LEAF TO FRUIT RATIO: PHOTOSYNTHETIC CAPACITY AND CARBOHYDRATE ACCUMULATION IN GRAPEVINES (CV. CHASSELAS)

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Abstract

A study of photosynthetic activity and carbohydrate content in the leaves, shoots, trunks and roots of *Vitis vinifera* L. (cv. Chasselas) was made with regard to the leaf-fruit ratio in grapevines on the experimental estate Agroscope Changins-Wädenswil ACW in Pully (Switzerland) between 1998 and 2002. Studies of variations in the leaf-fruit ratio or in the source-sink organ relationship on photosynthetic activity and the accumulation of carbohydrates in leaves, shoots, trunks and roots were carried out on a single Guyot trained system in the field. The reduction of grapevine leaf surface areas (LAI) by the removal of apexes (topping) and the complete removal of fruit clusters at the pea-size stage had little influence on leaf gas exchanges. Photosynthesis measurements taken 20 days after the first toppings showed that there was a slight increase in photosynthetic rates during the day with reduced LAI, irrespective of the yield. The influence of LAI on CO_2 assimilation diminished over the growing season, mainly in plants deprived of grape bunches. A high leaf to fruit ratio resulted in a small decrease in photosynthesis and stomatal conductance but favoured the accumulation of soluble sugars in leaves during the day. The exportation of leaf carbohydrates benefited from the presence of a sink organ, such as grape clusters, and a low leaf-fruit ratio. During the photoperiod, the accumulation and the export of foliage carbohydrates (both soluble and insoluble) increased with photosynthetic activity. The concentration of total leaf carbohydrates measured in the present experiments did not exert any retroactive inhibiting effect on photosynthetic activity. Seasonal dynamics of reserve carbohydrates (TNC = total non-structural carbohydrates) in roots, trunks and shoots were monitored. Starch mobilisation in roots occurred mainly between budburst and flowering. On the other hand, a constant carbohydrate accumulation in roots from flowering to leaf fall was observed. Leaf surface area of the grapevine had little influence on the carbohydrate concentration in shoots and fruit canes. Conversely, the starch content in trunks and root systems was higher at the beginning and at the end of the season. A relationship was established between the leaf to fruit ratio (exposed leaf area per kilogram of yield) and the carbohydrate content in roots at harvesting. The higher the fruit to leaf ratio, the more important is the starch content stored in the roots.

Key words: *Vitis vinifera*, leaf-fruit ratio, photosynthesis, leaves and roots carbohydrate content

Introduction

The photosynthetic activity of canopy plants is conditioned by physiological and climatic factors. Among physiological factors, the volume and proximity of sink organs (fruits), together with the extent of source organs (LAI), can be considered to influence leaf gas exchanges.

The regulation of photosynthesis, exerted by the demand of synthesised products from centres of consumption (sink organs), has been studied for many years in different plant species. In general, the removal of sink organs, such as fruits, leads to a decrease in leaf assimilation (FOYER *et al.*, 1995). Nevertheless, the effects of eliminating fruits on the photosynthetic capacity of perennial plants have proven to be relatively weak (ROM & FERREE, 1986) and largely dependant upon the timing of the removal during the growth period (DEJONG, 1986) and on the leaf-fruit ratio (source-sink) of the plant (EDSON *et al.*, 1993). In vine plants, close proximity of a sink organ exerts a significant influence on assimilation in the leaf positioned opposite the cluster, which manifests the highest rate of photosynthesis of all the canopy leaves over the greater part of the season (SCHULTZ, 1989). Eliminating part of the source organs (defoliation) generally gives rise to increased gaseous leaf exchanges in the remaining leaves (IACONO *et al.*, 1995). Reducing the LAI may also result in a modification of the partitioning of assimilated carbon, as several other studies on grapevines have shown (CANDOLFI-VASCONCELOS, 1990; HUNTER *et al.*, 1995; QUEREIX, 2001).

If photosynthetic activity remains high, even in the case of restricted sink organ activity and limited translocation of photosynthetic products, in most cases, an accumulation of starch and/or carbohydrate sucrose in source leaves results (PLAUT *et al.*, 1987). The increase in leaf sugar content may give rise to reduced photosynthetic activity (AZCON-BIETO, 1983) and stomatal conductance due to a deformation in the thylakoïdes (SCHAFFER *et al.*, 1986), a deficiency in inorganic phosphate (Pi) (PAUL et FOYER, 2001) caused by the inhibition of sucrose synthesis, or due to enzymes of the Calvin cycle (STITT *et al.*, 1990). Nevertheless, physiological processes in leaves would appear to be regulated in order to restore and maintain a balance between photosynthesis and exportation of assimilated carbon (QUEREIX, 2001).

The storage of non-structural carbohydrates in woods (KORKAS *et al*. 1996; WEYAND et SCHULTZ, 2006), trunks and roots of grapevines (BENETT *et al*. 2005) has rarely been investigated. The authors mentioned have, in particular, observed the influence of the training system and of defoliation on the TNC content of the perennial parts of vine plants during the growing season.

In the present study, tests were carried out in the field on *Vitis vinifera* (cv. Chasselas) in order to verify the hypothesis according to which gas exchanges, the capacity to accumulate and export leaf carbohydrates , as well as the stocking of carbohydrates in the perennial parts of the plant, are all influenced by the source-sink (leaf-fruit) relationship. An appreciation of the influence of the leaf-fruit ratio on photosynthesis and on leaf and root carbohydrate content was made by studies involving different levels of LAI and crop yield.

Materials and methods

The influence of leaf surface area (LAI)

Trials on varying leaf-fruit ratios were conducted in Switzerland from 1998 to 2002 at the Agroscope Changins-Wädenswil ACW Research Station, on a “Guyot” trained system (vertical plane) of vine plants (cv. Chasselas) spaced at distances of 200 cm x 85 cm. In a first series of experiments, the effects of reducing LAI area by topping were measured. The objective of topping was to maintain plant growth of the vines at two different levels of total leaf surface area per square metre of land (LAI = Leaf Area Index), that is at 2.5 m^2 and 4.5 m^2 LAI. In order to study the effect of yield load on leaf absorption capacity, a trial on limiting yield was conducted on both LAI variations after the flowering stage on the 01.07.98 (stage 27, EICHHORN and LORENZ, 1977). On the one hand, this trial involved the complete removal of clusters (0.0 kg/vine) and, on the other, keeping the total yield on each plant (3.0 ± 0.15 kg/vine).

Leaf gas exchanges and products of photosynthesis

Measurements of gase exchanges (assimilation chamber ADC-LCA3 in an open system) and the analysis of non-senescent primary carbohydrates during the day (soluble sugars and starch) were carried out on mature leaves, located in the median zone of the shoot (7-10 leaf insertion), under optimal environmental conditions (light saturation, no water, stress 25-30 °C). The analysis of soluble and insoluble carbohydrates of the leaves and different parts of the vine plant (shoots, trunks, roots) were made using the enzymatic method (Boehringer Mannheim) details of which can be found in ZUFFEREY (2000).

Potential exportation of photosynthetic products

The potential rate of carbon exportation from the source leaf to other organs of the plant was determined by the carbon balance method, such as measuring the difference between the net total photosynthetic rate of CO_2 and the variations in leaf carbohydrate content, carried out every two to three hours over a 24-hour period (ZUFFEREY, 2000).

Results and discussion

Content and exportation of leaf carbohydrates

Figure 1 illustrate the daily evolution on 7-8 August 1998 (ripening stage) in photosynthetic activity and the soluble and insoluble leaf carbohydrate content of primary leaves from vegetation exposed to the EAST and WEST sides (rows N-S). Starch accumulates in leaves as photosynthetic activity increases, during the morning in east-facing vegetation (Fig. 1E) and during the afternoon in sides exposed to the west. An identical pattern can be observed for sucrose (Fig. 1G-H). When photosynthetic activity exceeds the capacity for photosynthetic products to migrate away from the chloroplast, the subsequent rise in trioses-P (especially APG) associated with a drop in Pi (inorganic phosphate), stimulates the production of starch (FOYER, 1988). The daily evolution of leaf TNC confirms results observed in other studies on grapevines (CHAUMONT *et al.*, 1994; QUEREIX *et al.*, 199; HUNTER *et al.*, 1995). If light intensity and photosynthesis fall off for a while, a drop in starch concentration and leaf TNC is observed. During the night, leaf starches continues to be broken down so that carbohydrate exportation is maintained and sugar substrates are supplied for leaf respiration during the night.

The study of potential carbon exportation shows that carbohydrate translocation increases with photosynthetic activity in leaves (Fig. 2). During the photoperiod, carbon exportation represents 75% to 95% of assimilation. If photosynthesis drops off during daytime, the rate of carbon exportation exceeds that of assimilation. The flow of carbohydrates away from the leaf continues nocturnally. The exportation of leaf sugars becomes very low towards the end of the night. The potential accumulation of starch depends not only on whether conditions are favourable or not for photosynthesis (solar radiation, temperature, etc.), but also on the need for photosynthetic products by the sink organs (plant growth, berries, roots) (HUNTER *et al.*, 1995). Generally speaking, over a growing season, the potential exportation of carbohydrates falls off in parallel with photosynthetic activity (Fig. 2).

Source-sink relationship and photosynthetic capacity

A high leaf-fruit ratio led to a slight decrease in CO_2 assimilation (6 and 23 July, in addition to 25 August) (Fig. 3). Conversely, a low leaf-fruit ratio favoured the assimilation following the decrease in LAI and no modification in the high yield: slightly higher rates of photosynthesis are observed during the growing season under these conditions.

To sum up, volumes of foliage and fruits had only a minor influence on the photosynthetic activity of grapevine leaves in conditions met in the present study. The rapid plant growth observed in these trials contributed to raising the demand in photosynthetic products and thus reduced differences in photosynthetic behaviours.

The carbohydrate content in leaves differed mainly in the area of soluble sugars, which accumulated in greater quantities when the leaf-fruit ratio was high (Fig. 4). Starch content in leaves remained unchanged irrespective of the leaf-fruit volume. It increased during the daytime (Fig. 4B), and during the night starch withdrawal appeared greater in vines where the leaf-fruit ratio was low (high demand in photosynthetic products).

Trials undertaken by INTRIERI *et al.* (1997) on whole canopy assimilation have shown that global photosynthesis of a vine, in relation to total LAI , increases as the source-sink ratio diminishes. These results bring confirmation to those of various other authors (EDSON *et al.*, 1993; QUEREIX *et al.*, 2000).

Source-sink relationships determine not only the rates of carbon accumulation in leaves, but also their exportation. Low leaf-fruit ratios gave rise to lower concentrations of leaf carbohydrates whereas higher rates of carbon exportation, measured on average over a twenty-four hour period and at equivalent rates of photosynthesis, were observed when the leaf-fruit ratio was high (Table 1). The relatively low leaf carbohydrate contents observed in the present study exerted no inhibition on the photosynthetic activity of leaves. Starch concentration in leaves was below 0.3 mg/cm^2 during the day and total carbohydrate concentrations overall were below 0.8 mg/cm^2. Under the present experimental conditions, it appears that the exportation of synthesised sugars was fast enough to avoid temporary engorgement in leaf photo-assimilates. Sugar exportation is influenced by numerous factors, the most important of which are the rate of leaf photosynthesis and the level of leaf reserves, as well as environmental conditions (HO, 1986). Various authors (GEIGER, 1987; QUEREIX, 2001) have demonstrated that the carbon exportation rate is higher when the leaf-fruit ratio is low under optimal conditions for photosynthesis. The phenomenon of retroactive regulation of photosynthesis, brought about by the significant accumulation of carbohydrates in source organs, is only really effective for high concentrations of starch or soluble sugars in leaves (PAUL et FOYER, 2001).

Sugar content in roots

The evolution of carbohydrate content (soluble and insoluble) in roots over the season is presented in Figure 5. Overall, soluble sugars (sucrose, glucose, fructose) changed little throughout the growing period and represent a small part of the total TNC content in roots. The greater part of sugars is stored in the form of starch. An accumulation of root starch and TNC can be observed from the time of flowering (or a little before this stage) up until around the time of leaf fall. During the winter, TNC and root starch content remained stable. A mobilisation of root reserves was observed from budburst until around the time of flowering (decrease in TNC contents). Comparable results were obtained by WYAND and SHULTZ (2006). Throughout the three-year period of observation 1998-2000, it was possible to establish a relationship between the leaf-fruit ratio and the TNC content in roots measured after harvesting. High leaf-fruit ratios led to sizeable TNC content in roots (Fig. 6). Sugar content in berries could equally be correlated to the exposed leaf surface area/kg grapes. The source-sink relationship appears to be a good indicator of the carbohydrate storage potential of the perennial parts of grapevines.

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Table 1. Influence of the leaf to fruit ratio on leaf photosynthesis, on the average daily content of total leaf carbohydrates (TNC) and the potential exportation of carbon in mature leaves. Lsd = smallest significant difference at 5%. Ns = not significant. *= significantly different. Chasselas, Pully (Switzerland), 19 September 1998.

	Photosynthesis (mmol CO_2 $m^{-2}day^{-1}$)	**TNC** (mmol Glc eq. m^{-2})	**C-Export** (mmol Glc eq. $m^{-2}h^{-1}$)
Low leaf-fruit ratio	331.2	32.6	2.38
High leaf-fruit ratio	321.3	36.3	2.09
lsd (p=0.05)	ns	*	*

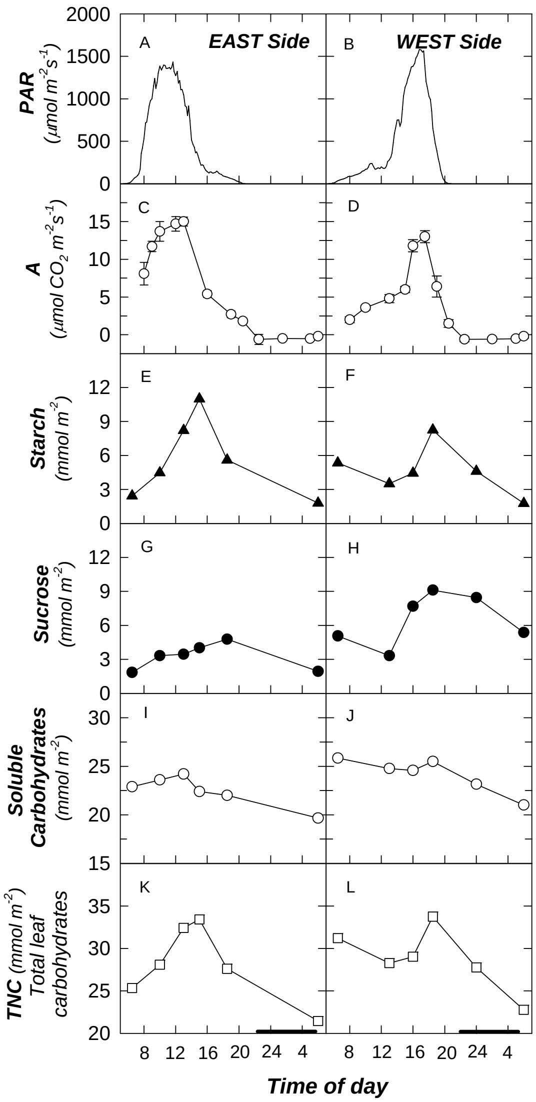


Fig. 1. Daily evolution of PAR, photosynthesis A, starch content, soluble carbohydrates and total leaf non-structural carbohydrates (TNC) of adult leaves in East and West sides of foliage (N-S row orientation). Chasselas, Pully (Switzerland), 7-8 August 1998.

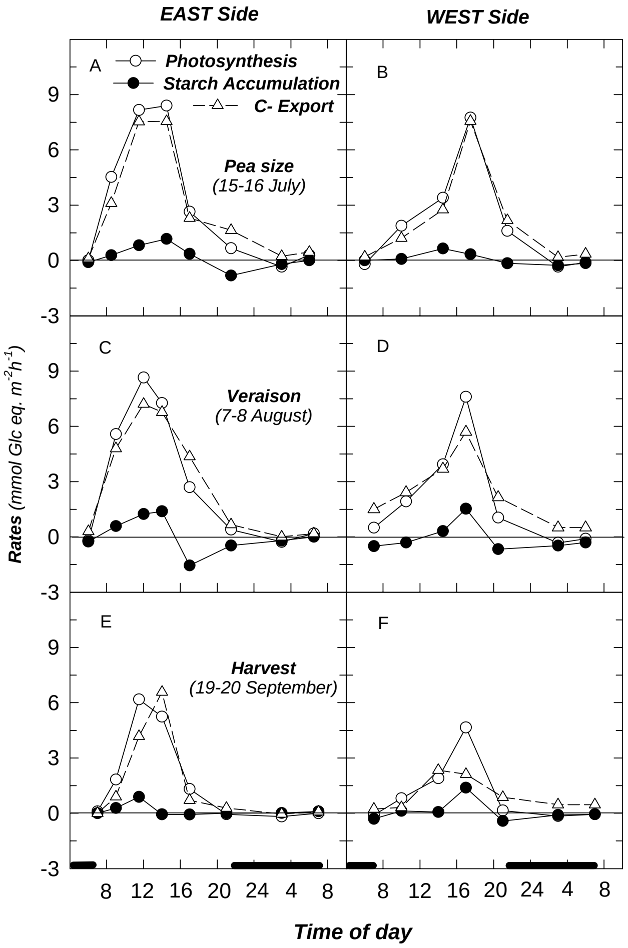


Fig. 2. Daily and seasonal evolutions of photosynthesis A, starch accumulation and C-Export of adult leaves in East and West sides of foliage (N-S row orientation). Chasselas, Pully (Switzerland), 1998.

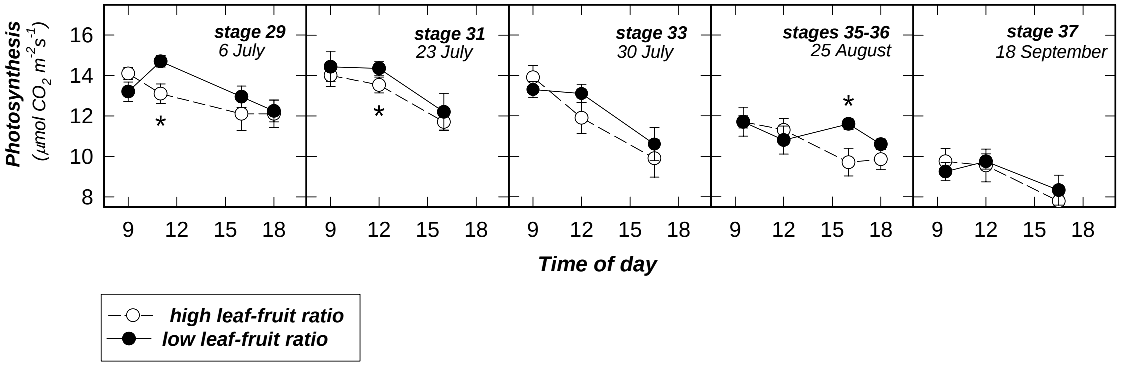
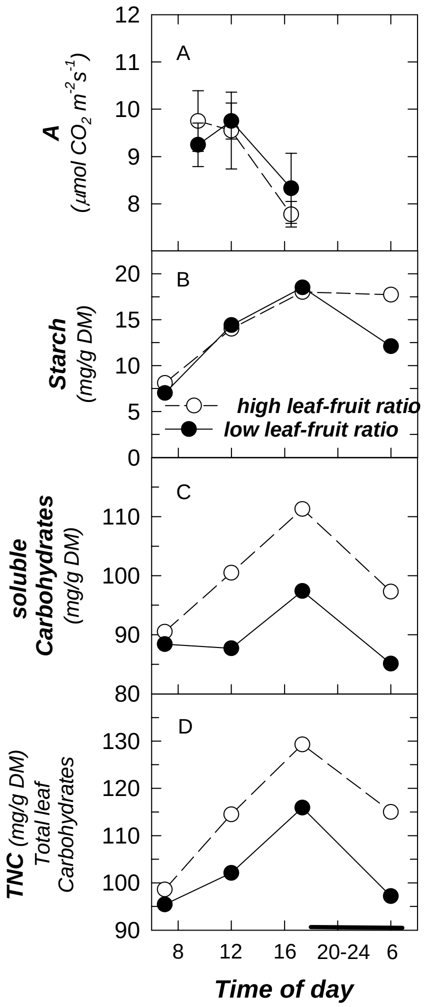


*Fig. 3. Daily evolution of photosynthesis A in mature leaves of vines with high or low leaf-fruit ratio. Vertical lines = standard error. * = differed significantly at 5% probability threshold. Chasselas, Pully (Switzerland), 1998.*



← *Fig. 4. Daily evolution of photosynthesis A, starch content, soluble carbohydrates and total leaf non-structural carbohydrates (TNC) of adult leaves in grapevines with high or low leaf-fruit ratio. Vertical lines = standard error. DM = dry matter. Chasselas, Pully (Switzerland), 18-19 September 1998.*

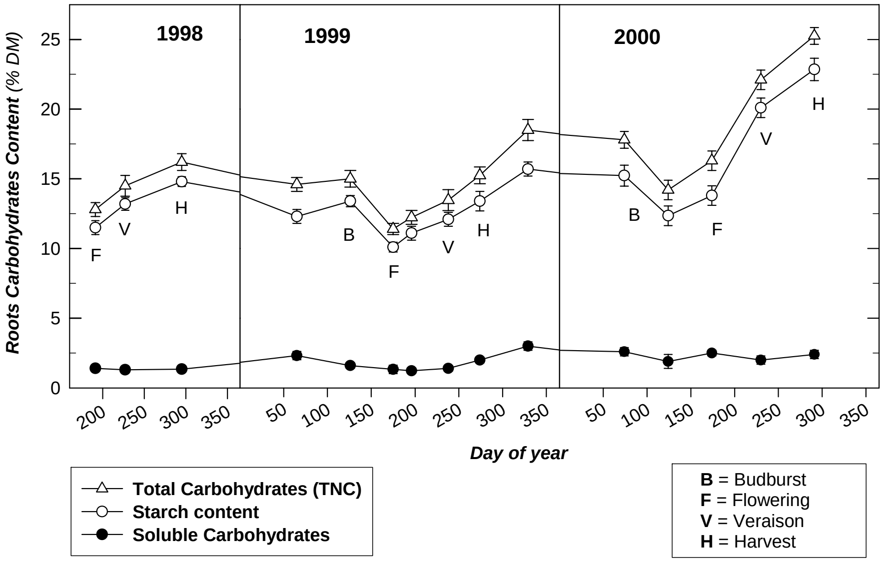


Fig. 5. Seasonal evolution of soluble carbohydrates, starch content and total non structural carbohydrates (TNC) in roots. Chasselas, Pully (Switzerland), 1998-2000.

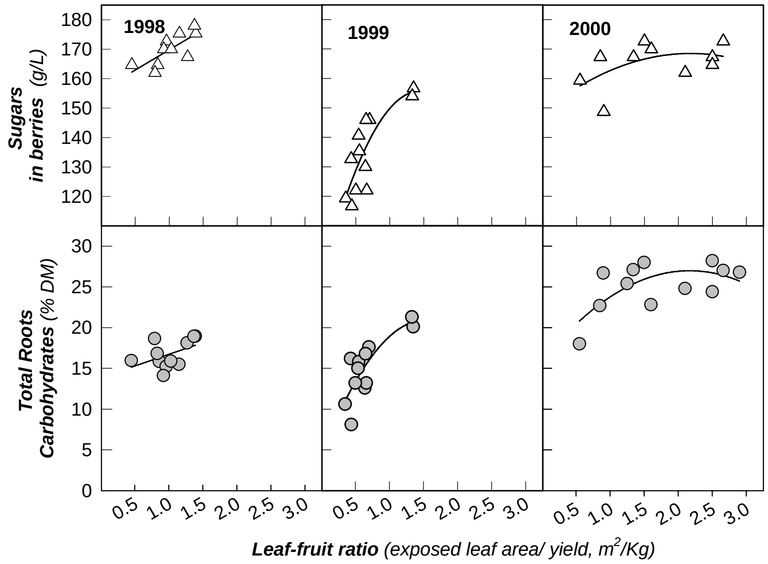


Fig. 6. Influence of the leaf to fruit ratio on sugar accumulation in berries and total non structural carbohydrate content (TNC) in roots. Chasselas, Pully (Switzerland), 1998-2000.