



Canopy profiles of starch and leaf mass per area in greenhouse tomato and the relationship with leaf area and fruit growth

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ABSTRACT

Better knowledge of patterns of carbon allocation in plants growing in CO₂-supplemented atmospheres may help to guide more efficient management of CO₂ applications in tomato greenhouses. Leaf starch and LMA (leaf mass per unit area) were investigated in commercially grown greenhouse tomato plants to determine the distribution and influence of leaf area and fruit load on these measures.

Leaf starch concentration and LMA exhibited similar profiles for the upper but not the lower shoot canopy. Maximum leaf starch was 10–20 g m⁻² for uppermost leaves and then declined rapidly with canopy depth, becoming negligible for leaves mid-canopy and lower. The canopy profile for LMA usually exhibited a linear decline with canopy depth, falling from 60 to 20 g m⁻². Accordingly, the relationship between LMA and leaf starch was stronger for upper canopy leaves. Maximum starch on a per leaf basis occurred in the top third of the canopy where leaves were close to full expansion. This was also the region where fruit growth was lowest. We concluded that leaves in canopy positions 7–9 are likely the most informative of plant carbon status. These leaves are high enough in the canopy to accumulate starch and are adjacent to fruit of significant growth rate.

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1. Introduction

Dosing greenhouse crops with CO₂ would be managed more effectively if growers had direct information about the carbon status and requirements of their crops. Current approaches to greenhouse CO₂ management are not immediately plant-based. Rather, they rely on CO₂ dosing rates or concentrations external to plants, and do not convey information on the ability of plants to assimilate and utilize CO₂. Therefore, growers do not currently know when CO₂ availability is optimal. In addition to atmospheric monitoring it would be useful if growers could track the carbon status of their crop and supply CO₂ according to the plants' ability to exploit that resource for fruit production.

To be useful in the management of CO₂ dosing, plant indicators of carbon status should be responsive to CO₂ enrichment and representative of the crop's ability to utilize carbon to support fruit production. Photosynthetic performance is an obvious candidate as it is the primary carbon input and is highly sensitive to atmospheric CO₂ availability. However, the measurement of whole-plant pho-

tosynthesis is not easily achievable for a large canopy like tomato, although there has been some progress made on modeling photosynthesis in relation to CO₂ concentration (Edwards, 2008).

Potentially a more useful assessment would be to monitor major end products of photosynthesis, such as sucrose or starch. Levels of these products depend both on the activities of photosynthesis and on carbon utilization by sinks. Therefore, they reflect the general carbon economy of the plant. Of these two measures, starch would seem to be the better candidate as its pools are usually larger and more stable than those of sucrose (Körner et al., 1995; Bertin et al., 1999). Starch accumulates in chloroplasts of photosynthetically active leaf cells when more assimilates are produced than the leaf is able to utilize or export to carbon sinks. Tomato plants with low sink strength are known to accumulate starch (Ammerlaan et al., 1986; Bertin and Gary, 1998). Plants growing in commercial greenhouses have been regarded as sink limited (Nederhoff, 1994) because some fruit are regularly removed to ensure uniform fruit growth. If commercial greenhouses are chronically oversupplying CO₂, resulting in assimilate production beyond what is needed for fruit growth, it would be expected that large amounts of starch would accumulate in the shoot canopy.

Leaf starch content in CO₂-enriched greenhouse tomato plants can build up sufficiently to cause detectable increases in leaf mass, reaching values as high as 43% of leaf dry mass (Edwards, 2008). Accordingly, increased leaf mass per unit area (LMA, the inverse of

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specific leaf area, SLA) is a recognized growth response to elevated CO₂ (Körner et al., 1995; Heuvelink and Marcelis, 1996; Bertin et al., 1999; Roumet et al., 1999) and be a useful surrogate for starch. Currently, it would be more convenient for growers to measure LMA then starch because sophisticated laboratory procedures are not required. However, in addition to starch, LMA will also be affected by structural and soluble constituents in leaves and its dependence on variation in starch needs to be thoroughly defined.

Therefore, it is worthwhile examining whether leaf starch and/or LMA are plant-based indicators which could be useful in managing greenhouse CO₂ dosing. In order to do this, information is required on how both of these measures vary in tomato canopies under commercial growing conditions, and to determine the influences of season, leaf area and fruit load. Specific objectives of this research were:

- (1) to determine the relationship between LMA and leaf starch,
- (2) to describe the vertical profiles of LMA and leaf starch in the shoot canopy during the production season,
- (3) to describe the interplay between fruit load and leaf starch in the canopy,
- (4) to ascertain if these measures could play a role in a plant-based approach to manage greenhouse CO₂ enrichment.

2. Materials and methods

2.1. Environment and crop culture in commercial greenhouses

In the summer of 2002 data were collected from beefsteak tomato plants growing in two commercial greenhouses located in the Lower Mainland of British Columbia (BC), Canada. The data collection was consistent among sites and there was considerable uniformity in both plant environment and crop culture among the greenhouses.

The two greenhouses were of Venlo design and clad with glass. All, or a sizable portion, of their areas were devoted to beefsteak tomato production. The greenhouses were: South Alder Greenhouses Ltd. (SA) located in Surrey, BC (N49°01'47", W122°43'33"), 4 ha in area and Gipaanda Greenhouses Ltd. (GI), also located in Delta, BC (N49°03'45", W122°06'16"), 7.3 ha in area. Greenhouse temperature, CO₂ concentration, relative humidity and global radiation (external to the greenhouse) for the experimental period were obtained from computer records maintained by the greenhouse managers (Table 1).

All plants in the study were the indeterminate, beefsteak tomato (*Lycopersicon esculentum* Mill.) cultivar Rapsodie (Syngenta Seeds Inc., Boise, ID). Both SA and GI greenhouses grafted Rapsodie onto the rootstock Maxifort (DeRuiter Seeds Inc., Tecumseh, ON) to increase plant vigour. The crops were maintained and fruit were harvested by the respective greenhouse staff according to conventional commercial practices for growing beefsteak tomatoes in the Lower Mainland of BC. Plants were raised in a high wire production system (Peet and Welles, 2005; Portree, 1996; van de Vooren et al., 1986), where normal commercial production starts in December with the planting of the new crop and ends in November the following year when crop removal is complete. The plants were obtained from a propagator and set into the greenhouses at a density of 2.5 plants per m². Plant density was increased twice during the year by training a side shoot from the main stem (also trained to the high wire). One shoot was allowed to develop soon after planting and a second (side) shoot was trained in February. By the end of March another side shoot was allowed to develop, increasing shoot density to a maximum of 3.75 shoots per m². This density was maintained until late August when a side shoot was removed. By mid-September the shoot density was further reduced to 2.5 heads

per m², and by early October the growing point was removed to promote development of the remaining fruit. Fruit harvesting typically commenced in mid-March and ceased by mid-October. In 2002 the production schedule was delayed for the crop in SA because plants were not set into the greenhouse until February. However, it should be noted that the high light levels in February 2002 increased the rate of crop development. Consequently, to some degree, the SA crop was able to catch up to the earlier plantings established in other greenhouses.

2.2. Collection of leaf length and fruit diameter data from plant canopies

Canopy profiles of leaf length and fruit load were measured *in situ* once per month (May–September) in 2002. On each day of data collection a row was randomly selected from the middle of the greenhouse. Within this row four plants (not contiguous) were selected for measurements and from each of these plants, six leaves at different levels in the canopy were marked for collection and analysis for starch and LMA. On each of these plants, the lengths of all leaves from a single shoot were measured, and their positions on the shoot were recorded.

Identification of leaf and truss positions in the tomato canopy can be complicated because of the indeterminate growth of the plant and the weekly removal of lower leaves and fruit. We followed the industry practice of identifying leaf position in the canopy as follows: descending from the shoot apex, leaf position 1 is the leaf closest to the youngest truss (identified as truss 1) with open flowers (Edwards, 2008). This leaf could be above or below the truss. Leaves in this position have reached approximately 40% of their full expansion, and leaves progressively younger than (i.e. above) leaf 1 were identified as 0, –1, –2, etc., and leaves progressively older (i.e. below leaf 1) were 2, 3, 4 and so on. Leaf length in cm was measured with a ruler from the base of the last pair of leaflets to the end of the terminal leaflet. The diameters (from calyx to the blossom end) of all the fruit on each truss were measured in mm with an electronic calliper. Trusses were labelled consecutively downward, starting with truss 1 being the truss containing mostly flowers at anthesis. Truss position in the canopy was also fixed relative to the closest leaf.

2.3. Calculation of leaf area, fruit volume and absolute growth rate

Leaf length and fruit diameter were converted to leaf area and fruit volume, respectively, by predetermined relationships. Leaf area was determined from an allometric function (Eq. (1)) that related blade length to leaf area for the cultivar Rapsodie (Edwards, 2008).

$$LA = e^{(-0.53+2.45 \times \ln(LL))} \quad (1)$$

where LA is leaf area in m² and LL is leaf length in meters. The fruit volume was calculated by assuming the fruit approximated a sphere (Eq. (2)):

$$FV = \frac{4}{3} \pi r^3 \quad (2)$$

where FV is fruit volume in cm³ and *r* is fruit radius in cm. Volume was calculated for each fruit on a truss and those values were added together to give a total volume of fruit for the truss. The absolute growth rate (AGR) in cm³ per day was calculated by determining the change in volume of fruit between consecutive trusses divided by seven. Generally trusses are produced at a rate of one per 7 days in commercial BC greenhouses. Negative AGR sometimes occurred for the three oldest trusses due to fruit harvesting. These values were coded as 0 for the analysis.

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