

## Carbohydrate reserves in grapevine (*Vitis vinifera* L. 'Chasselas'): the influence of the leaf to fruit ratio

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### Summary

Seasonal dynamics of total non-structural carbohydrates (TNC) in relation to the leaf-fruit ratio were measured over five years at different grapevine phenological stages in one- and two-year-old canes, trunks and roots of the cultivar 'Chasselas' (*Vitis vinifera* L.). Carbohydrates were mainly stored as starch in different parts of the grapevine during the growing season. Soluble carbohydrates represented only a small part (< 7 % of dry weight, DW) of the TNC. In the roots and trunks, the starch content fluctuated during the growing season, reaching the lowest values between budbreak and flowering depending on the year, and the highest values between harvest and leaf fall. The soluble sugar content increased in the trunks and the two-year-old canes during the winter period with the decrease in temperatures. A negative correlation was established between the average air temperature recorded during the seven days before sample collection for carbohydrate analysis, and soluble carbohydrate content in the trunks and two-year-old canes. The leaf-fruit ratio (source-sink), expressed by the "light-exposed leaf area·kg<sup>-1</sup> fruit", not only substantially influenced the soluble sugar content in berries but also the starch and TNC concentrations in the trunks and roots at harvest. Higher leaf-fruit ratios resulted in increased starch and TNC concentrations in the trunks and roots, which attained the maximum values when the leaf-fruit ratio neared 2.0 m<sup>2</sup> of light-exposed leaf area·kg<sup>-1</sup> fruit. Canopy height and leaf area had no predominant influence on the soluble sugars, starch contents, or TNC in the permanent vine parts.

**Key words:** carbohydrate reserves, total non-structural carbohydrates, starch, source-sink ratio, roots, wood.

### Introduction

The carbohydrates synthesized by leaves during photosynthesis have many functions. They are the building blocks of organic compounds, store energy, and form support structures, such as cellulose, hemi-cellulose, and gluco-protein. All plant parts can store carbohydrates, either temporarily (C reserves accumulated in leaves during daytime then used under stress conditions or during the night; FOYER 1988), or for a longer time, such as in the canes, trunks and roots (KELLER 2010).

In grapevines, the non-structural carbohydrates (TNC) in roots and wood fractions play a key role for the vine longevity and the quality potential at harvest. Indeed, TNC are not only involved in the protection against frost (KELLER 2010), but they also take part in the leaf area development, shoot growth as well as in the flower induction (YANG and HORI 1979, KELLER and KOBLET 1994, MURISIER and AERNY 1994). Furthermore is also established that rapid accumulation of soluble solids in berries at veraison is mainly due to the mobilization of TNC previously stored in the permanent organs. Studies of seasonal TNC variations in the canes, trunks and roots gave the opportunity to analyze TNC dynamics, for both soluble (sucrose, glucose, and fructose) and insoluble (starch) carbohydrates and their allocation between source and sink organs (WINKLER and WILLIAMS 1945, WILLIAMS 1996). In addition, other works demonstrated that climate (WAMPLE *et al.* 1993), water restriction (NDUNGU *et al.* 1997, ROGIERS *et al.* 2011), crop load (SMITH and HOLZAPFEL 2009), canopy management (WEYAND and SCHULTZ 2006) and grape variety (RÜHL and ALLEWELDT 1990) influenced C assimilation and TNC reserves, particularly in the permanent parts (trunks and roots). Canopy management including shoot topping and defoliation can also influence TNC reserves and allocation in plants by changing the source-sink ratio (SCHOLEFIELD *et al.* 1978, CANFOLDI-VASCONCELLOS and KOBLET 1990, VASCONCELLOS and CASTAGNOLI 2000, BENNETT *et al.* 2005). Recently, SMITH and HOLZAPFEL (2009) demonstrated that higher yielding grapevines were more dependent on the post-harvest period for the replenishment of TNC reserves, especially in the roots, than lower yielding vines. Under cool-climate conditions, it has been shown that a minimum leaf-fruit ratio approaching 10 to 20 cm<sup>2</sup> leaf-area/g fruit (KLEWER and DOKOOZLIAN 2005) or 1.0 to 1.4 m<sup>2</sup> light-exposed leaf area·kg<sup>-1</sup> fruit (MURISIER and ZUFFEREY 1997) is required for obtaining adequate grape maturation. MURISIER (1996) mentioned a correlation between the leaf-fruit ratio and the formation of TNC reserves in the woody parts and roots of the cultivar Chasselas. Finally, TNC reserves took part not only in vegetative and reproductive growth and energy requirements (respiration) but also in grapevine defense against biotic (JERMINE *et al.* 2010 a, b) and abiotic stress.

To analyze the seasonal dynamics of TNC reserves in different parts of the grapevine (roots and woody fractions), and to characterize the influence of the source-sink ratio, an experiment was conducted in the field on mature grapevines of 'Chasselas' with different leaf-fruit ratios. The variations of the leaf-fruit ratio were obtained

in manipulating the canopy height and the crop load. The seasonal dynamics of the TNC reserves was observed during 5 consecutive years in order to point out the inter and intra-annual mobilization and storage of TNC in the grapevines. The influence of the leaf-fruit ratio on the TNC content in the permanent parts of the grapevine at harvest was also investigated.

### Material and Methods

**Study site and plant material:** The experiment was conducted between 1998 and 2002 on *Vitis vinifera* L. 'Chasselas' (clone 14/33-4, rootstock 3309 C, planted in 1986) at the research station Agroscope Changins-Wädenswil ACW, in the experimental vineyard of Pully, Switzerland (46°32'N, 7°17'E). The plot was oriented South with a 10 % to 15 % slope. Vines were pruned in a vertical shoot positioning system (cane pruning), including six shoots per vine. Two planting densities, 4,900 vines·ha<sup>-1</sup> (2.4 x 0.85 m<sup>2</sup>) and 9800 vines·ha<sup>-1</sup> (1.2 x 0.85 m<sup>2</sup>), each comprising two heights of canopy (0.75 and 1.25 m) with the same trunk height (0.6 m), were compared. The soil of the vineyard in Pully is deep and fertile, with a high water holding capacity estimated to be above 200 mm on 2 meters soil depth. Annual precipitation and monthly precipitation are reported in Tab. 1. The climatic data were collected from the weather station located in the very plot used for this experiment ([www.météosuisse.ch](http://www.météosuisse.ch)).

**Leaf-fruit ratio variation:** Leaf-fruit ratio was manipulated in two ways (Tab. 2):

- 1) By varying the canopy height (H): two canopy heights (0.75 and 1.25 m) were maintained throughout the season by successive toppings. The first topping was conducted at the end of flowering on day of year (DOY) 182; the shoots were re-topped every three weeks.
- 2) By varying the yield: two levels of yield were compared by keeping 1 or 2 fruit clusters per shoot. Cluster dropping was completed when the grapes were pe-sized (DOY 190-200, depending on the year).

**Leaf area measurement:** Leaf area was determined non-destructively several times during the growing season, in 1998 and 2000, by measuring the length of each leaf lamina's two secondary lateral veins. Lengths were converted to areas using allometric equations developed from direct area measurements of previously harvested leaves ( $n = 200$ ;  $r^2 = 0.96$ ). All primary and lateral leaves on two shoots per vine (12 shoots per treatment) were measured to estimate the average leaf area per shoot. The average shoot leaf area was used to estimate total vine leaf area by multiplying it by the number of shoots per vine. The leaf area exposed to saturating light (PFD > 1,200  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) was estimated using Carbonneau's method (1995). This estimation takes into account the height of effective canopy (H), the canopy thickness (e), the row spacing (E) and the rate (in percentage) of canopy gaps (T), using the formula:

Light-exposed leaf area =  $[(2 \times H) + e] / [E \times (1 - T)]$ : Light-exposed leaf area was estimated every year at veraison (BBCH 81). The leaf-fruit or source-sink ratio was estimated using the ratio of light-

Table 1

Monthly precipitation totals (mm) at the experimental site in Pully, Switzerland, during the five study years in comparison to long-term averages (1960-1990)

	Precipitation (mm)					
	1998	1999	2000	2001	2002	Ø 30 years
January	85	58	18	202	41	72
February	21	120	125	38	77	68
March	39	55	58	322	56	76
April	165	123	108	160	41	75
May	34	153	55	113	191	93
June	42	175	48	193	77	111
July	51	68	157	139	115	107
August	68	209	137	82	106	121
September	222	144	74	148	47	108
Oktober	143	115	185	84	179	93
November	140	90	172	49	260	88
December	33	142	53	34	100	93
Annual Total	1044	1452	1190	1565	1290	1101

Table 2

Plant density, row spacing, foliage height and cluster number maintained per shoot of Chasselas grapevines in Pully, Switzerland from 1998-2002

Plant density (vines·ha <sup>-1</sup> )	Row spacing (m)	Foliage height (m)	Cluster per shoot
9800	1.2	0.75	1
			2
		1.25	1
			2
4900	2.4	0.75	1
			2
		1.25	1
			2

exposed leaf area to crop load per vine (light-exposed leaf area·kg<sup>-1</sup> fruit).

**Plant samples and carbohydrate analyses:** Samples of one-year-old canes, two-year-old canes (fruit canes), trunks and roots were collected from each vine plant during the main development stages of the grapevine following Lorenz *et al.* (1994) development scale (winter dormancy BBCH 0, budbreak BBCH 11, flowering BBCH 65, veraison BBCH 81, harvest BBCH 91 and leaf fall BBCH 97). At each phenological stage, three vines per treatment (12 vines total) were mechanically excavated, extracting the maximum possible quantity of roots. Approximately 1 kg of roots of all lengths and diameters were collected, immediately washed and frozen with liquid nitrogen. The roots were then stored at -20 °C. Wood samples were also collected destructively with pruning shears. Approximately 400 g of each of the three wood types (one- and two-year-old canes and trunk) was collected from each vine, frozen with liquid nitrogen, and stored at -20 °C for analysis. All root and wood samples were

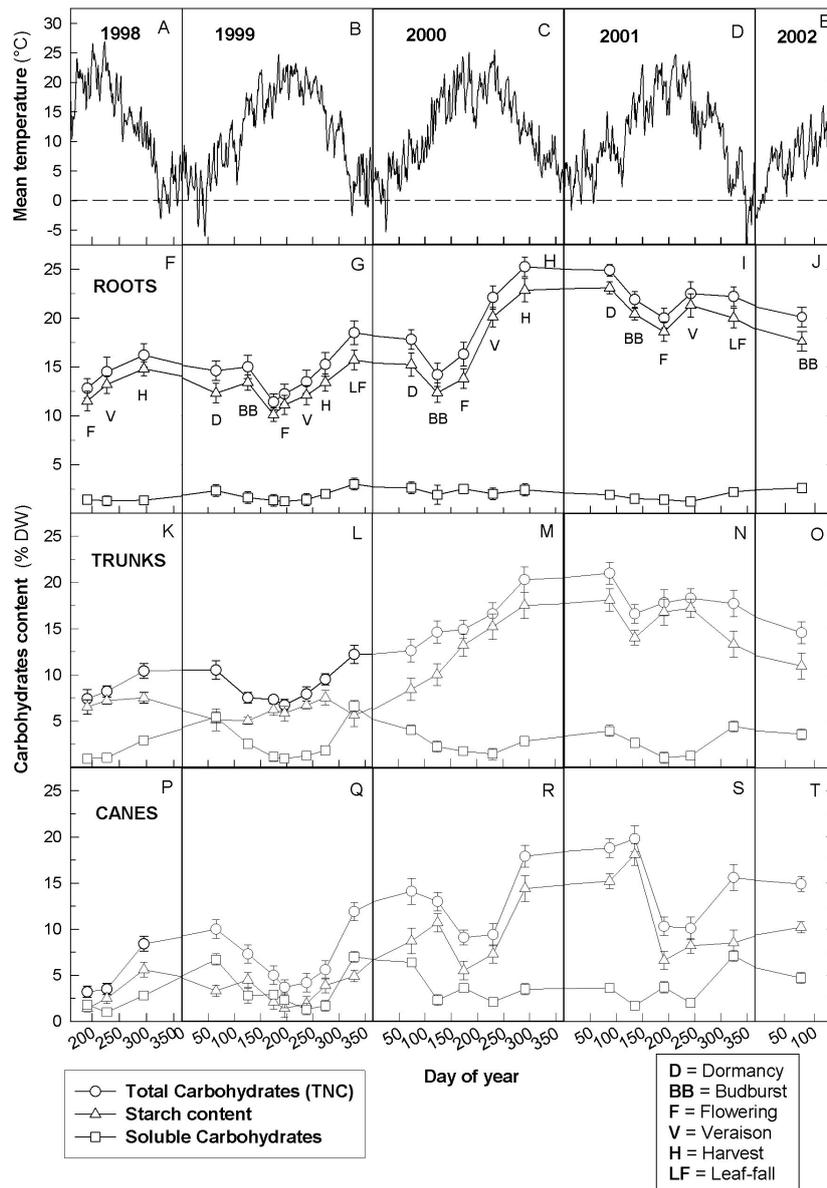


Fig. 1: Mean air temperature (A-E) and seasonal evolution of soluble carbohydrates (sucrose, glucose, and fructose), starch and total non structural carbohydrate (TNC) contents in the canes (P-T), trunks (K-O) and roots (F-E) of 'Chasselas' grapevines in Pully, Switzerland from 1998-2002. The means  $\pm 2 \times$  standard error,  $n = 12$ . DW: dry weight.

weighed before freezing in the field to determine their fresh weight, and then before cryo-dessication (freeze-drying) at Eurolyo laboratory, Chartres (France). Each freeze-dried sample was finely ground at 1,200  $\mu\text{m}$ . Soluble sugars (including glucose, fructose and sucrose) and starch were analyzed enzymatically (kit LISA 200C, CETIM, France) and then measured spectrophotometrically at 340 nm with an ELx800UV automated micro-plate reader (Bio-Tek Instruments Inc., Vermont, USA) as described by (GOMEZ *et al.* 2007).

**Yield and Fruit composition:** All grapes from each vine were harvested separately. The effective yield (crop load per vine) and berry weight (on 50 berries per vine) were measured. Grapes from each vine were crushed separately to quantify the soluble sugars, pH and total acidity.

**Statistical analysis:** Polynomial regressions and analyses of variance (ANOVA) were calculated with SigmaStat 3.1 (Systat Software, Point Richmond, CA).

## Results

**Seasonal TNC dynamics:** Seasonal dynamics of the soluble (sucrose, glucose and fructose) and insoluble (starch) carbohydrates in the roots, trunks and canes revealed that most the storage was in the form of starch (Fig. 1). In the roots (Fig. 1 F-J), the soluble sugars showed small variations and represented less than 3 % of dry weight (DW) during the season, while the starch content fluctuated between 12 % and 20 % of DW depending on the season. During each year, the root starch progressively increased just before flowering, increasing further between flowering and veraison. The accumulation of root starch continued through harvest until leaf fall, except in 2001. A decrease of starch in the roots was observed just before budbreak, sometimes lasting nearly until flowering.

In the trunks and canes (Fig. 1 K-T), starch was the dominant form of stored carbohydrates during the growing season, but in a lower concentration than in the roots. Con-

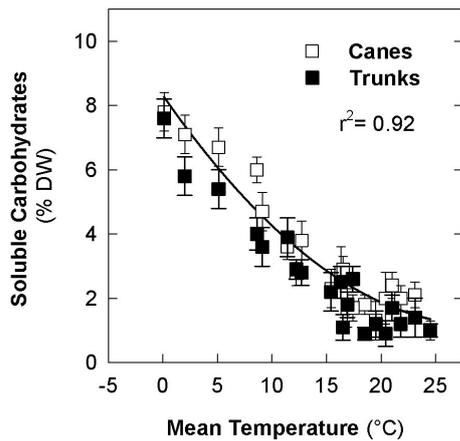


Fig. 2: Relationship between the cane and trunk soluble carbohydrates and the mean air temperature over the preceding 7 d in 'Chasselas' grapevines in Pully, Switzerland from 1998-2002. The means  $\pm 2 \times$  standard error,  $n = 12$ . DW: dry weight.

version of starch into soluble carbohydrates was observed during the winter, coinciding with lower temperatures. The starch level was the lowest around flowering period in the two-year-old cane wood. Soluble carbohydrate concentrations increased from 2-3 % to 7-8 % DW between DOY 300 (leaf fall) and DOY 60 (during the dormancy period). A correlation was established between soluble sugar concentrations in the canes and trunks and the average air temperature of the 7 d before sample collection (Fig. 2). The maximum sugar concentration in the reserve tissues was measured at the lowest average daily temperatures, around 0 °C in this experiment. The maximum level of TNC reserves was observed at leaf fall in all parts of the vine, and the minimum level of soluble sugar reserves was observed just before flowering. Planting density had no major impact on the TNC content in the shoots (one-year-old), canes (two year-old), trunks or roots (results not shown).

**Influence of leaf-fruit ratio:** Fig. 3 represents the seasonal evolution of leaf area per vine in 2000. The vines maintained at 0.75 m canopy height (H) had a leaf area of around 2.5 m<sup>2</sup>/vine from the end of flowering until harvest, while the vines with a 1.25 m tall canopy had a leaf area of about 4.5 m<sup>2</sup>/vine. Neither canopy height nor leaf area had any impact on the TNC content in the one- or two-year-old canes (Fig. 4 A-B). However, in the trunks and roots of the 0.75 m canopy vines, the TNC content measured in 2000 was lower in the winter (BBCH 0) and at budburst (BBCH 11) compared to the 1.25 m canopy vines (Fig. 4 C-D), and it was higher at veraison (BBCH 81). However, in 1998, 1999 and 2001, there was no significant impact of canopy height or leaf area on soluble sugars (Fig. 5 A-D), starch (Fig. 5 E-H), or TNC in the roots (Fig. 5 I-L). Similar results were observed in the trunks and one- and two-year-old wood (results not shown).

The leaf-fruit ratio (light-exposed leaf area/kg fruit) had a great impact on berry sugar content at harvest during the four years of this study (Fig. 6 A-D). The highest berry sugar contents were observed when the leaf-fruit ratio was above 1.5 m<sup>2</sup>/kg. Similarly, the TNC concentration in the trunks and roots – measured just before harvest (BBCH 91) – increased with a higher leaf-fruit ratio (Fig. 6 E-L).

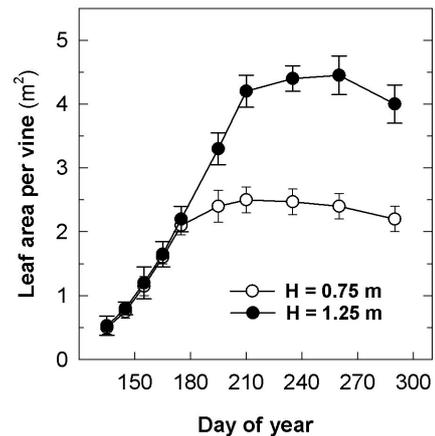


Fig. 3: Seasonal evolution of estimated leaf area per vine during the 2000 growing season for two different foliage heights (H = 0.75 m and 1.25 m) of 'Chasselas' grapevines in Pully, Switzerland in 2000. The means  $\pm 2 \times$  standard error,  $n = 6$ .

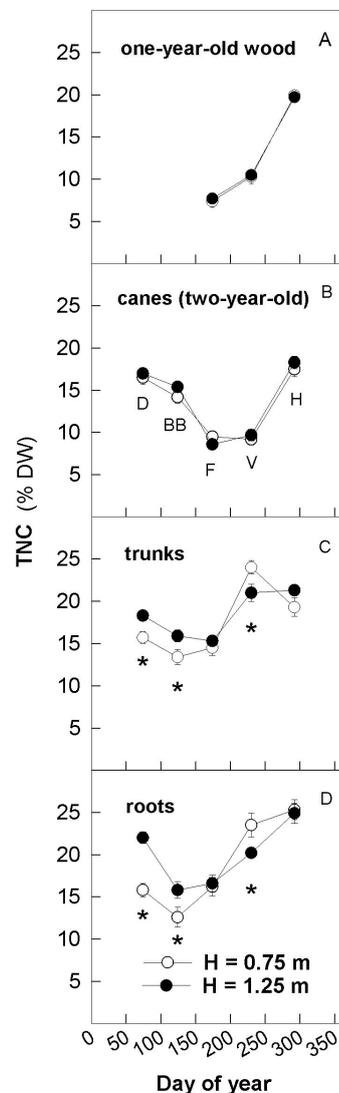


Fig. 4: Seasonal evolution of total non structural carbohydrates (TNC) in the one-year-old wood, canes, trunks and roots for two foliage heights (H = 0.75 m and 1.25 m) of 'Chasselas' grapevines in Pully, Switzerland in 2000. The means  $\pm 2 \times$  standard error,  $n = 6$ . DW: dry weight. \*denotes statistical significance at  $p < 0.05$ . **D**: dormancy, **BB**: budburst, **F**: flowering, **V**: veraison, **H**: harvest.

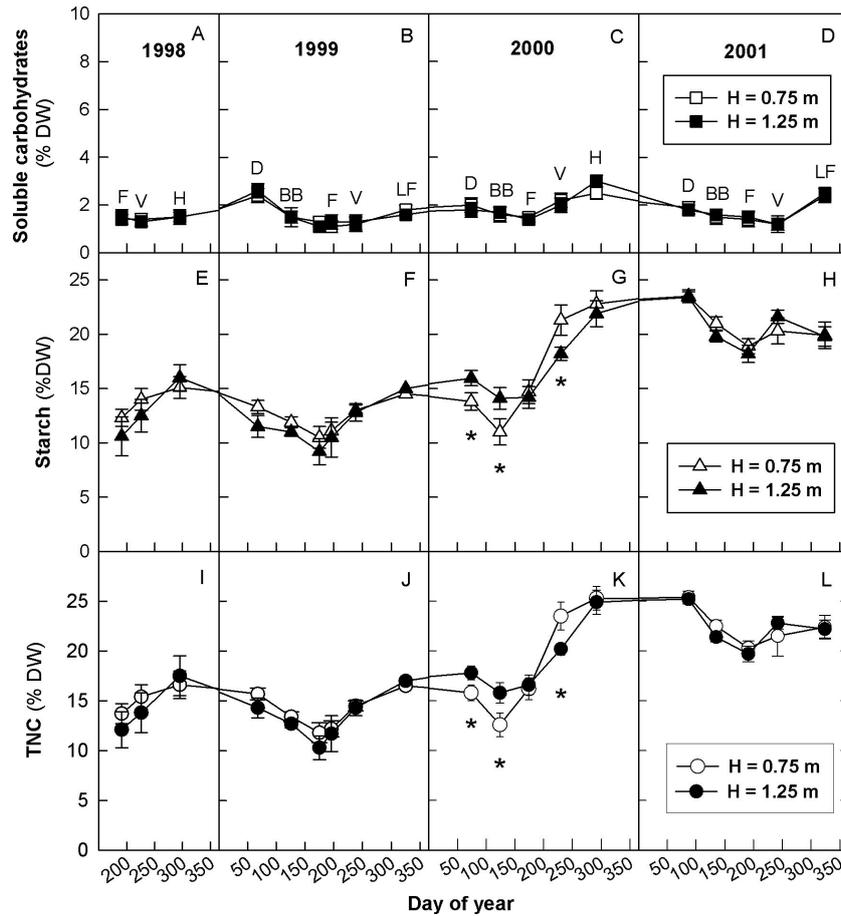


Fig. 5: Seasonal evolution of soluble carbohydrates, starch and total non structural carbohydrates (TNC) in the roots for two foliage heights ( $H = 0.75$  m and  $1.25$  m) of 'Chasselas' grapevines in Pully, Switzerland from 1998-2001. The means  $\pm 2 \times$  standard error,  $n = 6$ . DW: dry weight. \*denotes statistical significance at  $p < 0.05$ . **D**: dormancy, **BB**: budburst, **F**: flowering, **V**: veraison, **H**: harvest, **LF**: leaf-fall.

The curve fitting - calculated from 1998 to 2001- between leaf-fruit ratio and TNC contents shows that the highest TNC values were reached when the leaf-fruit ratio was above  $2.0 \text{ m}^2 \cdot \text{kg}^{-1}$ . Likewise, the TNC content in the roots was reduced by 50 % when the leaf-fruit ratio was around  $0.5 \text{ m}^2 \cdot \text{kg}^{-1}$ , in comparison to the maximum TNC values with a leaf-fruit ratio at  $2.0 \text{ m}^2 \cdot \text{kg}^{-1}$  (Fig. 7 C). Because TNC is mainly starch, a similar relation was observed between the leaf-fruit ratio and starch content in the trunks and roots (Fig. 7 B). On the other hand, the correlation between soluble carbohydrates and the leaf-fruit ratio was less obvious.

## Discussion

**Seasonal TNC variations:** Seasonal TNC dynamics show that 'Chasselas' stores carbohydrates as starch in the roots, trunks and one- and two-year-old wood. Soluble carbohydrates represented less than 7 % DW of TNC reserves in all grapevine parts, and even less in the roots ( $< 2$  %). These results confirm earlier observations of different grapevine cultivars (WINKLER and WILLIAMS 1945, EIFERT *et al.* 1961, SCHOLEFIELD *et al.* 1978, KOBLET *et al.* 1993, WILLIAMS 1996, BATES *et al.* 2002, ZAPATA *et al.* 2004, BENETT *et al.* 2005, WEYAND and SCHULTZ 2006, FIELD *et*

*al.* 2009, SMITH and HOLZAPFEL 2009) and on other woody species (LOESCHER *et al.* 1990). In cool climate conditions, maximum TNC values were observed at around 13-16 % DW in dormant grapevines (EIFERT *et al.* 1961, KORKAS *et al.* 1994, BATES *et al.* 2002; Weyand and Schultz 2006). In a hot climate, higher TNC values of above 30 % DW could be observed (WINKLER and WILLIAMS 1945, SCHOLEFIELD *et al.* 1978, SMITH and HOLZAPFEL 2009). In this study, intermediate TNC values (10-25 % DW) were observed in the trunks and roots. With 'Chasselas', root starch concentration reached maximum values during dormancy and then started decreasing just before budbreak and continued to drop until flowering. The starch decrease during this period could be partially explained by the root necrosis process (ZAPATA *et al.* 2001) and by the loss caused by sap bleeding after pruning (GLAD *et al.* 1992, CAMPBELL and STROTHER 1996). Besides root necrosis and sap bleeding, decline in starch reserves indicate that carbohydrate reserves in roots play a key role in leaf and root growth during the period from budbreak to flowering (MURISIER 1996). The rapid growth of shoots and leaves during this part of the season is mainly due to mobilization of TNC reserves and particularly starch (BATES *et al.* 2002, ZAPATA *et al.* 2004), while photosynthesis covers only a part of growth and energy requirements during this period (KOBLET and PERRET 1982, SCHULTZ *et al.* 1996, KELLER 2010).

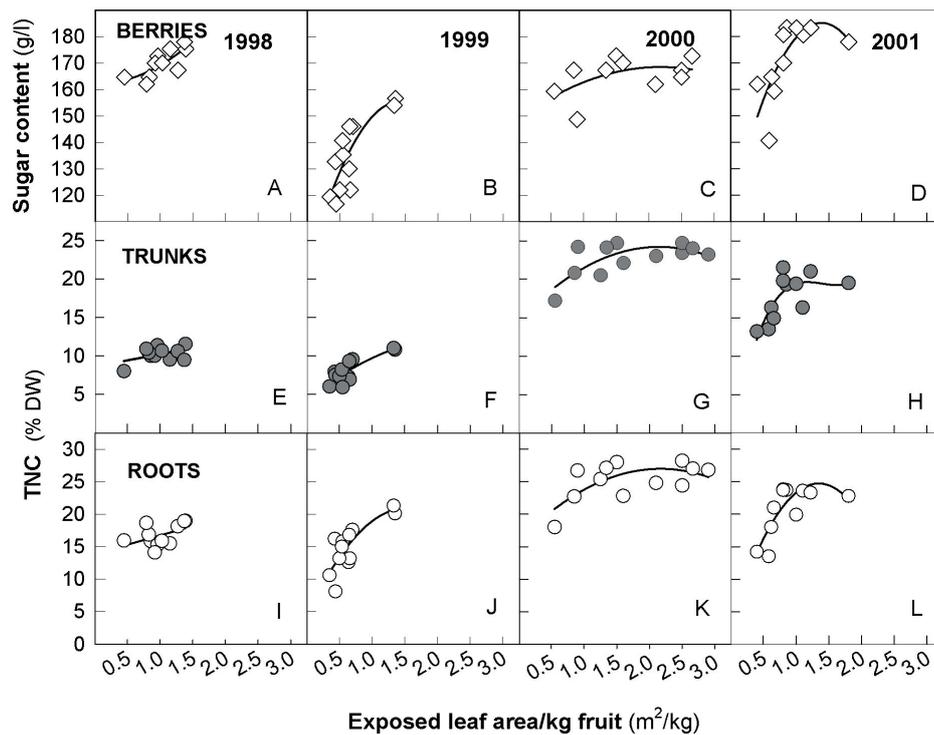


Fig. 6: Influence of the leaf to fruit ratio (light-exposed leaf area/kg fruit) on sugar accumulation in the berries and total non structural carbohydrate (TNC) in the trunks and roots at harvest time ( $n = 12$ ) in 'Chasselas' grapevines in Pully, Switzerland from 1998-2001. DW: dry weight.

In trunks and one- and two-year-old wood, starch was converted into soluble sugars during the winter, improving the wood frost resistance (WAMPLE and BARY 1992, WAMPLE *et al.* 1993, HAMMAN *et al.* 1996, KOUSSA *et al.* 1998). Because starch is osmotically inactive, it does not improve frost resistance by itself. Thus, grapevine acclimatization requires a conversion of starch – stored in phloem and xylem parenchyma cells – into soluble sugars (mainly sucrose), which allow the reduction of osmotic potential in the tissues and play the role of cryo-protectors (FENNEL *et al.* 2004, KELLER 2010). This conversion seems to be initiated by autumn temperatures below 5 °C (KELLER 2010) and by shorter days, and continues until the middle of winter. The phenomena is still present in this study, but less pronounced as per KELLER and LOESCHER's results (1989) on sweet berry. The starch content in wood fractions tended to increase between dormancy and budbreak (particularly in 2000) on 'Chasselas', as observed by WEYAND and SCHULTZ (2006) on 'Riesling'. These authors suggested that the starch increase was probably related to assimilation from sugars associated with an increase in ambient temperature before budbreak, which replenished starch depleted for maintenance of respiration in winter (MOONEY and GARTNER 1991). However, starch content in the one- and two-year-old wood decreased after budburst and reached its minimum value at cluster closure as per WEYAND and SCHULTZ' results (2006). In trunks, however, starch was accumulated from budburst until harvest.

The starch accumulation in roots and woody parts was more important at the end of the season 2000. This phenomenon could be partly explained by the lower rainfalls and the higher solar radiation observed in September 2000 in comparison to the three other years at the same period. These favorable climatic conditions maintained a high leaf

photosynthetic activity during fall 2000 (non published results). In opposite, the falls 1998 and 1999 were particularly rainy and cloudy with negative effects on canopy photosynthesis and TNC storage.

**Leaf-fruit ratio:** In this study, the source-sink relation - expressed by the ratio of light-exposed leaf area·kg<sup>-1</sup> fruit - clearly influenced the starch and TNC concentrations in the permanent parts of the grapevines (trunks and roots) at harvest. The TNC content in the roots strongly diminished when the leaf-fruit ratio was less than 1.5 m<sup>2</sup>·kg<sup>-1</sup>. The present results corroborate other studies (HOLZAPFEL *et al.* 2006, SMITH and HOLZAPFEL 2009) that showed the leaf-fruit ratio as an important factor of the process of carbohydrate refilling in roots before and after harvest. Moreover, these studies reported that higher yielding grapevines were much more dependent on climatic conditions during post-harvest period (hot inland region of New South Wales, Australia) in terms of TNC reserve replenishment compared to lower yielding grapevines.

In cool-climate conditions without water restriction, the observed late-season vegetative growth probably represented a powerful sink on TNC dynamics between veraison and harvest. Indeed, grapevines with greater leaf area ( $H = 1.25$  m;  $LA \cdot vine^{-1} = 4.5$  m<sup>2</sup>) accumulated less starch and less TNC in the trunks and roots around veraison in 1998 and 2000 compared to grapevines with smaller leaf area ( $H = 0.75$  m;  $LA \cdot vine^{-1} = 2.5$  m<sup>2</sup>). In this case, C-assimilation in grapevines with greater leaf area ( $LA \cdot vine^{-1} = 4.5$  m<sup>2</sup>) was mainly allocated to vegetative growth of secondary shoots, which were more numerous than in the grapevines with smaller leaf area (unpublished data). Nevertheless, TNC reserves at harvest were similar between the two canopy heights ( $H = 0.75$  m and  $H = 1.25$  m), showing an equilibrium between assimilation, translocation and

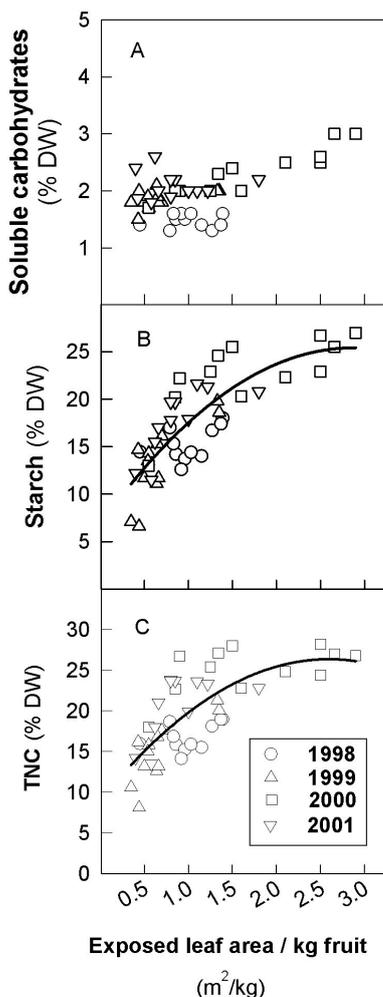


Fig. 7: Influence of the leaf to fruit ratio (light-exposed leaf area·kg<sup>-1</sup> fruit) on soluble carbohydrate, starch and total non structural carbohydrate (TNC) in the roots at harvest (n = 12) of 'Chasselas' grapevines in Pully, Switzerland from 1998-2001. DW: dry weight.

C-storage in the permanent parts of grapevine. Different canopy manipulation experiments (tipping, leaf removal) performed by VASCONCELOS and CASTAGNOLI (2000) have also illustrated that the leaf-fruit ratio could influence starch and TNC mobilization in the trunks of 'Pinot Noir' during dormancy. After two consecutive years of intensive defoliation (removal of all leaves of primary and secondary shoots), starch content in wood decreased markedly in contrast to the non-defoliated treatment in an experiment performed by CANDOLFI-VASCONCELOS and KOBLET (1990). Moreover, a positive correlation was reported by these authors between the soluble sugar content in the berries and the starch reserves in the wood, showing that the fruits and wood were both important sink organs for TNC storage during maturation, depending on the leaf-area per vine. The present study also showed a strong positive correlation between the starch reserve in the roots and the soluble sugar content in the berries at harvest ( $r = 0.85$ ;  $p < 0.01$ ) and they were dependent on the leaf-fruit ratio. Likewise, MURISIER (1996) also mentioned a positive correlation between the leaf-fruit ratio and TNC content (mainly starch) in the permanent parts of grapevine. In the present study, the low starch and TNC content in roots, measured at the end of the seasons 1998 and especially 1999, could mainly

be due to a lower leaf-fruit ratio, in comparison to 2000 and 2001, which reduced C-assimilation and storage. Another explanation for the lower starch content in roots could be the translocation of sugars from starch mobilization in roots and woody fractions to the berries during the ripeness when the weather conditions are unfavorable (high precipitations, low solar radiation).

The present results were obtained in well-watered grapevines, favorable to vegetative growth and even excess vigor in some years. The impact of water restriction represents a major factor not only in C assimilation, but also in TNC storage and allocation in the different sink organs of grapevines (CANDOLFI-VASCONCELOS *et al.* 1994, HOLZAPFEL *et al.* 2010). Future research would be required to study the effects of water stress in relation to the source-sink ratio on TNC reserves by grapevine.

### Conclusion

Grapevines store non-structural carbohydrates, mostly as starch, in the different parts of the perennial structure. An important mobilization of starch from roots and trunks was observed during the period from budburst to flowering and was related to the decrease of TNC reserves in the same organs. The lowest level of TNC was measured in roots and trunks at flowering time. From flowering until leaf fall, starch accumulated in the roots, trunks and one- and two-year-old wood. The highest level of TNC was measured at harvest and sometimes even later at leaf fall. The TNC and starch contents in roots were higher at the end of the season 2000 in comparison to the other years, probably due to the prevailing climatic conditions which were favorable to a high canopy photosynthesis. The leaf-fruit ratio – expressed by the ratio of light-exposed leaf area per kg fruit – strongly determined the starch and TNC contents in the trunks and roots at harvest. The starch and TNC concentrations increased along with the source-sink ratio up to a maximum value of about 2.0 m<sup>2</sup> of light-exposed leaf area per kg fruit. The root starch content doubled from 12 to 25 % D.W., when the leaf-fruit ratio increased from 0.5 to 2.0 m<sup>2</sup> of light-exposed leaf area per kg fruit. On the other hand, the relationship between soluble carbohydrates and leaf-fruit ratio was less obvious.

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