

Size, Biomass, and Nitrogen Relationships with Sweet Orange Tree Growth

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ABSTRACT. Growth and nitrogen (N) accumulation relationships based on tree size, rather than age, may provide more generic information that could be used to improve sweet orange [*Citrus sinensis* (L.) Osbeck] N management. The objectives of this study were to determine how orange trees accumulate and distribute biomass and N as they grow, investigate yearly biomass and N changes in mature orange trees, determine rootstock effect on biomass and N distribution, and to develop simple mathematical models describing these relationships. Eighteen orange trees with canopy volumes ranging between 2 and 43 m³ were dissected into leaf, twig, branch, and root components, and the dry weight and N concentration of each were measured. The N content of each tree part was calculated, and biomass and N distribution throughout each tree were determined. The total dry biomass of large (mature) trees averaged 94 kg and contained 0.79 kg N. Biomass allocation was 13% in leaves, 7% in twigs, 50% in branches/trunk, and 30% in roots. N allocation was 38% in leaves, 8% in twigs, 27% in branches/trunk, and 27% in roots. For the smallest tree, above-/below-ground distribution ratios for biomass and N were 60/40 and 75/25, respectively. All tree components accumulated biomass and N linearly as tree size increased, with the above-ground portion accumulating biomass about 2.5 times faster than the below-ground portion due mostly to branch growth. The growth models developed are currently being integrated in a decision support system for improving fertilizer use efficiency for orange trees, which will provide growers with a management tool to improve long-term N use efficiency in orange orchards.

Nitrogen is the most limiting nutrient for sweet orange production. Fertilization studies have traditionally emphasized N rate and timing effects on canopy growth and fruit yield (Koo, 1979, 1953; Reitz, 1956; Reuther et al., 1957; Sites et al., 1953). However, accurately determining the N input needed for maximum yield requires knowledge about root and shoot N requirements, since optimum plant growth and yield depend on maintaining an appropriate balance between vegetative and crop growth (Kramer and Boyer, 1995). Roots depend on shoots for carbohydrates, growth regulators, and some organic compounds, while shoots depend on roots for water and nutrients.

The relative proportions of total dry matter and N content allocated to above- and below-ground tree components change with age due to the growth of larger branches and trunks of older trees to support increased tree biomass. For example, Caruso et al. (1999) found that leaf and twig weight as a proportion of total peach [*Prunus persica* (L.) Batsch.] tree dry weight decreased with tree age while woody tissues increased. However, as with annual crops, tree size does not depend on age alone. Rootstock

(Castle, 1978, 1980), crop nutrition (Feigenbaum et al., 1987), irrigation (Parsons et al., 2001), and restriction of the root system (Mataa and Tominaga, 1998) can limit growth of an orange tree. Thus, orange trees of equal age can differ in size, biomass, and N content due to these factors. The ability to model root and shoot growth dynamics will improve our understanding of N uptake by orange trees, but data describing tree biomass and N accumulation as a function of tree size are not readily available.

Few predictive models have been developed specifically for use in sweet orange production. These models predict population and/or crop damage caused by citrus pathogens (Timmer and Zitko, 1996), scale insects (Arias-Reveron and Browning, 1995), irrigation scheduling (Xin et al., 1997), and crop flowering (Valiente and Albrigo, 2000). There are several predictive models developed to describe crop production. Crop–environment resource synthesis (CERES) was developed to model growth and yield of grain crops (Jones and Kiniry, 1987), while CROPGRO is the integration of a family of crop-specific models to predict legume and vegetable crop production (Hoogenboom et al., 1994; Scholberg et al., 1997; Wagner-Riddle et al., 1997). These are predictive, process-oriented models to simulate vegetative growth and reproductive development resulting in estimated dry matter growth (Quemada and Cabrera, 1995; Shen et al., 1998) and final yield (Batchelor et al., 1996; Gabrielle and Kengni, 1996; Heinemann et al., 2000; Jones and Luyten, 1998; Sexton et al., 1998) for given daily weather data, soil profile characteristics, and crop management conditions. Thus, developing functional

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relationships that capture tree growth and N accumulation dynamics as a function of tree size are essential for the development of a similar model for orange trees.

Considerable research and resources (Table 1) have been devoted to improving our understanding of how cultural, soil, and environmental factors influence biomass and N accumulation during orange tree development as a function of tree age but not tree size (Cameron and Appleman, 1935; Cameron and Compton, 1945; Feigenbaum et al., 1987; Kato et al., 1984; Mattos et al., 2003). It was reported that leaves of 3.5-, 7-, and 15-year-old 'Valencia' orange trees in California contained 40% to 50% of total tree N, while twigs and shoots contained approximately 10% of total N (Cameron and Appleman 1935; Cameron and Compton, 1945). Biomass proportions for 7-year-old 'Hamlin' orange trees grown in Florida (Mattos et al., 2003) were more like the 10-year-old trees than the 3.5-year-old trees dissected by Cameron and Appleman (1935) that had been grown in California. None of the above studies related biomass or N content of tree components to tree size measurements like canopy volume (TCV) or trunk cross-sectional area (TCSA).

Biomass and N distribution relationships based on tree size measurements rather than tree age would allow for the development of more universally applicable relationships that capture tree growth and N cycling dynamics, and could be integrated in a decision support system for orange production. Such a system in turn could be used to improve resource use efficiency and orange orchard management. We hypothesized that 1) we could define functional relationships correlating biomass and N partitioning of various orange tree components with tree size measured by TCSA or TCV; and 2) rootstock has a significant effect on orange

tree biomass and N partitioning. This information is a necessary component of a N budget for orange trees that can be used to fine-tune fertilizer recommendations to provide adequate N for growth and fruit production while minimizing nitrate leaching.

The objectives of this study were to 1) determine the distribution of biomass and N throughout orange trees as a function of tree size; 2) investigate how biomass and N content changes in mature orange trees after a 1-year period; 3) determine rootstock effect on mature orange tree biomass and N distribution; and 4) develop simple mathematical models to estimate how biomass and N are distributed throughout an orange tree knowing only TCSA or TCV.

Materials and Methods

The size of 18 orange trees ranging in age from 3 to 15 years was measured, followed by tree dissection and fresh weight measurement of constituent parts. The fresh and dry weights of representative tissue samples from each constituent part were measured, followed by nutrient concentration analysis. These data were used to estimate total dry mass and N content of each plant part. Finally, dry weight and N distributions throughout the tree were calculated. This study was performed in the fall and winter months to avoid tissue N reduction, particularly in woody tissues, due to N cycling within the trees during active growth.

Between Feb. and early Mar. 2001, six similar-sized 14-year-old 'Hamlin' orange trees were destructively sampled in a commercial orange orchard near Winter Garden in western Orange County, Fla. Three of the trees were budded on Swingle citrumelo [*C. paradisi* Macf. x *Poncirus trifoliata* (L.) Raf.]

Table 1. Summary of seven studies from literature sources comparing citrus biomass and N distribution on a proportion of total with tree age.

Source	Trees (no.)	Location	Cultivar	Age (years)	Tissue type	Weight proportion of total biomass (%)	N content proportion of total N (%)
Cameron and Appleman, 1935	15	California	Valencia	3.5	Leaves	31	62
					Branches	38	21
					Roots	31	17
Legaz and Primo-Millo, 1988	8	Spain	Valencia	4	Leaves	23	30
					Branches	29	19
					Lateral roots	46	41
					Fibrous roots	3	10
Mattos et al., 2003	6	Florida	Hamlin	6	Leaves	14	35
					Branches	46	28
					Lateral roots	26	14
					Fibrous roots	14	23
Cameron and Appleman, 1935	4	California	Valencia	10	Leaves	18	47
					Branches	61	39
					Roots	21	14
Cameron and Compton, 1945	36	California	Valencia	15	Leaves	17	45
					Branches	61	35
					Lateral roots	20	17
					Fibrous roots	2	3
Kato et al., 1984	1	Japan	Satsuma	21	Leaves	9	27
					Branches	65	45
					Lateral roots	19	14
					Fibrous roots	7	14
Feigenbaum et al., 1987	2	Israel	Shamouti	22	Leaves	8	25
					Branches	61	50
					Lateral roots	27	19
					Fibrous roots	4	4

rootstock, and three were on Carrizo citrange (*C. sinensis* × *P. trifoliata*) rootstock. This process was repeated between Jan. and Feb. 2002 using trees approximately the same size as those sampled in 2001. The trees were planted in 1987 at a spacing of 3 m within the row and 6.1 m between rows (556 trees/ha). All trees had been fertilized with nitrogen annually at a rate of 240 kg·ha⁻¹ applied in solution through a microirrigation system. The trees were irrigated with reclaimed water containing approximately 7 mg of NO₃-N per liter. The soil series at this site was Candler fine sand (hyperthermic, uncoated, Typic Quartzipsamment), a soil typically found in central Florida ridge orange orchards. It is an excessively drained, very rapidly permeable soil located in upland areas. The A and E horizons consist of single-grained fine sand, have a loose texture, and are strongly acidic. A Bt horizon is located at a soil depth of 2 m and includes loamy lamellae 0.1 to 3.5 cm thick and 5 to 15 cm long.

In Nov. 2001, seven various-sized 'Valencia' orange trees on Swingle citrumelo rootstock, varying in age from 3 to 15 years, were destructively sampled in a commercial orchard near Fort Meade in southern Polk County, Fla. These trees were planted at a spacing similar to the Hamlin trees at the Orange County location (3.3 × 6.5 m), and had been fertilized with dry N sources three or more times per year and were irrigated with well water. The soil series was Zolfo fine sand (sandy siliceous, hyperthermic, Grossarenic Entic Haplohumod), another typical central Florida ridge soil. Zolfo soil is also sandy, but slightly less well-drained than Candler. The A horizon consists of fine sand with single-grained, loose texture. The Bh horizon, between 4.0 and 5.0 cm thick at approximately 0.5 m, consists of fine sand coated with organic matter possessing weak granular to weak fine sub-angular blocky structure.

TREE CANOPY VOLUME AND TRUNK CROSS-SECTIONAL AREA. Changes in TCV or TCSA have been used to measure tree growth response to fertilizer rates (Whitney et al., 1991). Therefore, we measured tree size in this manner and correlated it with biomass and N concentration of various tree components. Canopy diameter of each tree was measured 1.5 m above the ground within and across the row. Tree height and hedgerow intercept measurements were made using a 5-m graduated pole. Hedgerow intercept is the height from the ground to the point at which the canopies of two trees meet in the row. These measurements have been used by Whitney et al. (1991) to determine canopy volume based on a spheroid model (Eq. 1):

$$TCV = (\pi/4)(IR)(CR)(HT)\{[1 - (1 - (INT/HT)^2)]/3\} \quad [1]$$

where TCV = tree canopy volume (cubic meters); IR = within-row spacing (meters); CR = cross-row spacing (meters); HT = canopy height (meters); and INT = canopy intercept height (meters).

Trunk diameter 5 cm above the ground was measured in both within-row and across-row directions. Trunk cross-sectional area was determined for each tree, assuming an elliptical shape. The largest of the trees measured were just reaching containment size, but had not yet completely filled the tree-allocated space.

TREE BIOMASS FRESH WEIGHT. Fresh weight of leaves, twigs, branches, trunk tap root, and roots were measured. Twigs were defined as being <7 mm in diameter; and branches were separated by diameter into three categories of small branches, medium branches, and large branches, with diameters of 7 to 15 mm, 15 to 30 mm, and >30 mm, respectively. Roots were, likewise, separated into small, medium, and large, having diameters of <4 mm, 4 to 20 mm, and >20 mm, respectively. Field weights and three samples of each plant part category were collected for

each tree using the following protocol: twigs less than 7 mm in diameter and attached leaves were cut from the tree with leaves intact. These twigs were placed into a plastic container and weighed on a portable balance. During cutting, one twig out of 20 was placed into a separate container and weighed separately. Leaves were removed from the selected twig and weighed. Branches 7 mm in diameter and greater were cut into 15- to 30-cm segments, separated into the three size ranges noted above, and weighed separately. Two to three samples equal to ≈5% of the fresh weight of each size category were removed from each container and placed into plastic bags. Any leaves attached to these branches were removed and weighed prior to weighing the branch segments. The trunk and taproot were cut into pieces and weighed, and three longitudinal slices of each were retained as separate sub-samples.

A vertical 0.3-m-deep cut through the roots was made with a shovel in a rectangular pattern 3 m within-row × 6.1 m across-row with the tree stump at its center. The bulk of the root system was extracted using a front-end loader equipped with a rake. All roots were removed from the excavation to a depth of 1 m, washed, blotted dry, separated into size categories, and weighed in the field.

SAMPLE PROCESSING AND N ANALYSIS. The area of 50 random leaves from each sample was measured. Each branch segment was cut into at least five disks approximately 0.5 to 1 cm thick that facilitated the removal of bark from the wood. Likewise, the bark was removed from each horizontal trunk slice. The bark and wood from the branch and trunk disks were weighed separately to determine the fresh mass proportion of bark to wood for each size category.

Samples were dried at 70 °C to a constant weight before recording dry weight. Drying time ranged from 3 d for leaves to a maximum of 10 d for trunk tissue. Total tissue dry weight for each tree was determined by multiplying fresh weights by the respective tissue dry matter content. All tissues were ground using a Cyclotec mill (1093 Sample Mill; Tecator Manufacturing, Hoganas, Sweden) for leaf tissue and Wiley mill (model 1; Arthur Thomas Manufacturing Co., Philadelphia) for woody tissue. The ground tissues were digested using a 12-vessel digestion unit (model K435; Buchi Analytical, New Castle, Del.). The digest was analyzed for total Kjeldahl N according to USEPA method 351.2 using a steam distillation instrument (model B339; Buchi Analytical).

LEAF AREA, BIOMASS AND N WEIGHT ESTIMATION. Specific leaf area (cm²·g⁻¹) was determined for a 50-leaf subsample by dividing total leaf area by leaf dry weight. Total leaf area was estimated by multiplying the mean specific leaf area by the estimated total dry leaf weight for the corresponding tree. Leaf area index (LAI) was determined for each tree by dividing the leaf area by the corresponding cross-sectional canopy area using the in-row and cross-row measurements. Dry weights for each tissue type and size category were estimated by multiplying the total field fresh mass by the mean percent dry mass of three sub-samples. N accumulation by each tissue type was estimated by multiplying its total dry weight by its mean N concentration. Total tree dry weight and N content were determined by summing the tissue categories. The above-ground dry weight and N contents were determined by summing the estimated values for leaf, twig, total branch, and trunk components. The below-ground biomass and N accumulation was the sum of total root and taproot values. Percentages of total biomass and N weight were determined for each tissue.

Since the soil, climatic, and management conditions in the Polk County orchard were similar to those in Orange County, it was assumed that tree growth there followed similar biomass and N partitioning patterns. Data from both sites were combined to determine relationships of dry weight and N accumulation to TCV and TCSA.

STATISTICAL ANALYSIS. Since the two groups of mature 'Hamlin' trees were dissected ≈ 12 months apart, year ($n = 6$) of sampling was considered a variable along with rootstock ($n = 6$) in the analysis of variance, using the SAS general linear models (GLM) procedure (SAS Institute, Cary, N.C.). Linear and non-linear regression analyses were used to relate leaf area and LAI to tree size. The relationships of biomass, N weight, biomass distribution percentage, and N weight distribution percentage of each tree component to tree size were analyzed using linear regression.

Results and Discussion

MATURE ORANGE TREE BIOMASS DISTRIBUTION. The total fresh weight of individual mature orange trees ranged from 120 to 194 kg/tree. TCV was between 27 and 43 m³, and TCSA ranged from 65 to 172 cm². Approximately 70% of total mature 'Hamlin' tree dry weight (not including fruit) was above ground, with the remaining amount in the root system. About two-thirds of the above-ground dry weight was comprised of branches. Large roots and the tap root constituted more than half of the below-ground dry weight (Table 2).

Year of sampling (2001 vs. 2002) had no effect on dry weight of any tree component except medium roots. Total above-ground dry weight of 'Hamlin' trees on Carrizo rootstock was significantly greater than trees on Swingle, but the two rootstocks used in this study did not affect below-ground dry weight. Carrizo rootstock trees also had a higher percentage of large branch and total branch biomass compared with Swingle. On a percentage basis, taproot biomass was significantly greater for trees on Swingle than those on Carrizo. Dry weight allocation to leaves, twigs,

small branches, medium branches, and trunk were similar for both rootstocks. Dry matter allocation to tree roots (excluding tap root) was highly variable, averaging $\approx 20\%$.

Total leaf area increased with tree size (Fig. 1). The two rootstocks in this study did not affect leaf area, which averaged 107.4 ± 18.7 m²/tree (mean \pm SE) for the mature 'Hamlin' trees. Neither rootstock nor tree size affected LAI, which averaged 10.1 ± 1.5 m²-m⁻² canopy ground coverage. The LAI was within the 9 to 11 range found by Syvertsen and Lloyd (1994) for mature orange trees, but was much higher than the 3 or less normally associated with agronomic row crops (Flenet et al., 1996). The dense canopy of an orange tree is thought to be a result of its development as an understory plant in subtropical rainforests (Syvertsen and Lloyd, 1994).

MATURE ORANGE TREE N DISTRIBUTION. Neither year nor rootstock included in this study affected tissue N concentration within any of the mature 'Hamlin' orange tree components sampled. Therefore, year or rootstock differences in N mass allocation among each tissue category were mostly due to differences in biomass. Mean total Kjeldahl N concentrations in g·kg⁻¹ within mature tree parts were as follows: leaves, 24.7 ± 1.3 ; twigs, 11.2 ± 1.6 ; small branches, 4.7 ± 0.4 ; medium branches, 4.1 ± 0.4 ; large branches, 4.2 ± 0.4 ; trunk, 4.9 ± 0.5 ; small roots, 15.6 ± 1.5 ; medium roots, 10.4 ± 1.7 ; large roots, 4.9 ± 1.6 ; tap root, 4.3 ± 0.7 . Mean N concentration (g·kg⁻¹) for mature orange fruit collected in 2002 was 12.0 ± 1.6 with accumulations for the two rootstocks of 302 and 258 g/tree for trees on Carrizo and Swingle, respectively.

Neither sampling year nor rootstock affected total, above-ground, or below-ground N accumulation (Table 3). Leaf, twig, branch/trunk, and root N comprised 37%, 8%, 28%, and 27% of total tree N, respectively. Year and rootstock did not affect above-ground N allocation among tree parts except large branches, where there was interaction between year of sampling and rootstock. Carrizo trees had $\approx 50\%$ more N in large branches compared with Swingle (Table 3). Below ground, there was a higher percentage

Table 2. Dry matter accumulation and allocation between tree components for 12 mature 'Hamlin' orange trees as affected by year of sampling and rootstock.

Factor	Dry wt		Dry wt allocation													
	Total	Above	Below	Above ground							Below ground					
		ground	ground	Leaves	Twigs ^z	Branches ^y			Trunk ^x	Total	Roots ^w					
						Small	Medium	Large			Small	Medium	Large	Tap	Total	
	kg/tree		(% of total tree wt)													
2001	97.5	69.2	28.3	13	6	17	12	19	48	4	70	5	5	10	10	30
	$\pm 12.9^v$	± 15.7	± 4.9	± 1.1	± 2.3	± 2.1	± 3.8	± 9.0	± 7.1	± 1.4	± 7.8	± 1.3	± 1.6	± 2.2	± 7.1	± 7.8
2002	90.8	64.9	26.3	12	7	15	9	21	45	4	69	6	7	6	9	31
	± 16.3	± 15.9	± 8.2	± 1.3	± 1.6	± 2.4	± 3.6	± 2.8	± 4.3	0.9	± 8.2	± 1.0	± 0.3	± 1.8	± 4.7	± 6.4
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS	NS	NS
Carrizo	104.3	77.0	26.6	12	7	16	10	24	50	4	73	6	6	7	7	27
	± 10.2	± 11.0	± 5.0	± 1.2	± 1.0	± 1.6	± 2.8	± 3.3	± 3.2	± 0.8	± 4.3	± 1.6	± 1.2	± 2.5	± 2.5	± 4.0
Swingle	82.6	54.7	27.9	13	6	16	10	16	42	4	67	6	6	9	13	33
	± 14.9	± 9.4	± 8.9	± 1.1	± 2.8	± 3.3	± 5.3	± 6.0	± 4.6	± 1.5	± 7.8	± 0.5	± 1.8	± 2.4	± 6.5	± 7.8
	NS	*	NS	NS	NS	NS	NS	**	*	NS	NS	NS	NS	NS	*	NS

^zTwigs refer to tree branches <7 mm in diameter.

^yBranches were separated into three categories by diameter: small = 7–15 mm; medium = 15–30 mm; and large >30 mm.

^xTrunk tissue is defined as the aboveground main stem after all branches were removed.

^wRoots were separated into three categories by diameter: small <4 mm; medium = 4–20 mm; and large >20 mm. Tap root was defined as the vertical member after all roots were removed.

^vSE.

NS, *, **Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

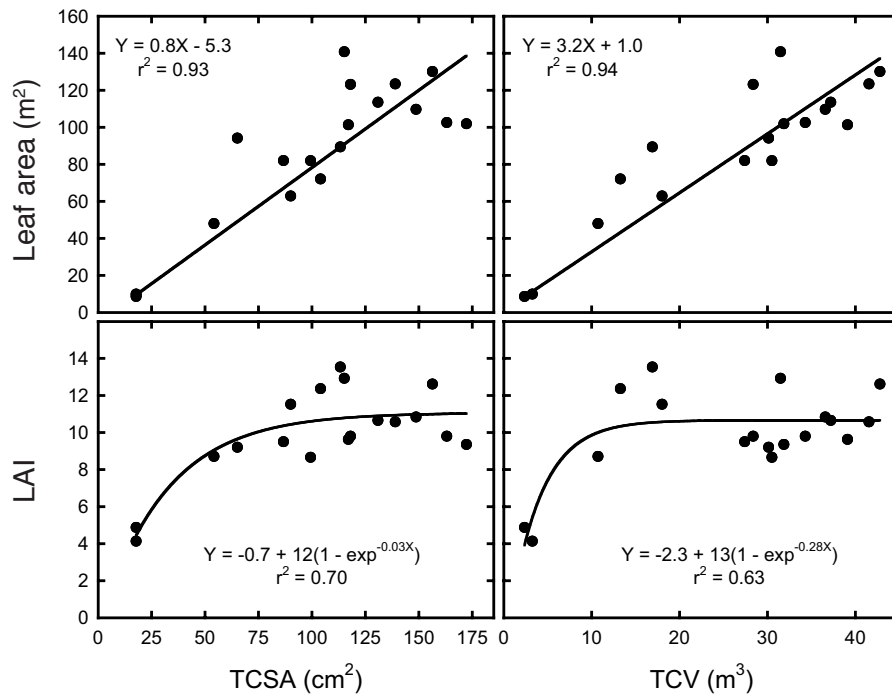


Fig. 1. Orange tree leaf area and leaf area index (LAI) as a function of trunk cross-sectional area (TCSA) and tree canopy volume (TCV) for all 18 trees used in this study.

of N in large roots of trees sampled in 2001 than those in 2002, and trees on Carrizo rootstock had a slightly higher N percentage in medium roots compared with trees on Swingle (Table 3).

RELATIONSHIPS OF LEAF AREA AND LAI TO TREE SIZE. The two methods of measuring tree size were well correlated, described by the equation

$$TCSA \text{ (cm}^2\text{)} = 10.1 + 3.19 \text{ TCV (m}^3\text{)}, r^2 = 0.93$$

Total leaf area per tree was linearly proportional to both TCV and TCSA (Fig. 1). LAI increased rapidly from 4 to 10 as TCSA increased from 20 to 80 cm² and as TCV increased from 2 to 10 m³, with little further increase above these ranges (Fig. 1). These relationships can be used to parameterize light interception functions for orange tree photosynthesis and growth model.

BIOMASS AND N CONTENT OF TREE COMPONENTS AS A FUNCTION OF TREE SIZE. Significant relationships were found between dry biomass and tree size (Tables 4 and 5). Orange tree dry weight accumulation of all tree components increased linearly as tree size increased. Biomass accumulation by above-ground tree components correlated slightly better (higher r² value) with TCV growth compared with TCSA. Conversely, three of the four root components correlated slightly better with TCSA. Comparison of regression slopes revealed that as tree size increased, the above-ground portion of the tree accumulated biomass ≈2.5 times faster than the below-ground portion. This rate of biomass accumulation is indicative

of non-limitation on growth from inter-tree competition for light and soil water resources.

Compared with leaves, biomass weights for twig, trunk, and root categories had greater variation that resulted in lower r² and higher RMSE. The medium branch masses varied more than the small or large branch categories, possibly indicating inconsistent and/or incomplete separation of tree components into appropriate diameter ranges. Correlations of trunk and taproot weights with

Table 3. Nitrogen accumulation and allocation between tree components for 12 mature ‘Hamlin’ orange trees as affected by year of sampling and rootstock.

Factor	N wt			N allocation												
	Total	Above ground	Below ground	Above ground						Below ground						
					Leaves	Twigs ^z	Branches ^y			Trunk ^x	Roots ^w					
						Small	Medium	Large	Total		Total	Small	Medium	Large	Tap	Total
	kg/tree			(% of total tree N)												
2001	0.81	0.60	0.21	38	8	10	6	9	25	2	72	10	6	6	5	28
	±0.11 ^v	±0.12	±0.02	±3.2	±2.6	±1.4	±1.8	±3.9	±3.0	±0.8	±4.7	±3.2	±2.1	±1.2	±2.9	±4.7
2002	0.77	0.57	0.20	37	8	9	5	11	24	2	74	10	7	4	5	26
	±0.19	±0.15	±0.05	±2.6	±1.3	±1.2	±2.0	±1.5	±3.0	±0.7	±4.5	±1.6	±0.9	±0.7	±2.6	±4.5
	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	**	NS	NS
Carrizo	0.87	0.65	0.22	36	9	9	5	12	26	2	75	10	7	4	25	
	±0.12	±0.11	±0.28	±3.9	±1.3	±1.1	±1.4	±1.8	±2.4	±0.6	±3.5	±3.0	±1.2	4±1.3	±1.2	±3.4
Swingle	0.69	0.50	0.19	38	8	9	5	8	23	2	72	10	6	5	6	27
	±0.13	±0.10	±0.05	±0.2	±2.5	±1.9	±2.6	±3.0	±2.2	±0.9	±5.6	±1.6	±1.3	±1.6	±3.0	±5.6
	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	*	NS	NS	NS

^zTwigs refer to tree branches <7 mm in diameter.

^yBranches were separated into three categories by diameter: small = 7-15 mm, medium = 15-30 mm, and large >30 mm.

^xTrunk tissue is defined as the above-ground main stem after all branches were removed.

^wRoots were separated into three categories by diameter: small <4 mm, medium = 4-20 mm, and large >20 mm. Tap root was defined as the vertical member after all roots were removed.

^vSE.

^wThere was interaction between year of sampling and rootstock for percentage of total tree N in large branches. N allocation data for large branches are as follows: Carrizo (2001), 12%; Carrizo (2002), 11%; Swingle (2001), 5%; Swingle (2002), 10%.

^{ns, *, **}Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 4. Linear regression analysis² of dry weight and N accumulation in tree components as a function of trunk cross-sectional area (TCSA) for all 18 trees in this study. Root mean square errors (RMSE) of the regressions are included as a measure of error in the estimation.

Y	Intercept (Y ₀)	Slope (a)	r ²	RMSE	P
<i>Dry weight (kg/tree)</i>					
Total	-3.80	0.69	0.83	14.26	<0.0001
Above ground	-9.06	0.56	0.82	11.76	<0.0001
Leaves	0.67	0.08	0.77	2.05	<0.0001
Twigs	-0.19	0.06	0.51	2.47	0.0009
Small branches	-2.52	0.12	0.73	3.45	<0.0001
Medium branches	-0.38	0.08	0.45	3.99	0.0023
Large branches	-7.28	0.19	0.63	6.72	<0.0001
Total branches	-10.18	0.40	0.79	9.23	<0.0001
Trunk	0.65	0.02	0.49	1.03	0.0012
Below ground	2.23	0.18	0.57	6.90	0.0003
Small roots	0.31	0.04	0.74	0.96	<0.0001
Medium roots	0.40	0.04	0.67	1.27	<0.0001
Large roots	0.21	0.05	0.42	2.64	0.0034
Tap root	1.31	0.05	0.19	4.50	0.0213
<i>N weight (g/tree)</i>					
Total	-6.35	5.80	0.81	126.86	<0.0001
Above ground	-9.25	4.37	0.78	104.16	<0.0001
Leaves	17.00	2.09	0.74	55.59	<0.0001
Twigs	-1.91	0.57	0.54	23.96	0.0006
Small branches	-7.64	0.56	0.71	16.26	<0.0001
Medium branches	3.38	0.30	0.38	17.76	0.0068
Large branches	-24.67	0.74	0.59	28.07	0.0002
Total branches	-28.93	1.61	0.75	41.84	<0.0001
Trunk	4.58	0.10	0.38	5.85	0.0064
Below ground	3.33	1.42	0.74	37.62	<0.0001
Small roots	-0.53	0.57	0.73	15.58	<0.0001
Medium roots	-1.66	0.40	0.71	11.66	<0.0001
Large roots	0.69	0.24	0.45	12.01	0.0024
Tap root	4.83	0.21	0.25	16.28	0.0357

²Y = Y₀ + aX, where X = TCSA, and Y₀ and a are regression coefficients.

TCV and TCSA were poor compared with those for other tree components. Variation in dry matter allocation to root and tap root were apparently due to differences in root density distribution of the two rootstocks.

N weight accumulation by tree components was also significantly related to tree size in a linear fashion (Tables 4 and 5). As tree size increased, the above-ground portion of the tree accumulated N more than three times faster than the below-ground portion. In addition to the biomass increase differences between them, the above-ground tree parts contained an average of ~20% more N than the roots on a unit weight basis.

RELATIVE BIOMASS AND N CONTENT DISTRIBUTION AMONG TREE COMPONENTS. The ratio of above-ground to below-ground biomass and N content ranged from 3:2 to 3:1 across the range of tree sizes analyzed. As tree size increased from small to large, the relative amount of biomass allocated to above-ground tree parts increased from ~60% to 80% (Fig. 2). This increase was due to biomass accumulation by branches, which increased from 20% to 55% of tree dry weight as tree size increased; thus the relative amount of biomass allocated to leaves, twigs, trunk, and roots decreased as branch mass increased.

Relative root biomass above 1-m depth was subject to the

Table 5. Linear regression analysis² of dry weight and N accumulation in tree components as a function of tree canopy volume (TCV) for all 18 trees in this study. Root mean square errors (RMSE) of the regressions are included as a measure of error in the estimation.

Y	Intercept (Y ₀)	Slope (a)	r ²	RMSE	P
<i>Dry weight (kg/tree)</i>					
Total	7.24	2.48	0.93	9.18	<0.0001
Above ground	0.23	1.99	0.91	8.39	<0.0001
Leaves	2.35	0.29	0.80	1.96	<0.0001
Twigs	0.33	0.21	0.66	2.07	<0.0001
Small branches	-0.76	0.45	0.85	2.58	<0.0001
Medium branches	1.42	0.27	0.44	4.04	0.0028
Large branches	-4.23	0.69	0.71	5.97	<0.0001
Total branches	-3.57	1.41	0.87	7.15	<0.0001
Trunk	1.12	0.07	0.49	1.03	<0.0001
Below ground	4.11	0.66	0.71	5.64	0.0012
Small roots	1.30	0.11	0.65	1.13	<0.0001
Medium roots	1.57	0.12	0.56	1.48	<0.0001
Large roots	0.42	0.20	0.60	2.19	<0.0001
Tap root	0.83	0.22	0.35	4.03	0.0093
<i>N weight (g/tree)</i>					
Total	84.28	20.83	0.91	85.00	<0.0001
Above ground	57.86	15.76	0.89	74.34	<0.0001
Leaves	58.06	7.18	0.77	52.77	<0.0001
Twigs	0.18	2.30	0.77	16.91	<0.0001
Small branches	-0.10	2.08	0.84	11.99	<0.0001
Medium branches	8.71	1.07	0.41	17.30	0.0043
Large branches	-16.25	2.80	0.73	22.82	<0.0001
Total branches	-7.64	5.95	0.89	27.28	<0.0001
Trunk	7.25	0.32	0.34	6.05	0.0115
Below ground	27.03	5.05	0.82	31.38	<0.0001
Small roots	13.82	1.85	0.67	17.33	<0.0001
Medium roots	7.27	1.35	0.70	11.95	<0.0001
Large roots	1.45	0.97	0.65	9.59	<0.0001
Tap root	4.49	0.87	0.39	14.63	0.0055

²Y = Y₀ + aX, where X = TCV, and Y₀ and a are regression coefficients.

greatest decrease with increase in tree size. Roots constituted 30% of small tree dry weight, but only 15% of large tree dry weight (Fig. 2). The tap root averaged ~9% of total tree weight regardless of size, although the variation was high. There was no consistent trend regarding which tree size measurement correlated better with changes in the relative amount of biomass allocated to the various tree parts. Leaves and roots correlated better with TCV; branches correlated better with TCSA; and no difference was detected for twigs and trunk (Fig. 2).

The relationships of relative N content in each tree component to tree size were less well-defined than the relative biomass relationships. Only the percentage of total tree N allocated to leaves, branches, and the trunk were significantly influenced by tree size, and correlated better with TCV compared with TCSA (Fig. 3). The relative amount of N residing in branches increased as trees grew larger, but decreased in the leaves and trunk. N weight percentage in the above-ground, below-ground, twig, root, and tap root components remained constant (74%, 26%, 8%, 30%, and 4%, respectively) regardless of tree size. Leaves showed the greatest difference between biomass partitioning and N partitioning; the leaves of the largest trees held only ~12% of tree dry weight, but ~38% of the N weight.

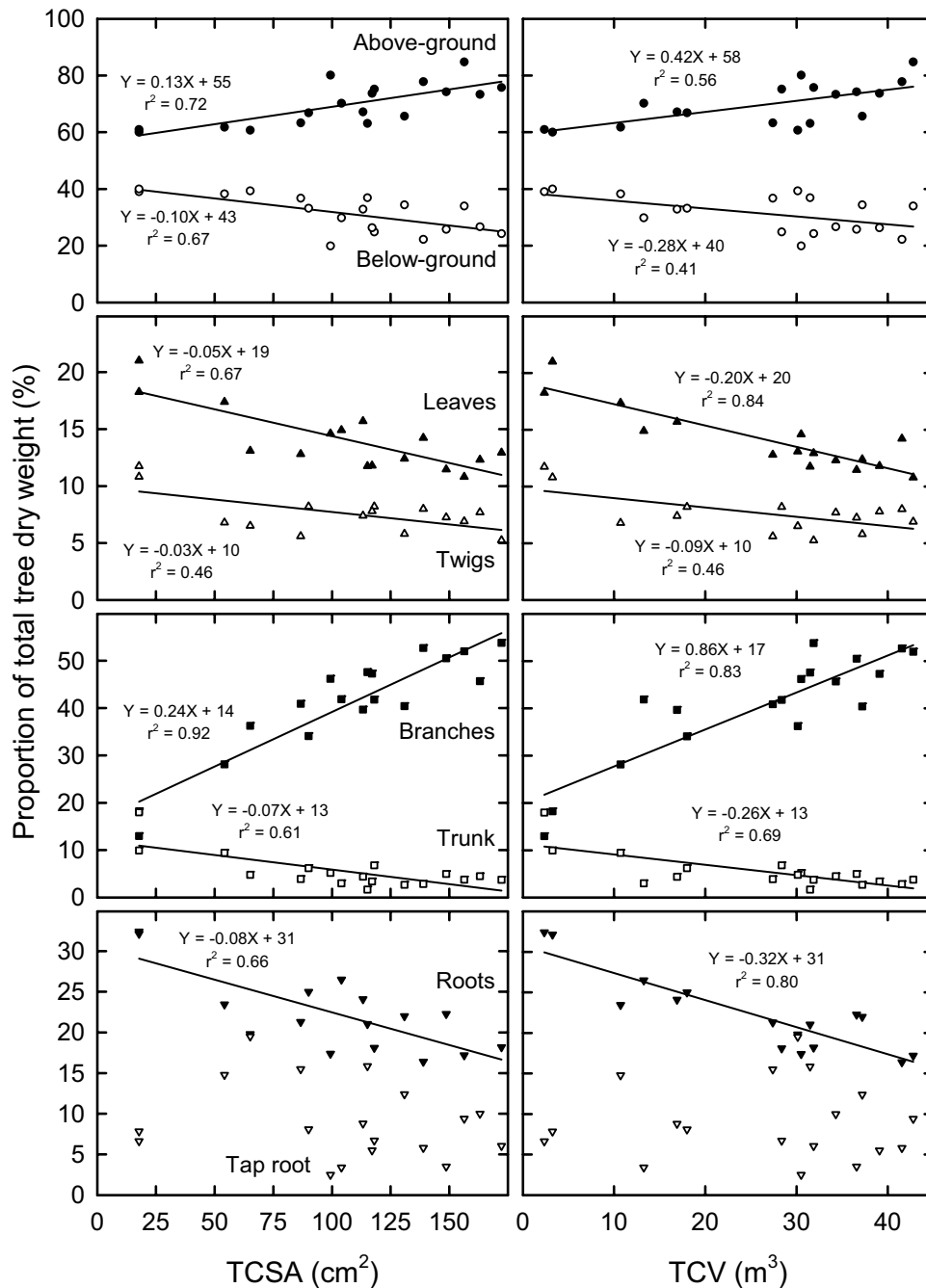


Fig. 2. Dry weight allocation to above-ground, below-ground, leaf, twig, branch, trunk, root (not including tap root), and tap root components as a function of orange tree trunk cross-sectional area (TCSA) and tree canopy volume (TCV) for all 18 trees used in this study.

Conclusions

As orange trees grow, branches increase in diameter through accumulation of xylem tissue, eventually developing a scaffold branch structure of large-diameter branches. The relationship of total tree biomass and N weight to TCV and TCSA was linear, indicating a constant rate of accumulation with increase in tree size. This result implies that the partitioning of biomass and N accumulation in all plant parts occurs at rates specific to the tree component. Therefore, the total biomass and/or N weight of an orange tree can be estimated for any tree size.

Percentage of biomass and N weight of woody tree parts (large

branches and trunk) increased while those of leaves and twigs decreased with increase in TCV and TCSA. Caruso et al. (1999) found similar results in peach trees, where the relative proportion of leaf and twig dry weights decreased with tree age. It can be concluded that to support the increase in total tree weight, the biomass and N content of woody branches and trunk increases at a higher rate compared with leaves and twigs. However, it appears that LAI is a limiting factor in leaf and twig biomass accumulation since the ratio of leaf area to ground area under the canopy remained constant with increase in tree size for medium and large trees. Thus, once the total biomass and N weight of a tree is estimated from tree size measurement, the weights of individual tree parts can be estimated. Regression equations (Tables 4 and 5) can be used to simulate biomass and N partitioning in an orange tree growth (excluding fruit) model.

Leaf area of both young (small) and mature (large) orange trees was correlated with tree size as measured by TCSA and TCV. Leaf area index increased rapidly for young orange trees and then reached a maximum value of 10 by age 3 to 4 years. This information can be used to model orange light interception and total photosynthesis as a function of tree size.

Biomass and N partitioning of specific orange tree components with tree size was captured in generic linear relationships. A favorable outcome for modeling purposes was that the rootstocks used in this study did not have a significant effect. Changes in orange tree dry weight and N content were linearly related to TCV and TCSA. Total biomass and N allocated to leaf, branch, and root tissue measured here compared

well with 10- and 15-year-old trees harvested by Cameron and Appleman (1935) and Cameron and Compton (1945).

Partitioning of biomass and N decreased for leaves and twigs, increased for branches, and remained constant for trunk and tap-root with increase in tree size. While mature orange trees grown on Swingle citrumelo rootstock were consistently smaller than trees of similar age grown on Carrizo citrange, mass partitioning of tree parts based on tree size was similar for both rootstocks. Rootstock effects in this paper only apply to the two rootstocks used in this study under Florida conditions. Thus, no generalizations regarding rootstock effects on biomass and N accumulation can be made; however, the two rootstocks used represent 60%

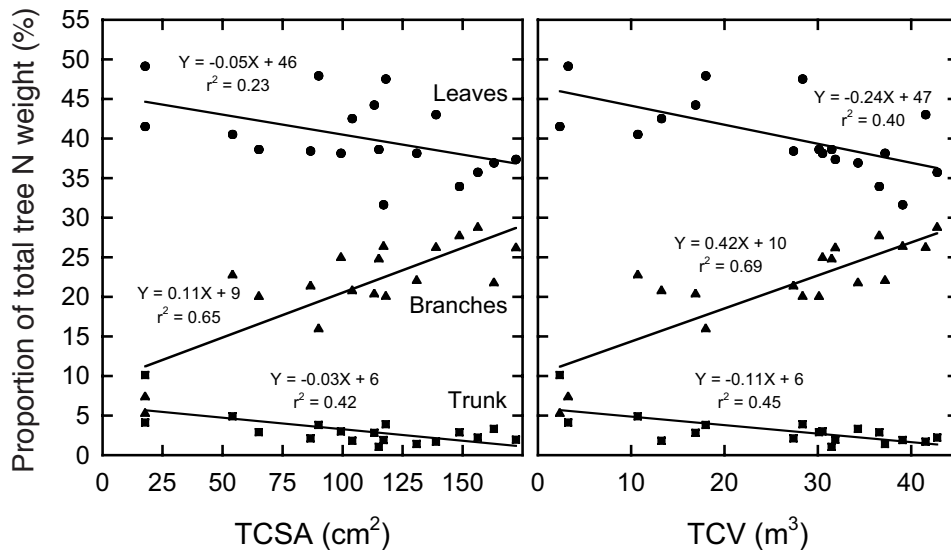


Fig. 3. N weight allocation to leaf, branch, and trunk as a function of orange tree trunk cross-sectional area (TCSA) and tree canopy volume (TCV) for all 18 trees used in this study.

to 70% of the orange acreage in Florida (Florida Department of Agriculture and Consumer Services, 2004). Significant differences in large and total branch biomass were correlated with tree size as measured by TCV and TCSA. Hence, the percentages of total biomass for specific tree components were similar for both rootstocks, indicating that above-ground biomass is partitioned about equally as trees grow. Therefore, the biomass and N accumulation relationships developed in this study can be used as the basis to parameterize models estimating orange tree photosynthesis, growth, and N use with change in tree size that will provide a new opportunity to improve long-term N use efficiency in orange orchards.

Literature Cited

Arias-Reveron, J.M. and H.W. Browning. 1995. Development and mortality of citrus snow scale under constant temperature and relative humidity. *Environ. Entomol.* 24:1189–1195.

Batchelor, W.D., J.W. Jones, and K.J. Boote. 1996. Comparisons of methods to compute peanut seed size distribution by crop growth models. *Trans. Amer. Soc. Agr. Eng.* 39:737–744.

Cameron, S.H. and D. Appleman. 1935. The distribution of total nitrogen in the orange tree. *J. Amer. Soc. Hort. Sci.* 30:341–348.

Cameron, S.H. and O.C. Compton. 1945. Nitrogen in bearing orange trees. *J. Amer. Soc. Hort. Sci.* 46:60–68.

Caruso, T., P. Inglese, F. Sottile, and F.P. Marra. 1999. Effect of planting system on productivity, dry-matter partitioning and carbohydrate content in above-ground components of 'Flordaprince' peach trees. *J. Amer. Soc. Hort. Sci.* 124:39–45.

Castle, W.S. 1978. Citrus root systems: Their structure, function, growth, and relationship to tree performance. *Proc. Intl. Soc. Citricult.* 1:62–69.

Castle, W.S. 1980. Fibrous root distribution of 'Pineapple' orange trees on rough lemon rootstock at three tree spacings. *J. Amer. Soc. Hort. Sci.* 105:478–480.

Feigenbaum, S., H. Bielora, Y. Erner, and S. Dasberg. 1987. The fate of ¹⁵N labeled nitrogen applied to mature citrus trees. *Plant Soil* 97:179–187.

Flenet, F., J.R. Kiniry, J.E. Board, M.E. Westgate, and D.C. Reicosky. 1996. Row spacing effects on light extinction coefficients of corn, sorghum, soybean and sunflower. *Agron. J.* 88:185–190.

Florida Department of Agriculture and Consumer Services. 2004. Florida citrus budwood protection program—Annual report. Bur. of Citrus Budwood Registration, Div. Plant Ind., Fla. Dept. Agr. Consumer Serv., Tallahassee.

Gabrielle, B. and L. Kengni. 1996. Analysis and field-evaluation of the CERES models' soil components: Nitrogen transfer and transformation. *Soil Sci. Soc. Amer. J.* 60:142–149.

Heinemann, A.B., G. Hoogenboom, G.A. Georgiev, R.T. de Faria, and J.A. Frizzone. 2000. Center pivot irrigation management optimization of dry beans in humid areas. *Trans. Amer. Soc. Agr. Eng.* 43:1507–1516.

Hoogenboom, G., J.W. White, J.W. Jones, and K.J. Boote. 1994. BEANGRO: A process oriented dry bean model with a versatile user interface. *Agron. J.* 86:182–190.

Jones, C.A. and J.R. Kiniry. 1987. CERES-MAIZE: A simulation model of maize growth and development. Texas A&M Univ. Press, College Station.

Jones, J.W. and J.C. Luyten. 1998. Simulation of biological processes, p. 19–62. In: R.M. Peart and R.B. Curry (eds.). *Agricultural systems modeling and simulation*. Marcel Dekker, New York.

Kato, T., Y. Makoto, and S. Tsukahara. 1984. Storage forms and reservoirs of nitrogen used for new shoot development in Satsuma mandarin trees. *J. Jpn. Soc. Hort. Sci.* 52:393–398.

Koo, R.C.J. 1979. The influence of N, K, and irrigation on tree size and fruit production of 'Valencia' orange. *Proc. Fla. State Hort. Soc.* 95:10–13.

Kramer, P.J. and J.S. Boyer. 1995. *Water relations of plants and soils*. Academic Press, New York.

Mataa, M. and S. Tominaga. 1998. Effects of root restriction on tree development in Ponkan mandarin. *J. Amer. Soc. Hort. Sci.* 123:651–655.

Mattos, D., D.A. Graetz, and A.K. Alva. 2003. Biomass distribution and nitrogen-15 partitioning in citrus trees on a sandy Entisol. *Soil Sci. Soc. Amer. J.* 67:555–563.

Parsons, L.R., T.A. Wheaton, and S.W. Castle. 2001. High application rates of reclaimed water benefit citrus tree growth and fruit production. *HortScience* 36:1273–1277.

Quemada, M. and M.L. Cabrera. 1995. CERES-N model predictions of nitrogen mineralized from cover crop residues. *Soil Sci. Soc. Amer. J.* 59:1059–1065.

Reitz, H.J. 1956. Timing fertilization of citrus in the Indian River area. *Proc. Fla. State Hort. Soc.* 69:58–64.

Reuther, W., P.F. Smith, G.K. Scudder, and G. Hrcnciar. 1957. Responses of 'Valencia' orange trees to timing, rates, and ratios of nitrogen fertilization. *J. Amer. Soc. Hort. Sci.* 70:223–236.

Scholberg, J.M.S., K.J. Boote, J.W. Jones, and B.L. McNeal. 1997. Adaptation of the CROPGRO model to simulate the growth of field-grown tomato, p. 133–151. In: M.J. Kropff, P.S. Teng, P.K. Aggarwal, J. Bouma, B.A.M. Bouman, J.W. Jones, and H.H. van Laar (eds.). *System approaches for agricultural development: Application of systems approaches at the field level*. Kluwer, Dordrecht, The Netherlands.

Sexton, P.J., W.D. Bachelor, K.J. Boote, and R. Shibles. 1998. Evaluation of CROPGRO for prediction of soybean nitrogen balance in a Midwestern environment. *Trans. Amer. Soc. Agr. Eng.* 41:1543–1548.

Shen, J., W.D. Batchelor, J.W. Jones, J.T. Ritchie, R.S. Kanwar, and C.W. Mize. 1998. Incorporation of a subsurface tile drainage component into a soybean growth model. *Trans. Amer. Soc. Agr. Eng.* 41:1305–1313.

Sites, J.W., I.W. Wander, and E.J. Deszyck. 1953. The effect of fertilizer timing and rate of application on fruit quality and production of 'Hamlin' oranges. *Proc. Fla. State Hort. Soc.* 66:54–62.

Syvetsen, J.P. and J.J. Lloyd. 1994. Citrus, p. 342–387. In: B. Schaffer and P.C. Andersen (eds.). *Handbook of environmental physiology of fruit crops*, Vol. II. Sub-tropical and tropical crop. CRC Press, Boca Raton, Fla.

Timmer, L.W. and S.E. Zitko. 1996. Evaluation of a model for prediction of post bloom fruit drop of citrus. *Plant Dis.* 80:380–383.

Valiente, J.L. and L.G. Albrigo. 2000. Modeling flowering date of sweet orange [*Citrus sinensis* (L.) Osbeck] trees in central Florida based on historical weather records. *Proc. Intl. Citrus Congr.* 1:296–299.

Wagner-Riddle, C., T.J. Gillespie, L.A. Hunt, and C.J. Swanton. 1997. Modeling a rye cover crop and subsequent soybean yield. *Agron. J.* 89:208–218.

Whitney, J.D., A. Elezaby, W.S. Castle, T.A. Wheaton, and R.C. Littell. 1991. Citrus tree spacing effects on soil water use, root density and fruit yield. *Trans. Amer. Soc. Agr. Eng.* 34:129–134.

Xin, J., F.S. Zazueta, A.G. Smajstrla, T.A. Wheaton, J.W. Jones, P.H. Jones, and D.D. Dankel. 1997. CIMS—An integrated real-time computer system for citrus microirrigation management. *Appl. Eng. Agr.* 13:785–790.