Fruit were harvested from each tree and transported to the packinghouse facility at CREC. Total fruit yield (kg/tree), fruit number, and individual fruit weights were determined using a two-lane, 12.5-cm roller/cup spacing, Colour Vision Blemish Sorter optical sizing unit (Victoria, Australia) comparable to systems found in commercial packinghouses. The unit was equipped with proprietary hardware (BVP 555 video processing card) and software (BlemishSort version 4.8) for data collection. Soluble solids in the juice ($^{\circ}$ Brix), and ratio of juice $^{\circ}$ Brix to percentage acid were determined in a 9-kg fruit subsample using USDA standard

computerized test equipment commonly found in Florida processing plants and present at CREC. Soluble solids per tree were calculated from $^{\circ}$ Brix in juice.

Fresh weight of leaves removed from each tree was measured. A random subsample of 200 leaves from each tree was weighed, and the area of each leaf determined using a portable leaf area meter (LI-3000; LI-COR, Lincoln, Nebr.). The total number of leaves removed and total leaf area of each tree were estimated based on the fresh weight of removed leaves from each tree, and the fresh weight and area of the 200-leaf subsample.

Statistical analysis. Effects of defoliation treatments were tested for significance using regression analysis and orthogonal comparisons where appropriate. Statistical Analysis Systems Software for PC (SAS Institute Inc., Cary, N.C.) was used for all data analyses.

Results

Removed leaf area and leaf size. The estimated leaf area (Fig. 1) and leaf number (data not shown) removed increased linearly with increasing defoliation levels in 'Hamlin' and 'Valencia'. Although the total estimated leaf area removed in the 50% defoliation treatment tended to decrease in the second and third year, defoliation had no significant effect on the following year's calculated total leaf area or total leaf number in either cultivar. Thus, there was no evidence that 50% defoliation significantly reduced total canopy size over the two year period. The first year of 50% defoliation reduced average single leaf area in 'Hamlin', whereas average leaf area was reduced only after 2 years of defoliation in 'Valencia' (Fig. 2).

Yield and fruit quality. Fruit yield was not affected by any defoliation treatment over 2 consecutive years in 'Hamlin' orange trees (Table 1). Similarly, yield was not significantly affected by defoliation in 'Valencia' except that 50% defoliation reduced yield when compared to the nondefoliated control 1 year after the first defoliation treatment in 2003. Defoliation treatments had no effect on fruit number per tree (data not shown), and fruit weight was not affected by defoliation of 'Hamlin' after two consecutive years (Fig. 3). Fruit weight was not affected after 1 year of defoliation in 'Valencia' but fruit from the 50% defoliated trees were smaller than those from any other treatments after 2 consecutive years of leaf removal. Defoliation did not affect $^{\circ}$ Brix and $^{\circ}$ Brix to acid ratio of the juice in 'Hamlin' and 'Valencia' trees (Table 2). Yield expressed as soluble solids per tree was not affected by defoliation treatment in 'Hamlin'. However, removal of 50% of the 'Valencia' leaves significantly decreased fruit yield and

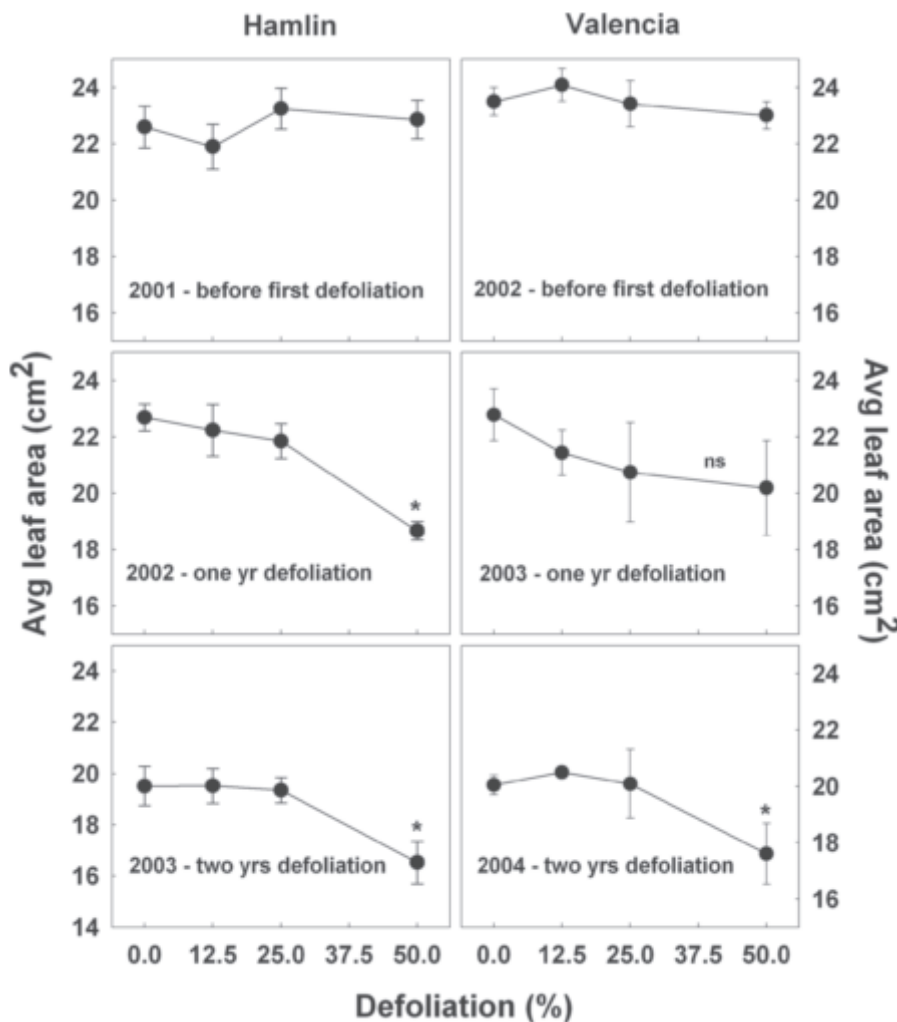


Fig. 2. Effect of defoliation on average individual leaf area in 'Hamlin' and 'Valencia' orange trees. In 'Hamlin', leaves were removed for the first time in November 2001 and again in November in 2002 and 2003. In 'Valencia', leaves were removed for the first time in March 2002 and again in March 2003 and 2004. Data are means \pm SE ($n = 4$). ns, *Nonsignificant or significant difference at $P \leq 0.01$.

fruit soluble solids yield when compared with control trees in 2003 but this did not occur after the second year of defoliation in 2004.

Ratio of leaf area or leaf number to fruit number. Ratio of leaf area to fruit number (Fig. 4) was not significantly affected by defoliation treatment in 'Hamlin'. In 'Valencia', however,

50% defoliated trees had the lowest ratio of leaf area to fruit number.

Fruit weight and ratio of leaf area to fruit number. When data were pooled from all defoliation treatments, there was a positive linear relationship between fruit weight at harvest and leaf area to fruit number ratio in 'Hamlin'

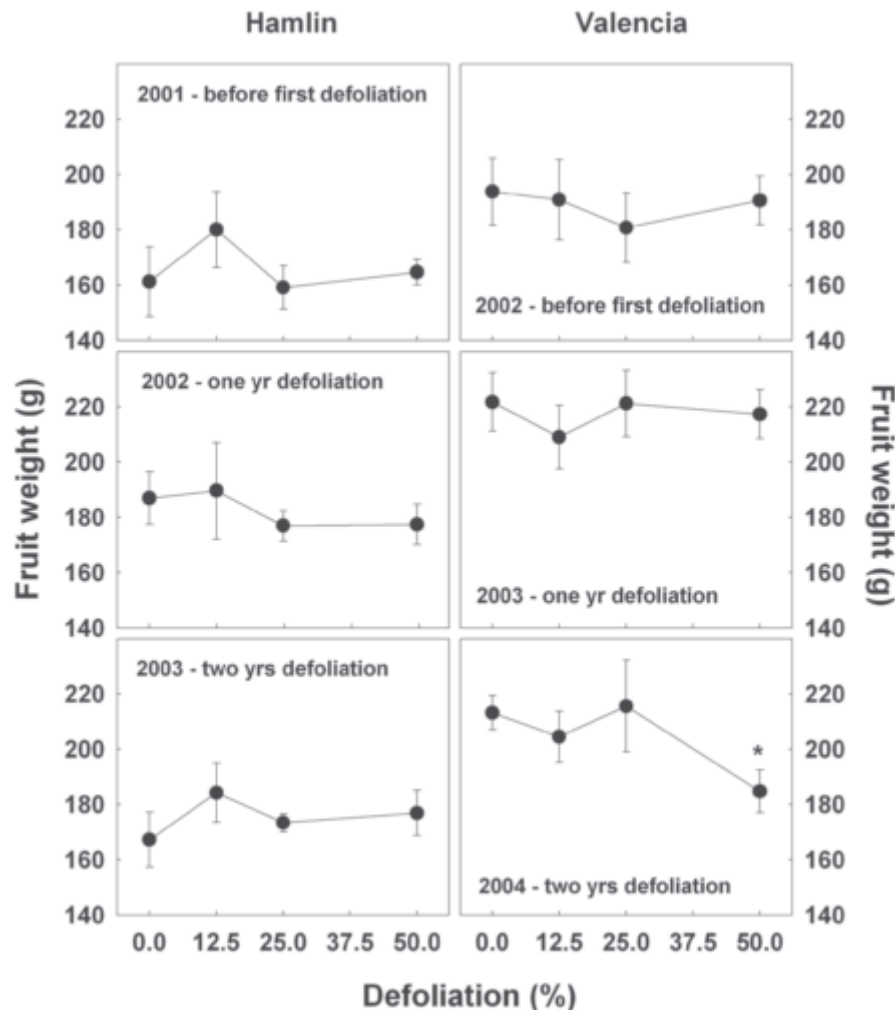
in all 3 years (Fig. 5). Average leaf number to fruit ratios followed similar patterns as leaf area to fruit number ratios (data not shown). In 'Valencia', a positive linear relationship existed between fruit weight at harvest and leaf area or leaf number to fruit number ratio after the second year but not after the first year of defoliation (Fig. 6).

Table 1. Effect of annual defoliation on yield of 'Hamlin' and 'Valencia' orange trees in 2 consecutive years (n = 4).

Defoliation (%)	Yield (kg/tree)		
	2001 ^z	2002	2003
Hamlin			
0	86.75	87.64	82.18
12.5	69.12	79.55	79.44
25	80.52	91.39	86.48
50	80.95	98.76	89.69
Significance			
Linear	NS	NS	NS
Quadratic	NS	NS	NS
0 vs. 50	NS	NS	NS
Valencia			
	2002 ^z	2003	2004
0	98.07	126.62	125.82
12.5	87.53	105.05	117.15
25	97.99	110.12	98.14
50	99.81	100	108.03
Significance			
Linear	NS	NS	NS
Quadratic	NS	NS	NS
0 vs. 50	NS	*	NS
0 vs. 25	NS	NS	NS

^zBefore initial defoliation treatment. Defoliation treatment was conducted in late November in 'Hamlin' oranges, and late March in 'Valencia' oranges, respectively.

^{NS} Nonsignificant or significant at $P \leq 0.05$, respectively.



Discussion

Removal of 25% or less of the 'Valencia' leaves in late March when spring flush leaves were fully expanded had no significant effect on fruit yield, soluble solids yield, or the following year's average leaf area. Thus, up to 25% of the total leaf area in healthy citrus trees was apparently not required to support normal fruit yield. Similarly, defoliation up to 20% in apple (Flore and Irwin, 1983), 20% in sour cherry (Layne and Flore, 1992), 25% in tomato (Stacey, 1983), or 40% in hybrid poplar clones (Bassman et al., 1982) had no significant effect on fruit yield, vegetative growth, or dry weight accumulation. Some level of defoliation can be compensated for by increasing photosynthetic rates of remaining leaves (Iglesias et al., 2002; Layne and Flore, 1992; Syvertsen, 1994). Increased photosynthetic rates after partial defoliation have been attributed to enhanced Rubisco activity and RuBP regeneration capacity (Layne and Flore, 1992; von Caemmerer and Farquhar, 1984; Wareing et al., 1968). Although 50% defoliation of 'Valencia' orange trees significantly increased photosynthetic rates of some of the remaining leaves (Garcia-Sanchez and Syvertsen, unpublished data), removal of 50% leaves in late March exceeded the tree's compensation ability since average leaf size decreased the following year and average fruit weight decreased after 2 years of defoliation. Fruit yield and soluble solids decreased after 1 year of defoliation but this effect disappeared after the second year of defoliation.

Reducing total leaf area by removal of 50% of 'Hamlin' leaves in late November, had no effect on fruit size and yield the following year. Similarly, shading 'Satsuma' mandarin trees in winter and presumably lowering winter-time photosynthesis rates, had no effect on bud break and flowering the next spring (Garcia-Luis et al., 1995; Wu et al., 1988). Since leaf area removed from 'Hamlin' orange trees in November was replaced by new leaves during the following spring before fruit set, there was no disruption in leaf area supporting young fruit set and development. Subsequent leaf size on the 50% defoliated trees was reduced, however, implying that early spring vegetative growth may have been limited by carbohydrate supply. This agrees with previous reports that new spring flush leaves are not net exporters

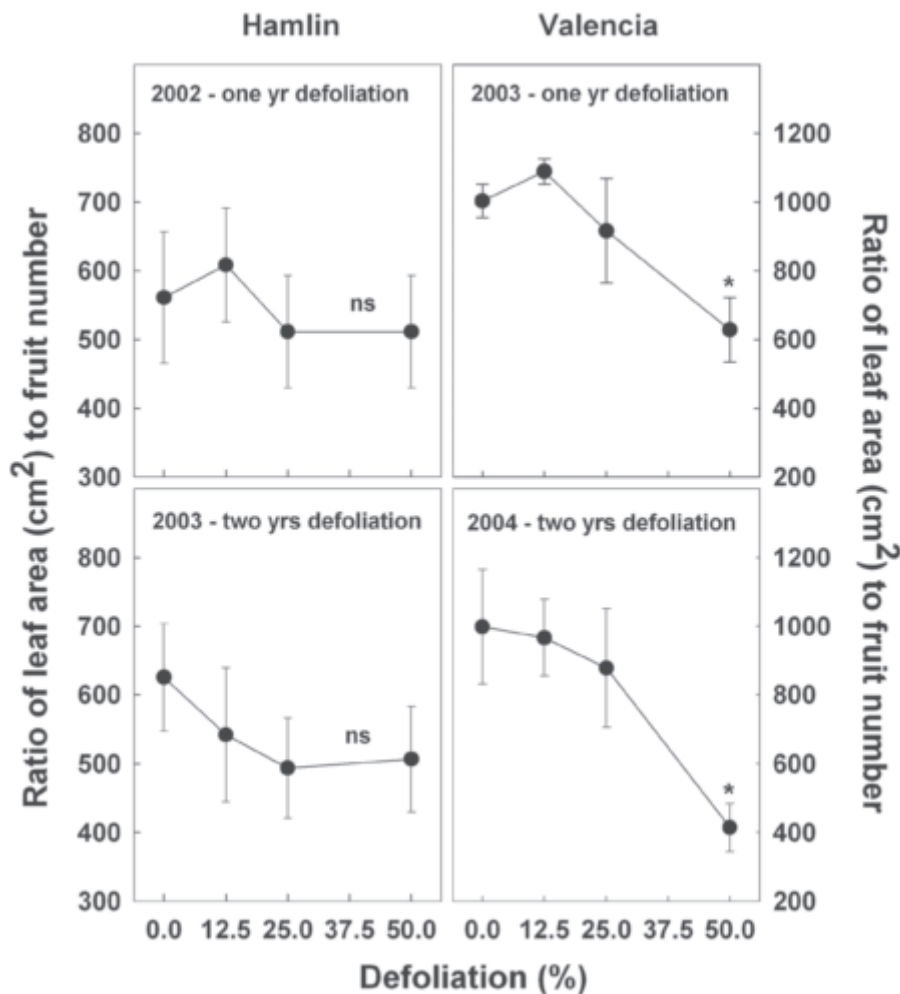
Fig. 3. The effect of defoliation on fruit size in 'Hamlin' and 'Valencia' orange trees. In 'Hamlin', leaves were removed for the first time in November 2001 and again in November 2002 and 2003. In 'Valencia', leaves were removed for the first time in March 2002 and again in March 2003 and 2004. Data are means \pm SE (n = 4). *Significant difference at $P \leq 0.01$.

Table 2. Effects of annual defoliation on juice quality of 'Hamlin' and 'Valencia' oranges in 2 consecutive years (n = 4).

Defoliation	Hamlin			Valencia		
	2001 ^z	2002	2003	2002 ^z	2003	2004
Brix						
0	10.61	10.1	11.43	12.42	11.45	12.47
12.5	10.4	10.12	11.28	12.69	11.81	12.82
25	10.69	10.25	11.57	12.6	11.48	12.38
50	10.84	10.54	11.57	12	11.67	12.46
Significance						
Linear	NS	NS	NS	NS	NS	NS
Quadratic	NS	NS	NS	NS	NS	NS
0 vs. 50	NS	NS	NS	NS	NS	NS
Ratio of Brix to % acid						
0	14.61	16.36	20.63	12.67	14.24	11.96
12.5	14.84	15.96	20.75	12.36	14.83	12.64
25	14.95	16.04	21.64	12.37	14.72	12.51
50	15.12	16.41	20.96	12.16	15.64	12.83
Significance						
Linear	NS	NS	NS	NS	NS	NS
Quadratic	NS	NS	NS	NS	NS	NS
0 vs. 50	NS	NS	NS	NS	NS	NS
Soluble solids (kg/tree)						
0	5.31	5.17	5.35	7.36	8.44	9.18
12.5	4.16	4.74	5.02	6.8	7.07	8.03
25	4.93	5.51	5.58	7.59	7.4	7.11
50	5.1	6.17	5.85	7.25	6.91	7.75
Significance						
Linear	NS	NS	NS	NS	NS	NS
Quadratic	NS	NS	NS	NS	NS	NS
0 vs. 50	NS	NS	NS	NS	*	NS
0 vs. 25	NS	NS	NS	NS	NS	NS

^zBefore initial defoliation treatment. Defoliation treatment was conducted in late November in 'Hamlin' oranges and late March in 'Valencia' oranges, respectively.

NS,*Nonsignificant or significant at $P \leq 0.05$, respectively.



of photosynthates until about 20 d after full bloom, and that carbohydrates used for new leaf growth come mainly from reserves and current photosynthates from older leaves (Akao et al., 1981; Ruan, 1993). Root growth may also have been affected by partial defoliation (Syvertsen, 1994) but results from an adjacent block of trees showed that removal of all new leaves and young fruit had only a small effect on root growth (Yuan et al., 2001). Therefore, 25% or less defoliation probably had little impact on citrus root growth under the conditions of this study.

Since fruit weight increased linearly with increasing ratio of leaf area to fruit number in both 'Hamlin' and 'Valencia' trees, fruit enlargement was apparently limited by leaf area. Previous results from girdled branches showed that fruit weight at harvest increased with leaf area per fruit in grapefruit (Fishler et al., 1983), grape (Winkler, 1930), peach (Weinberger and Cullinan, 1932), and litchi (Roe et al., 1997). Little increase in grapefruit weight occurred, however, as leaf area per fruit increased from 1.0 to 2.0 m², suggesting that 1.0 m² of leaves per fruit was sufficient to support fruit development and that any excess carbohydrates were allocated to vegetative growth or storage (Fishler et al., 1983). Based on our results, about 800 cm² leaf area (about 40 leaves) per fruit for 'Valencia' or 980 cm² (about 49 leaves) leaf area per fruit for 'Hamlin' were required to produce high quality orange fruit of about 200 g, or 100 count per carton of fresh packed oranges. Additional experiments with wider ranges of leaf area to fruit number ratios will be required to determine the critical point at which fruit size fails to increase with increasing leaf area to fruit ratio.

In conclusion, fruit weight and yield were not affected by annual defoliation of up to 25% of the canopy leaf area for 2 consecutive years. This suggests that otherwise healthy 'Hamlin' and 'Valencia' orange trees have excess leaf area that is not required to develop a normal crop load or that citrus trees have the ability to compensate for such levels of leaf removal by increasing photosynthetic rates of remaining leaves. Once leaf loss reached the 26% to 50% range, trees were unable to compensate so that individual leaf size was reduced but not total tree canopy volume. Annual removal of 50% of 'Valencia' leaves in the springtime reduced average fruit weight after 2 years and reduced fruit yield after one year but not after the second year. This work is a first step towards providing a better understanding of the effects of annual leaf loss in citrus trees and critical leaf areas for crop production over two consecutive seasons. When abscission agents become available for routine mechanical harvesting of citrus, they will be used annually for the life of the tree (≥ 20 years). Several natural and synthetic abscission agents that loosen mature fruit have been assumed unacceptable because they caused up

Fig. 4. Effect of defoliation on ratio of leaf area to fruit number in 'Hamlin' and 'Valencia' oranges. 'Hamlin' and 'Valencia' were harvested in late November and late March, respectively. Data are means \pm SE (n = 4). NS,*Nonsignificant or significant difference at $P \leq 0.01$.

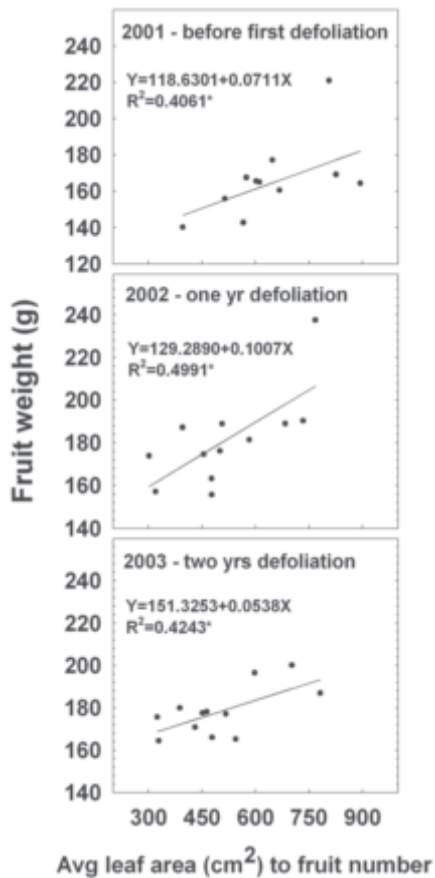


Fig. 5. Relationship between fruit size and ratio of leaf area to fruit number in 'Hamlin'. *Significant adjusted R^2 values at $P \leq 0.05$, respectively.

to 25% defoliation (Burns et al., 2003a; Burns et al., 2003b; Pozo et al., 2004a; Pozo et al., 2004b). These abscission agents may now become more promising since yield and tree health were not affected by this level of defoliation. Since abscission agents can also wound tissue and alter metabolism, such effects will need to be considered when fully assessing the consequences of these abscission agents.

Literature Cited

Akao, S., S. Tsukahara, H. Hisada, and S. Ono. 1981. Contribution of photosynthetic assimilates to development of flower and spring flush in *Citrus unshiu* Marc. J. Jpn. Soc. Hort. Sci. 50:1-9.

Bassman, J., W. Myers, D. Dickmann, and L. Wilson. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid polars in northern Wisconsin. Can. J. For. Res. 12:1-9.

Burns, J.K. 2002. Using molecular biology tools to identify abscission materials for citrus. HortScience 37:459-464.

Burns, J.K., R.S. Buker, and F.M. Roka. 2005. Mechanical harvesting capacity in sweet orange is increased with an abscission agent. HortTechnology (in press).

Burns, J.K., L.V. Pozo, C.R. Arias, B. Hockema, V. Rangaswamy, and C. Bender. 2003a. Coronatine and abscission in citrus. J. Amer. Soc. Hort. Sci. 128:309-315.

Burns, J.K., L.V. Pozo, R. Yuan, and B. Hockema. 2003b. Guanfacine and clonidine reduce defoliation and phytotoxicity associated with abscission agents. J. Amer. Soc. Hort. Sci. 128:42-47.

Byers, R.E., C.G. Lyons, Jr., K.S. Yoder, J.A. Barden, and R.W. Young. 1985. Peach and apple thinning

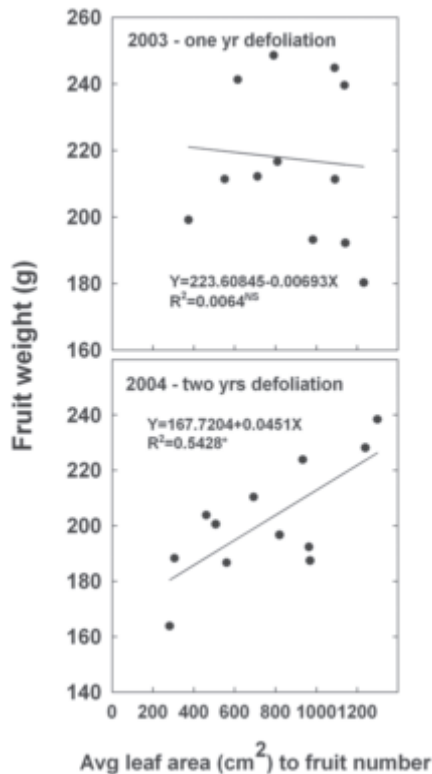


Fig. 6. Relationship between fruit weight and ratio of leaf area to fruit number in 'Valencia' oranges. ^{NS}Non-significant or significant adjusted R^2 values at $P \leq 0.05$, respectively.

by shading and photosynthetic inhibition. J. Hort. Sci. 60:465-472.

Byers, R.E., J.A. Barden, and D.H. Carbaugh. 1990. Thinning of spur 'Delicious' apples by shade, terbacil, carbaryl, and ethephon. J. Amer. Soc. Hort. Sci. 115:9-13.

Ferree, D.C. and J.W. Palmer. 1982. Effects of spur defoliation and ringing during bloom on fruiting, fruit mineral level, and net photosynthesis of 'Golden Delicious' apple. J. Amer. Soc. Hort. Sci. 107:1182-1186.

Fishler, M., E.E. Goldschmidt, and S.P. Monselise. 1983. Leaf area and fruit size in girdled grapefruit branches. J. Amer. Soc. Hort. Sci. 108:218-221.

Flore, J.A. and C. Irwin. 1983. The influence of defoliation and leaf injury on leaf photosynthetic rate, diffusive resistance, and whole tree dry matter accumulation in apple. HortScience 18:72.

Garcia-Luis, A., F. Fornes, and J.L. Guardiola. 1995. Leaf carbohydrates and flower formation in *Citrus*. J. Amer. Soc. Hort. Sci. 120:222-227.

Goldschmidt, E.E. 1999. Carbohydrate supply as a critical factor for citrus fruit development and productivity. HortScience 34:1020-1024.

Hansen, P. 1970. ¹⁴C-studies on apple trees. VI. The influence of the fruit on the photosynthesis of leaves, and the relative photosynthetic yields of fruits and leaves. Physiol. Plant. 23:805-810.

Iglesias, D.J., L. Liso, F.R. Tadeo, and M. Talon. 2002. Regulation of photosynthesis through source:sink imbalance in citrus is mediated by carbohydrate content in leaves. Physiol. Plant. 116:563-572.

Layne, D.R. and J.A. Flore. 1992. Photosynthetic compensation to partial leaf area reduction in sour cherry. J. Amer. Soc. Hort. Sci. 117:279-286.

Lenz, F. 1978. Photosynthesis and respiration of citrus as dependent upon fruit load. Proc. Intl. Soc. Citricult. 1:70-71.

Mehouachi, J., D. Serna, S. Zaragoza, M. Agusti, M. Talon, and E. Primo-Millo. 1995. Defoliation increases fruit abscission and reduces carbohydrate levels in developing fruits and woody tissues of *Citrus unshiu*. Plant Sci. 107:189-197.

Moss, G.I. 1976. Thinning 'Washington' navel and 'Late Valencia' sweet orange fruits with photosynthetic inhibitors. HortScience 11:48-50.

Pozo, L., A. Redondo, U. Hartmond, W.J. Kender and J.K. Burns. 2004a. 'Dikegulac' promotes abscission in citrus. HortScience 39(7):1655-1658.

Pozo, L., R. Yuan, I. Kostenyuk, F. Alferrez, G.Y. Zhong, and J.K. Burns. 2004b. Differential effects of 1-methylcyclopropene on citrus leaf and mature fruit abscission. J. Amer. Soc. Hort. Sci. 129:473-478.

Roe, D.J., C.M. Menzel, J.H. Oosthuizen, and V.J. Doogan. 1997. Effects of current CO₂ assimilation and stored reserves on lychee fruit growth. J. Hort. Sci. 72:397-405.

Ruan, Y.L. 1993. Fruit set, young fruit and leaf growth of *Citrus unshiu* in relation to assimilate supply. Scientia Hort. 53:99-107.

Stacey, D.L. 1983. The effect of artificial defoliation on the yield of tomato plants and its relevance to pest damage. J. Hort. Sci. 58:117-120.

Syvrtsen, J.P. 1994. Partial shoot removal increases net CO₂ assimilation and alters water relations of *Citrus* seedlings. Tree Physiol. 14:497-508.

Syvrtsen, J.P., C. Goni, and A. Otero. 2003. Fruit load and canopy shading affect leaf characteristics and net gas exchange of 'Spring' navel orange trees. Tree Physiol. 23:899-906.

von Caemmerer, S. and G.D. Farquhar. 1984. Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO₂) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta. 161:320-329.

Wareing, P.E., M.M. Khalifa, and K.J. Treharne. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature (London) 220:453-457.

Weinberger, J.H. and F.P. Culliman. 1932. Further studies on the relation between leaf area and size of fruit, chemical composition and fruit bud formation in Elberta peaches. Proc. Amer. Soc. Hort. Sci. 29:23-27.

Winkler, A.J. 1930. The relation of number of leaves to size and quality of table grapes. Proc. Amer. Soc. Hort. Sci. 27:158-160.

Wu, G.L., L.C. Zhang, F. Zhang, Y.L. Ruan, and J.S. Liu. 1988. A study on the physiology of overwintering 'Satuma' trees under straw sheds. China Citrus 17:3-6.

Wunsche, J.N., J.W. Palmer, and D.H. Greer. 2000. Effects of crop load on fruiting and gas-exchange characteristics of 'Braeburn'/M.26 apple trees at full canopy. J. Amer. Soc. Hort. Sci. 125:93-99.

Yuan, R. and D.W. Greene. 2000a. Benzyladenine as a chemical thinner for 'McIntosh' apples. I. Fruit thinning effects and associated relationships with photosynthesis, assimilate translocation, and nonstructural carbohydrates. J. Amer. Soc. Hort. Sci. 125:169-176.

Yuan, R. and D.W. Greene. 2000b. Benzyladenine as a chemical thinner for 'McIntosh' apples. II. Effects of benzyladenine, bourse shoot tip removal, and leaf number on fruit retention. J. Amer. Soc. Hort. Sci. 125:177-182.

Yuan, R., U. Hartmond, A. Grant, and W.J. Kender. 2001. Physiological factors affecting response of mature 'Valencia' orange fruit to CMN-pyrazole. I. Effects of young fruit, shoot, and root growth. J. Amer. Soc. Hort. Sci. 126:414-419.

Yuan, R. and H. Huang. 1988. Litchi fruit abscission: Its pattern, effect of shading and relation to endogenous abscisic acid. Scientia Hort. 36:281-292.