CARBOHYDRATE SUPPLY AND DEMAND DURING FRUIT DEVELOPMENT IN RELATION TO PRODUCTIVITY OF GRAPEFRUIT AND 'MURCOTT' MANDARIN

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Abstract

A comparison was conducted between grapefruit (Citrus paradisi Macf. cv. Marsh seedless), [large fruit, high, regular yields] and mandarin (Citrus reticulata cv. Murcott) [small fruit, alternate bearing].

To determine fruit demand, maximal fruit absolute growth rate (AGR) and fruit relative growth rate (RGR), trees were trunk girdled and extremely thinned (grapefruit); alternatively, 'Off' and regular (control) trees were used (Murcott). Fruit growth was followed weekly and transformed into carbohydrate consumption by CHNOS analysis (McDermitt and Loomis, 1981), and respiration measurements.

In grapefruit, fruit thinning resulted in higher AGR and RGR throughout most of fruit development, suggesting long periods of source limitation. Calculation of the daily available carbohydrate also indicated that in grapefruit, fruit demand for carbohydrate exceeded the supply.

In 'Murcott', 'Off' fruit revealed relatively low AGR values, though higher than 'On' fruit throughout the season. During stage I of fruit development RGR values were unstable and not unequivocally indicative for sink- or source limitations. However, fruit absolute demand was significantly lower than the calculated supply during stage I and the beginning of stage II. Source limitation occurred only when fruit size reached about 20 g (FW), 120 days after anthesis.

It is suggested that fruitlet size is a major factor in the source-sink interplay of developing fruits. Murcott fruit development is sink limited for the first three months due to its remarkably small initial size (about 6 mgFW). When source limitation takes over, the self-thinning mechanisms are not fully active any more. Fruit number per tree remains higher than desired, resulting in small fruit size at harvest and overcropping symptoms. In grapefruit, on the other hand, initial fruitlet size is large (72 mgFW) and fruit number per tree is adjusted by the self-thinning mechanism to the available supply during stage I, thus preventing crop overload and resource depletion.

1. Introduction

Alternate bearing and relatively low yields are common among 'easy peeling' cultivars of Citrus. Some of the productivity problems of that group may be represented by the 'Murcott' mandarin, which has become an important cultivar in Israel. In spite of recent improvements, 'Murcott' trees still tend to alternate bearing, fruits are small (70150 g/fruit) and the average 'On' year yield is ca. 30-40 tons/hectare. Chemical thinning (down to 400-500 fruit/tree) is an obligatory practice to keep fruit size distribution within the commercial range.

Grapefruit trees, on the other hand, are known to bear regular, heavy yields (60-80

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tons/hectare) of relatively large (250-400 g/fruit) fruit. The final number of fruit per grapefruit tree (400-500) is determined by the tree itself.

Photosynthetic source-sink imbalance is suspected to be the reason behind those differences in productivity (Goldschmidt and Koch, in press).

Periods of source- or sink-limited growth may be identified by two methods. The first, as suggested by Pavel and DeJong (1993), compares the relative growth rates (RGR) of fruit developing under extremely low crop conditions (non-limiting source) and control fruits. Source limitation is indicated when higher RGR are observed for low crop level (LCL) fruit in comparison with control fruit. If, in spite of the non-limiting source condition, the RGR of LCL fruit fails to increase above that of control fruit, then growth is assumed to be sink limited.

An alternative way to identify source-sink imbalance is by estimation of the daily photosynthetic demand and supply within a tree. The absolute growth rate (AGR) of sink organs generally reflects the balance between the available photoassimilate and the demand for it at a time. AGR is the result of, and not the cause for the partitioning procedure. Sink organ demand is determined by its potential growth rate under non-limiting source condition and is considered as the driving force of carbon flux and partitioning (Patrick et al 1988). The calculated total daily demand of LCL developing fruits, including respiratory losses, can be matched with an estimate of the daily amount of photosynthates available in a tree.

Goldschmidt and Monselise (1977) established the basic physiological assumptions for modelling Citrus productivity. A dynamic mathematical model has been developed to describe and study quantitatively the problems of Citrus productivity (Harpaz et al. 1992). Improvement of this model requires better insight into the physiological mechanisms involved with fruit development. Goldschmidt and Koch (in press) have recently reviewed different aspects of source-sink relations in Citrus trees. The objective of the present study has been to identify periods of source-sink imbalance during fruit development and to relate them to the cropping behaviour of grapefruit and 'Murcott'.

2. Materials and Methods

Grapefruit trees were trunk girdled and thinned from ca. 400 to ca. 40 fruit per tree at the end of June drop (1 July). Individual fruit were followed weekly for AGR and RGR determination. In another experiment, uniform grapefruit branches, 1 m long, were thinned at bloom to 20 flowers. Fruitlet growth and abscission were followed and compared to control. In 'Murcott', 'Off' trees fruit were compared to control (fruit of regularly cropping trees) throughout the season. Volumetric fruit growth was transformed to dry matter units using calibration data.

The cost of fruit growth was calculated using the method of McDermit and Loomis (1981). Dry matter was analysed for CHNOS content and results were transformed to Glucose Equivalents. Fruit respiratory losses were measured, calculating Rg and Rm (Amthor 1990) (data not shown), to determine the single fruit daily demand for carbohydrate (gGlucose fr⁻¹ day⁻¹):

\[ Fr.Demand = PotFrGr \times Conv1 + Rm \times Conv2 \]

Where: PotFrGR is the daily growth rate of a fruit, growing under condition of unlimited carbon source (gDW day⁻¹), Conv1 is the conversion coefficient for Glucose to fruit dry matter (gGLU gDW⁻¹), including direct respiratory losses (after McDermit and Loomis, 1981), Rm is maintenance respiratory losses of the whole fruit at 25°C (gCO₂ day⁻¹) and Conv2 is the conversion coefficient of respiratory CO₂ to Glucose. Conv1 was relatively high at the early stage of fruit growth, 1.6, but declined quickly to the level of 1.3 and 1.2 for grapefruit and 'Murcott', respectively, and remained without further change until harvest.
Daily supply of photoassimilate within a tree was estimated using integration of numerous CER measurements (Licor 6250) under different conditions and included data of diurnal cycle of four sides of the tree. Light penetration into the canopy and the hysteresis behaviour have been considered as well. The estimates for whole tree photosynthesis were compared with the data and model estimates recently published by Severtsen and Lloyd (1994).

3. Results and discussion

Extreme fruit thinning and trunk girdle resulted in immediate enhancement of fruit growth in grapefruit (Fig. 1A). The average final fresh weight of an LCL fruit was about 700g, more than twice the control. Results were similar for 'Murcott' 'Off' fruit (Fig. 1B), however maximal fruit fresh weight was much smaller than for grapefruit, for a longer growth period. Evidently, the potential fruit size is much larger for grapefruit than for 'Murcott'.

The reason for this difference may be either different RGR, or initial fruit size (ovary size), or both. RGR analysis did not reveal any advantage for grapefruit. On the contrary, 'Murcott' RGR often appeared to be higher than that of grapefruit (Fig. 1-C,D). This may indicate that initial fruit size is the most important factor determining fruit potential AGR. Indeed, ovary fresh weight was about 72mg (25mgDW) for grapefruit, and only 6mg (2mgDW) for 'Murcott'.

The RGR of LCL grapefruit was higher than that of control fruit during early, as well as during later fruit developmental stages (Fig. 1-C), indicating the prevalence of source limitation during most of the season. The RGR of 'Murcott' fluctuated and seemed much more sensitive to transient environmental stresses, such as temperature and water deficiency. No significant difference between LCL and control fruit' RGR could be observed during more than a month after bloom. Later in the season source limitation were more clearly revealed by the higher RGR for 'Off' fruits (Fig. 1-D).

As might be expected, LCL grapefruit AGR was much higher than that of 'Murcott' (Fig. 2), suggesting a higher daily carbohydrate demand on a single fruit basis. Focusing on the first 80 days after bloom it could be observed, that grapefruit AGR increased very fast as compared with 'Murcott' (Fig. 3). In fact, both 'Off' and control 'Murcott' fruit attained remarkably low values during more than 50 days after bloom.

Considering the similar RGR values for both cultivars, it may again be concluded that the tiny initial fruit size of 'Murcott' is responsible for the relatively low rate of demand revealed by that fruit (Fig. 4). About 90 days after bloom, the calculated daily demand for grapefruit was more than 1.5 gGlucose day⁻¹ fr⁻¹ (as against only 0.14 for 'Murcott'). The single fruit demand of 'Murcott' increased up to 0.5-0.6 towards the end of fruit development.

The differences in productivity of the two cultivars does not evolve from photosynthetic capacity, as indicated by the data shown in table 1: The maximal and average leaf carbon exchange rates (CER) for grapefruit and 'Murcott' are within the same range. A full description of the estimation of whole Citrus tree photoassimilation (Bustani, unpublished data) is beyond the scope of this paper. The estimates of 170-200 for a grapefruit tree, and 95-110 gGlucose tree⁻¹ day⁻¹ for 'Murcott' in an ordinary summer day in the coastal plane in Israel seem reasonable and are in good agreement with data presented recently by Syvertsen and Lloyd (1994). On a ground area basis, total daily photoassimilation of both cultivars is within the same range, since planting density for 'Murcott' is as twice as for grapefruit.

Assuming that the photoassimilate supply is stable throughout the summer, it may be divided by the single fruit demand, to result in estimates of the largest number of fruit per tree permitted by the supply each day during fruit development. As expected, the number of fruit permitted for a 'Murcott' tree was very high at the beginning, and remained high for a long period (Fig. 5). During the first 40 days, the actual number of fruit per tree was smaller than permitted, indicating again sink limitation. On the
contrary for grapefruit, the actual number of fruit per tree was larger than permitted, hence most of fruit abscission continually occurred during the first 3 months of fruit development may be related to source limitation.

The substantial fruitlet abscission observed in 'Murcott' during early stages of fruit developments can not be attributed to an overall shortage of carbohydrate within the tree. It may be the outcome of interactions between individual fruit, local source and limited translocation capacity (Bustan et al. 1995) within the small branch level which still need further study.

The single fruit demand is not the only determinant of fruit size and number. Ninety days after anthesis, when June drop had terminated, the number of fruits per grapefruit tree was about 450, compared to about 250 predicted by the model. The situation was principally the same for 'Murcott' at the same time, but the numbers were different; the actual number of fruit per tree was above 2000, whereas the predicted number was about 1500. The "exchange" between fruit size and number (Goldschmidt and Monselise 1977) appears to take place quite early, indicating the existence of competition between individual fruit, and the further complexity of the self-thinning mechanism. It may be asked what is the "persistence threshold" for a fruit - the minimum amount of photoassimilate required for its retention. More precise physiological definitions of this factor are essential, if better quantitative predictions of yield are to be achieved by mechanistic models of fruit trees productivity.

The grapefruit tree seems to have the ability of controlling its crop load, adjusting an appropriate number of fruits to the available carbon source. In 'Murcott', the overall demand for carbohydrate obtained by the fruit is too low for a very long period. Later on, it is too late for the tree to adjust the fruit number to the increasing demand, since self-thinning mechanisms seem not to be fully sensitive any more. The too large number of fruit per tree results in severe overloading symptoms. It is suggested, therefore, that efforts should be made to increase the initial fruit size, which appears to be the key parameter of the Murcott productivity problem.

Acknowledgement

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References


Pavel EW and DeJong TM. 1993. Source- and sink-limited growth periods of
Figure 1 - fruit growth and relative growth rate of grapefruit (A,C) low crop load (LCL) (■) vs. control (□) fruit, compared to fruit of 'Murcott' (B,D) 'Off' (●) vs. regular cropping trees (control)(○).
Figure 2 - absolute growth rate (AGR) of LCL (■) vs. control (□) grapefruit fruit (left), compared to 'Murcott' (right) 'O'ff (●) vs. control (○) fruit throughout the season.

Figure 3 - absolute growth rate (AGR) of LCL (▲) vs. control (△) grapefruit fruit (left), compared to 'Murcott' (right) 'O'ff (●) vs. control (○) fruit during stage I of fruit development, until 80 days after bloom.
Table 1 - Net carbon exchange rate measurements and estimates for whole tree daily photoassimilation in grapefruit and 'Murcott', Jul.-Sep. 1992.

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<th>grapefruit</th>
<th>'Murcott'</th>
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<tr>
<td>maximal net CER</td>
<td>12.7</td>
<td>13.2</td>
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<td>μmolCO₂ M⁻² s⁻¹</td>
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<td>average net CER (leaves in direct irradiation)</td>
<td>5.8±1.8</td>
<td>5.6±2.1</td>
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<td>μmolCO₂ M⁻² s⁻¹</td>
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<tr>
<td>average net CER (all canopy surface)</td>
<td>2.62</td>
<td>2.74</td>
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<td>daily CO₂ assimilation</td>
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<td>140-165</td>
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<td>gCO₂ tree⁻¹ day⁻¹</td>
<td></td>
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<tr>
<td>daily Glucose production</td>
<td>170-200</td>
<td>95-110</td>
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<td>gGLU tree⁻¹ day⁻¹</td>
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Figure 4 - the daily demand for carbohydrate (Glucose) as obtained by grapefruit and 'Murcott' single LCL and 'Off' fruit, respectively. Respiratory losses were included.

Figure 5 - the maximal number of fruit per tree permitted by the daily supply and single fruit demand within grapefruit and 'Murcott' trees.