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The Carbohydrate Balance of Alternate-bearing Citrus Trees and the Significance of Reserves for Flowering and Fruiting[1]

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Abstract. **Two alternate bearing 'Wilking' mandarin (*Citrus reticulata* Blanco) trees, an "on" and an "off" tree were uprooted and dissected into 11 organ types. Starch and soluble sugar concentrations were determined for each organ. Starch concentrations were 3.6 (leaves) to 17.4 (medium roots) times higher in the "off" tree. Soluble sugar concentrations were 1.5 (leaves) to 1.9 (medium roots) times higher in the "off" tree. A total dry matter, starch and soluble sugar balance was compiled for each tree. The "off" tree contained 13.26 kg starch and 10.66 kg soluble sugars; as against 2.95 kg starch and 6.75 kg soluble sugars in the "on" tree (excluding the fruit). The majority of this reserve pool would presumably be recycled and used for next year's crop. Removal of fruit by mid-summer permitted reasonable flower bud differentiation the following year, connected with a build up of the starch reserve levels.**

A considerable portion of the dry matter produced through photosynthesis is deposited in cell walls as cellulose, hemicellulose and lignin and therefore not available for further utilization by the plant. Starch and soluble carbohydrates, on the other hand, constitute a reserve pool which may be put back into use for vegetative and reproductive growth. The presence of carbohydrate reserves in leaves, stems, trunk and root of citrus trees (1, 8–11, 14, 16–18, 20, 21) as well as in other woody plants is well documented (12).

In the present study we were concerned with the size of the reserve pool accumulated during the "off" year and with its potential contribution to the formation of the next crop. It is not enough, in such a case, to determine the *concentrations* of starch and soluble sugars in tree organs. It is necessary to estimate the *total amounts* of the reserve materials in the tree. An overall balance sheet of carbohydrates and dry matter must therefore be compiled. This was done in the present study for 2 'Wilking' mandarin trees, an "on" and an "off" tree. 'Wilking' mandarin trees are prone to an absolute alternate bearing habit which involves lack of flowering in "off" years (2, 14).

Materials and Methods

Two trees of about the same size were selected from a plot of 15-year-old 'Wilking' mandarin trees grafted on sour orange, growing on heavy loam at the Acre experimental farm, which contained "on" and "off" trees at the same time. The "on" trees were thinned by hand. Trees were sprayed with KNO_3 on April to avoid collapse due to mineral deficiencies (18).

The dissection experiment was conducted on February 1978. The selected "on" and "off" trees were dissected to 11 organ types, as recorded in Table 1. Trees were carefully lifted by a tractor equipped with a trencher which was introduced beneath the main root system (60 cm depth). The roots were rinsed with water to remove the soil and left in the open for 30 minutes before fresh weight determinations. Estimates of root recovery were 87% for major roots, 75% for medium roots ($d > 0.5$ cm), and 50% for minor roots ($d < 0.5$ cm); root weights were corrected according to these estimates. Five replicate samples were taken for each of 11 organ types, from each tree. Samples were oven-dried at 65°C, ground to fine powder and analyzed for starch content according to Thievend et al. (19) as described recently by Ben Gad et al. (1, 6). Soluble sugars were determined in 80% ethanol extracts by the anthrone method. Results are expressed as mg glucose.g^{-1} dry weight.

Eight "on" trees and 4 "off" trees from the same plot were used in a separate experiment to examine the effects of complete removal of fruit on fruiting and carbohydrate levels (2, 8, 14). The "on" trees were hand thinned as usual. Four trees were completely defruited on July 22, 1978, while the other 4 served as controls. Leaves and thin twigs were sampled from all 12 trees on February 12, 1979. The spring flush was surveyed on March 11, 1979. Numbers and types of buds were recorded on 12 shoots/tree.

Results and Discussion

The "off" and "on" status was reflected strongly in the starch concentrations in tree organs (Table 1). The soluble sugars content was affected similarly, but to a lesser extent, in accordance with previous reports (8, 9). During the "off" year starch levels were highest in roots, higher than in leaves and branches. Soluble sugar levels were very high in the fruit, and quite high also in leaves and twigs. The presence of starch in the fruit is somewhat surprising. The results may, however, reflect some degradation of other polysaccharides by the amyloglucosidase enzyme preparation.

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Table 1. Starch and soluble sugar concentrations in organs of “off” and “on” trees of ‘Wilking’ mandarin.

	Starch ($mg \cdot g^{-1}$ dry matter)			Soluble sugar ($mg \cdot g^{-1}$ dry matter)		
Organ	“Off”	“On”	“Off/on”	“Off”	“On”	“Off/on”
Fruit	—	38.2	—	—	407.0	—
Leaves	122.6	33.8	3.6	178.2	121.6	1.5
Twigs; diam <1 cm	97.0	25.7	3.8	102.6	83.6	1.2
Branches; diam = 1-3 cm	73.9	20.4	3.6	70.4	47.0	1.5
Branches; diam = 3-5 cm	78.2	17.0	4.6	55.8	40.2	1.4
Branches; diam >5cm	76.6	19.0	4.0	70.6	47.8	1.5
Trunk above graft union	80.2	38.4	2.1	50.4	43.2	1.2
Trunk beneath graft union and main root	96.1	46.7	2.0	47.2	58.4	0.8
Major roots	124.6	17.5	7.1	56.0	47.8	1.2
Roots; diam >0.5 cm	163.2	9.4	17.4	77.2	40.0	1.9
Minor roots; diam <0.5 cm	179.8	19.2	9.4	67.8	52.0	1.3

[z] Averages of 5 replicate plant material samples obtained from a single tree.

The off/on ratio gives some idea about the availability of reserves in various tree organs for reutilization. The ratio is very high for starch in the root system (7 to 17), it is lower in leaves and branches (3 to 5) and in the trunk it does not exceed 2. The levels of starch in the trunk remain relatively high during the “on” year, suggesting that starch deposited in the trunk is not easily mobilized and recycled. The off/on ratio is much lower for soluble sugars than for starch. Starch seems therefore to behave as a true reserve material, which may accumulate in high concentrations and may then be almost completely depleted.

The overall balance of dry matter, starch and soluble sugar for the “off” and “on” trees is presented in Table 2. Comparison of the dry matter data shows that the 2 trees were similar in size, except for the root system which appeared to be more developed in the “off” tree.

The fruit produced by the “on” tree contained 25.8 kg dry matter. The sum of starch and soluble sugar accumulated in the “off” tree reached 23.9 kg. From the off/on ratios given in Table 1 it may be estimated that about 75% of the starch and 33% of the soluble sugar, together about 13.5 kg, are available for reutilization. Even when allowing for certain losses due to investment of energy in mobilization and biochemical transformations, the amounts of reserve materials seem to be very significant and may satisfy a considerable portion of the dry matter requirements of the forthcoming crop.

What are the steps in the sequence of events leading to productivity for which carbohydrate levels may be limiting? The ‘Wilking’ mandarin is an absolute biennial bearer, meaning that no flowers are formed during the “off” year. Can the depletion of carbohydrate reserves during the “on” year be responsible for the lack of flowering in the subsequent season? A hint in that direction was obtained in a fruit removal experiment (Table 3). Removal of all fruits from “on” trees in July allowed starch to reaccumulate before flower bud differentiation. The medium levels of starch in leaves appear to be well correlated with the medium flowering response, as revealed in the percentage of shoot types (4, 5). The number of buds/shoot also reached an intermediate position, between the “off” and “on” treatments.

The hypothesis that low carbohydrate levels are responsible for the lack of flowering in ‘Wilking’ mandarin during “off” years was rejected by Lewis et al. (14) on the grounds that thinning changed the production cycle without significantly affecting carbohydrate levels. Similarly, Jones et al. (8) working with ‘Valencia’ orange found that the effectiveness of thinning treatments was not clearly correlated with carbohydrate levels. In our experiment, however, the rate of flower bud differentiation resulting from removal of fruit appeared to be well correlated with the partial recovery of starch levels (Table 3). Smith’s data (18) also pointed to carbohydrates as a major factor in alternate bearing ‘Murcott’ tangerine trees. It may be relevant to point out that Lewis et al. (14) and Jones et al. (8) relied solely on carbohydrate determinations in leaves, while it is clear from Smith (18) and from our data (Tables 1, 2) that leaves are not always the most sensitive indicator organs. Anyway, the correlations between fruiting and starch levels were always higher than correlations with soluble sugars or total carbohydrate levels (8, 9). The differences in root starch levels were particularly striking (9, 18). Our data confirm these observations.

The levels of starch determined in the present study in “off” trees organs are considerably higher than those reported previously for ‘Wilking’ mandarin (14) and among the highest in the citrus literature for both leaves and roots (1, 8–11, 16–18, 20, 21). The high concentrations of starch in roots suggest them to be

Table 2. Total amounts of dry matter, starch, and soluble sugar in organs of “Off” and “On” ‘Wilking’ mandarin trees. Data based on percentage dry matter determined for each organ in 5 replicates and on the data of Table 1.

	“Off” tree			“On” tree		
Organ	Dry matter (kg)	Starch (g)	Soluble sugar (g)	Dry matter (kg)	Starch (g)	Soluble sugar (g)
Fruit[z]	—	—	—	25.80	986.0	10499.0
Leaves	10.58	1298.0	1885.5	7.72	261.0	938.4
Twigs; diam <1 cm	6.49	629.0	665.8	6.78	174.0	567.0
Branches; diam = 1–3 cm	21.21	1568.0	1493.3	20.98	428.0	986.2
Branches; diam = 3–5 cm	24.44	1912.0	1363.8	24.60	419.0	989.0
Branches; diam >5 cm	23.22	1778.0	1639.3	29.14	553.0	1393.0
Trunk above graft union	14.37	1152.0	724.3	14.08	541.0	608.1
Trunk beneath graft union and main root	7.20	691.0	399.7	6.82	319.0	398.5
Major roots[y]	15.04	1874.0	842.3	7.40	130.0	353.5
Roots; diam >0.5 cm[y]	20.43	3334.0	1577.2	12.24	115.0	489.4
Minor roots; diam <0.5 cm[y]	1.06	191.0	72.1	0.60	11.5	31.1
Total per tree (kg)	144.04	13.26	10.66	156.16	3.94	17.25

[z] Fruit fresh weight was 148 kg.

[y] Corrected according to root recovery estimates; see Materials & Methods.

Table 3. Effect of fruit removal by midsummer on midwinter leaf starch content and spring flush of alternate bearing 'Wilking' mandarin trees^{z}.

Treatment	Starch (mg • g^{-1} dry wt)	Buds/shoot (No.)	Shoot types (%)		
			Vegetative	Mixed	Flower
"On" year	90.4 ± 4.0	15.2	99.9	0.1	0.0
"Off" year	160.5 ± 23.2	39.6	3.1	39.0	57.9
"On" year, defruited	119.6 ± 1.5	29.6	25.7	50.2	24.1

^{z}Avg. from 4 trees/treatment.

a strong, actively accumulating "sink" in the absence of fruit. It may be calculated from our data that up to 40% of starch in the tree was deposited in the roots of the "off" tree, as against less than 10% in the "on" tree. A strong diversion of carbohydrates towards the root system in "off" trees has been reported previously by Shimizu et al. (17).

Whereas our present data emphasize the significance of carbohydrate levels they do not rule out the involvement of mineral nutrition (Golomb and Goldschmidt, unpublished data) and hormonal balance (4, 7) in the alternate bearing syndrome of 'Wilking' mandarin. On the other hand, the role of carbohydrate reserves is probably not confined to the process of flower bud differentiation, which in itself does not appear to require much energy. Fruit set and development certainly require high amounts of energy and may be limited by the availability of carbohydrate supplies.

The present study gives some insight into the problems of carbohydrate balance in biennially-bearing trees, problems which have not been studied in detail until now. The biochemistry and physiology of starch turnover in tree organs is one aspect which warrants further study. The fact that the tree draws so heavily upon its reserves suggests that it has difficulties in providing the photosynthate required for fruit development during the "on" year. Does the tree reach optimum photosynthetic efficiency throughout its biennial cycle? 'Wilking' trees overloaded with fruit have only 2/3 of the normal chlorophyll content in the leaves (unpublished data), indicating that some obstruction of their photosynthetic system may have occurred. On the other hand, does the tree photosynthetize efficiently during the "off" year in the absence of the major photosynthetic sink — the fruit? Recent studies in apple (15) and model plants of citrus (13) suggest the existence of feedback mechanisms which restrict photosynthetic activity in defruited trees, as already demonstrated in annual crops (3). Studies along these lines are currently being conducted by our group with alternate bearing 'Wilking' mandarin trees.

Literature Cited

1. Ben-Gad, D. Y., A. Altman, and S. P. Monselise. 1979. Interrelationships of vegetative growth and assimilate distribution of *Citrus limettoides* seedlings in response to root-applied GA$_3$ and SADH. Can. J. Bot. 57:484–490.
2. Galliani, S., S. P. Monselise, and R. Goren. 1975. Improving fruit size and breaking alternate bearing in 'Wilking' mandarins by ethephon and others agents. HortScience 10:68–69.
3. Geiger, D. R. 1976. Effects of translocation and assimilate demand on photosynthesis. Can J. Bot. 54:2337–2345.
4. Goldschmidt, E. E. and S. P. Monselise. 1972. Hormonal control of flowering in citrus trees and other woody perennials. p. 758–766. In: D. J. Carr (ed.) Plant Growth Substances 1970. Springler Verlag, Berlin.
5. Goldschmidt, E. E. and S. P. Monselise. 1977. Physiological assumptions toward the development of a citrus fruiting model. Proc. Intern. Soc. Citriculture 2:668–672.
6. Hassid, W. Z. and E. F. Neufeld. 1964. Quantitative determination of starch in plant tissue. p. 33–36. In: R. L. Wistler (ed.) Methods in carbohydrate chemistry. Vol. 4.
7. Jones, W. W., C. W. Coggins, Jr., and T. W. Embleton. 1976. Endogenous abscisic acid in relation to bud growth in alternate bearing 'Valencia' orange. Plant Physiol. 58:681–682.
8. Jones, W. W., T. W. Embleton, E. L. Barnhart, and C. B. Cree. 1974. Effect of time and amount of fruit thinning on leaf carbohydrates and fruit set in 'Valencia' oranges. Hilgardia 42:441–449.
9. Jones, W. W., T. W. Embleton, and C. W. Coggins, Jr. 1975. Starch content of roots of 'Kinnow' mandarin trees bearing fruit in alternate years. HortScience 10:514.
10. Jones, W. W., T. W. Embleton, M. L. Steinacker, and C. B. Cree. 1970. Carbohydrates and fruiting of 'Valencia' orange trees. J. Amer. Soc. Hort. Sci. 95:380–381.
11. Jones, W. W. and M. L. Steinacker. 1951. Seasonal changes in concentrations of sugar and starch in leaves and twigs of citrus trees. Proc. Amer. Soc. Hort. Sci. 58:1–4.
12. Kozlowski, T. T. and T. Keller. 1966. Food relations of woody plants. Bot. Rev. 32:293–382.
13. Lenz, F. 1979. Fruit effects on photosynthesis, light- and dark-respiration. p. 271–281. In: R. Marcelle, H. Clijsters, and M. van Poucke (eds.) Photosynthesis and plant development. Dr. W. Junk, Publ. The Hague.
14. Lewis, L. N., C. W. Coggins, Jr., and H. Z. Hield. 1964. The effects of biennial bearing and NAA on the carbohydrate and nitrogen composition of 'Wilking' mandarin leaves. Proc. Amer. Soc. Hort. Sci. 84:147–151.
15. Monselise, S. P. and F. Lenz. 1980. Effect of fruit load on photosynthetic rates of budded apple trees. Gartenbauwiss. 45:220–224.
16. Sharples, G. C. and L. Burkhart. 1954. Seasonal changes in carbohydrates in the Marsh grapefruit tree in Arizona. Proc. Amer. Soc. Hort. Sci. 63:74–80.
17. Shimizu, T., H. Torikata, and S. Torii. 1978. Studies on the effect of crop load on the composition of Satsuma mandarin trees. V. Analysis of production processes of bearing and non-bearing trees based on the carbohydrate economy. J. Japan. Soc. Hort. Sci. 46:465–478.
18. Smith, P. F. 1976. Collapse of 'Murcott' tangerine trees. J. Amer. Soc. Hort. Sci. 101:23–25.
19. Thievend, P., C. Mercier, and A. Guilbort. 1972. Determination of starch with glucoamylase. p. 100–105. In: R. L. Wistler & J. N. BeMiller, (eds.) Methods of carbohydrate chemistry. Vol. 6.
20. Wallerstein, I., R. Goren, and S. P. Monselise. 1974. The effect of girdling on starch accumulation in sour orange seedlings. Can. J. Bot. 52:935–937.
21. Yelenosky, G. and C. L. Guy. 1977. Carbohydrate accumulation in leaves and stems of 'Valencia' orange at progressively colder temperatures. Bot. Gaz. 138:13–17.