ODC 160.22:164.4:176.1 *Acer saccharum* Marsh.

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Carbohydrate Levels in Current-year Shoots of Sugar Maple

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Abstract

Diurnal changes in carbohydrate concentrations in leaves and current-year stems of a mature sugar maple tree were studied in June and September. In leaves, alcohol-soluble sugar concentration was highest in the morning and lowest in late afternoon or early evening; diurnal changes in starch lagged about 5 hours behind changes in sugar. Carbohydrate concentrations in current-year stems did not vary diurnally. Leaves weighed much more than current-year stems and contained a higher concentration of sugar and starch. In leaves, sugar concentration was higher in September than it had been in June; starch concentration was much higher in June. The opposite was true for current-year stems; sugar concentration was slightly lower in September than it had been in June, but starch concentration was much higher.

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SEASONAL CHANGES in carbohydrate levels in roots, bolewood, and twigs of sugar maple (*Acer saccharum* Marsh.) have been reported by Jones and Bradlee *(1933)*, Witherell *(1963)*, Marvin and others *(1971)*, and Wargo *(1971)*. All found starch to be at a maximum in early fall and at a minimum in winter.

These previous studies have dealt with woody material at least 1 year old. My data are based on carbohydrate levels in current-year shoots of a mature sugar maple tree in Vermont. This is a report on diurnal changes in starch and alcohol-soluble sugars during a 2-day period in late June after shoot elongation had ceased and during a 1-day period in mid-September before leaf coloration and abscission.

METHODS

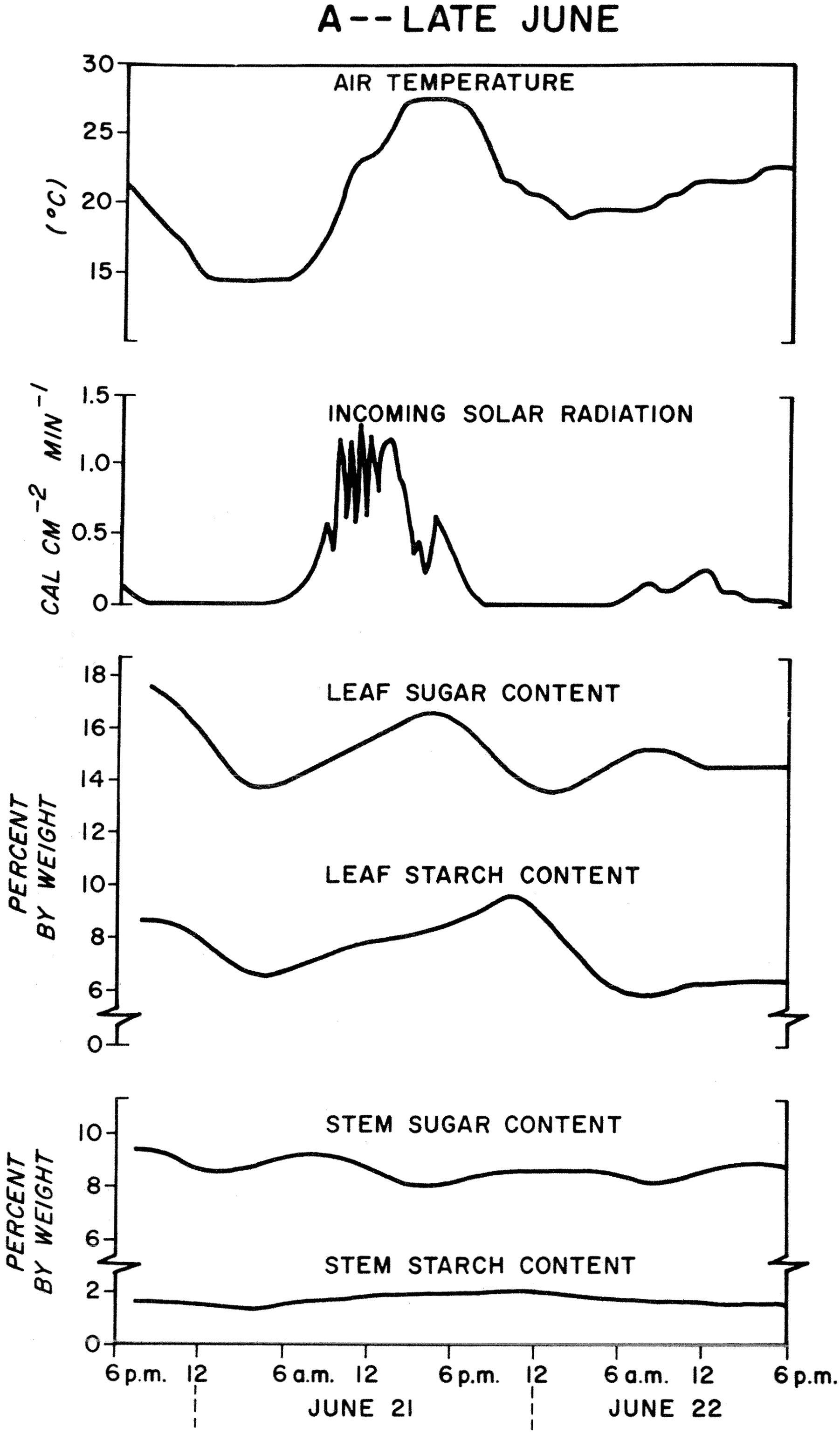
Current-year shoots, about 7 to 27 cm long, were collected at 2-hour intervals from a single open-grown mature sugar maple tree in Fairfax, Franklin County, Vermont. The tree was 59 cm in dbh; total height was 15.5 m; and crown diameter was 11.6 m. Shoots were collected in late June after elongation had ceased, and in mid-September while leaves were still green. In June they were collected during the 46-hour period 8 pm 20 June to 6 pm 22 June. In September, they were collected during the 24-hour period 10 am 13 September to 10 am 14 September.

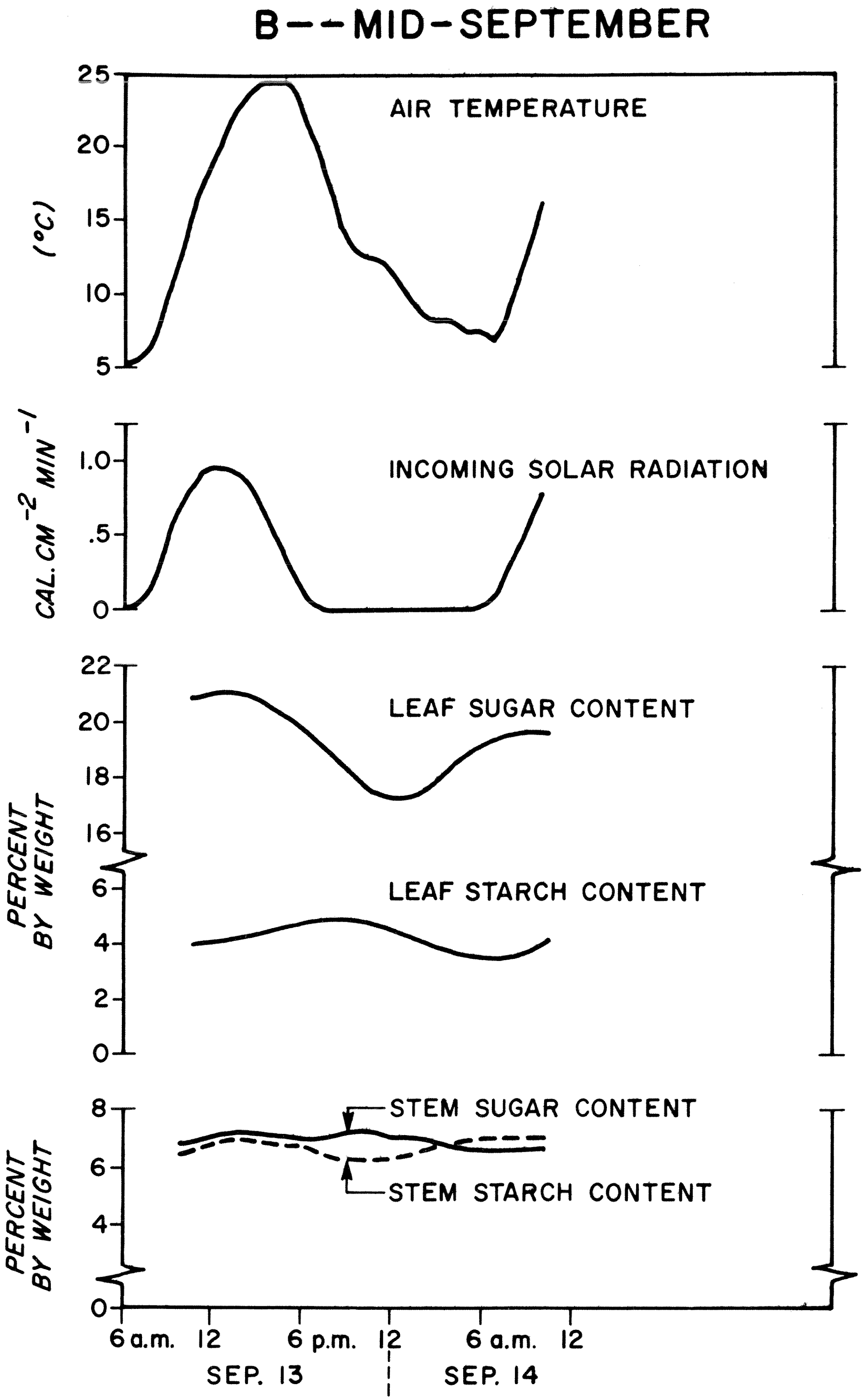
The study tree's crown, as projected onto the ground, was divided into 10 sections to eliminate possible effects of aspect on carbohydrate content. Ten shoots were collected at each 2-hour interval, one from each section. Leaves were removed immediately after shoots were collected. (The term "shoot" refers to the entire current-year growth, and the term "stem" refers to the shoot minus its leaves.)

The 10 stems (including the bark) and 10 sets of leaves were cut up, and 2 leaf and 2 stem samples (approximately 2 gm each) were placed in glass jars and covered immediately with hot 80-percent ethanol. Oven-dry weights of remaining plant material were recorded for estimating total amounts of carbohydrate. Selected samples were stored in the alcohol-filled jars until they were analyzed for starch and sugar with standard procedures.

Air temperature (measured about 4 feet above ground in an instrument shelter) and solar radiation (measured in the open) were monitored during the study period (fig. 1). Scattered clouds were evident on 20 and 21 June. The sky was overcast on 22 June, and about 2 cm of rain fell. Skies were clear throughout the September test period.

Figure 1.—Diurnal changes in air temperature, incoming solar radiation, and leaf and stem sugar and starch content in current-year shoots of sugar maple. A, from samples collected in late June. B, from samples collected in mid-September.




B--MID-SEPTEMBER
AIR TEMPERATURE
(°C)
25
20
15
10
5
INCOMING SOLAR RADIATION
CAL. CM^-2 MIN^-1
1.0
.5
0
LEAF SUGAR CONTENT
LEAF STARCH CONTENT
PERCENT BY WEIGHT
22
20
18
16
6
4
2
0
STEM SUGAR CONTENT
STEM STARCH CONTENT
PERCENT BY WEIGHT
8
6
4
0
6 a.m.
12
6 p.m.
12
6 a.m.
12
SEP. 13
SEP. 14

RESULTS

Amount and Distribution of Carbohydrates

In June, current-year shoots weighed an average of 3.42 gm and contained about 800 mg of carbohydrates (table 1). Approximately two-thirds of this was alcohol-soluble sugar, and one-third was starch. At this time, leaves made up 93 percent of the total shoot weight, had 96 percent of the sugar, 99 percent of the starch, and 97 percent of the total carbohydrates.

The average weight of all leaves on a shoot increased by 0.25 gm from June to September, and there was a moderate increase in total carbohydrate content (from 771 to 849 mg). The composition of leaf carbohydrates changed markedly during this period: leaf sugar increased from 495 to 697 mg, whereas leaf starch decreased from 276 to 152 mg.

The statistical probability of June to September changes in leaf weight, leaf sugar content, leaf starch content, stem weight, stem sugar content, and stem starch content were evaluated with a "t" test; differences were highly significant (probabilities less than 0.01) for all comparisons.

The dry weight of stems more than doubled during the 3-month period June to September, and total carbohydrate content increased from 25 to 85 mg. Stems of current-year shoots had contained only 3 percent of all carbohydrates in June, but this had increased to 9 percent by September. This change was primarily the result of a marked increase in starch. Stem starch increased from 4 mg in June (1 percent of the total starch) to 42 mg in September (22 percent of the total starch). Stem sugar content also increased. Stems had only 4 percent of the total sugar in June; this increased slightly to 6 percent in September. But the increase in stem sugar (from 21 to 43 mg) was less than the corresponding increase in stem dry weight. Thus the concentration of stem sugar decreased from 8.6 to 6.7 percent.

Diurnal Variations

Diurnal variations in carbohydrate levels were not nearly so well defined as seasonal differences. Variations within replications sometimes exceeded variations between sampling times. However, curves for the data revealed consistent diurnal changes in leaf carbohydrates (fig. 1). Curves are based on a 3-point moving average of the data.

Sugar concentrations tended to be lowest early in the morning and highest in late afternoon or early evening. Diurnal changes in leaf starch lagged about 5 hours behind leaf sugar in those minimum and maximum amounts. In June, the daily minimum concentration of total carbohydrates (alcohol-soluble sugar plus starch) was about three-fourths the maximum. Diurnal patterns in September were similar, but sugar concentrations tended to be lowest earlier in the morning and highest

Table 1.—Carbohydrate levels in sugar maple leaves and stems during June and September[1]

Item		June			September		
		Leaves	Stem	Total shoot	Leaves	Stem	Total shoot
Total dry weight	gm	3.17	0.25	3.42	3.61	0.64	4.25
Sugar content:							
Concentration[2]	pct.	15.6	8.6	15.1	19.3	6.7	17.4
Amount	mg.	495	21	516	697	43	740
Starch content:							
Concentration[2]	pct.	8.7	1.7	8.2	4.2	6.6	4.6
Amount	mg.	276	4	280	152	42	194
Total carbohydrates:							
Concentration[2]	pct.	24.3	10.3	23.2	23.5	13.3	22.0
Amount	mg.	771	25	796	849	85	934

[1] June values are the average of those for the period 10 a.m. 21 June through 8 a.m. 22 June; September values are the average for those for the period 10 a.m. 13 September through 8 a.m. 14 September.

[2] Concentration as percentage of dry weight.

earlier in the afternoon. Also, leaf starch concentrations did not vary as much diurnally in September.

We did not find consistent patterns of diurnal fluctuations in stem carbohydrates. Observed differences were more likely due to sampling or analytical procedures.

DISCUSSION

Amount and Distribution of Carbohydrates

Leaf starch content decreased from 276 mg in late June, soon after leaves became fully expanded, to 152 mg in mid-September, when leaves were becoming senescent. During the comparable period, leaf sugar increased from 495 to 697 mg. The seasonal reduction in leaf starch may be due to hydrolysis of "reserve starch", or to a decrease in the synthesis of "assimilation starch". Reserve starch is formed from translocated sugars and is synthesized in storage organs; assimilation starch is a transient form, synthesized in leaf chloroplast *(Akazawa 1965)*.

In sunflower leaves, less photosynthate is assimilated into starch at 10°C than at 20°C *(Smith 1944)*. The average air temperature in our study area was 6°C lower in mid-September than it had been in late June. This may partially explain why the concentration of leaf starch was lower in September whereas the concentration of leaf sugar was higher. It may also explain why diurnal changes in leaf starch were smaller in September than they had been in June. Another, perhaps more important, reason for the September reduction in leaf starch is that maple leaves were becoming senescent at this time. Starch is characteristically hydrolyzed to sugar in senescent leaves *(Salisbury and Ross 1969)*.

Stems contained only 4 mg of starch in June, but 42 mg in September. Current-year stems were undoubtedly importing carbohydrates from leaves in late June. Much of this was being assimilated into plant biomass; consequently, these developing stems contained very little starch. Total carbohydrate reserves in stems were probably at a maximum in mid-September. Starch is also maximum at about this time.

Sugar-starch interconversions are thought to be temperature-dependent. Witherell *(1963)* reported a net conversion of sugar to starch in dormant maple stems when the temperature was 10°C or higher. The average air temperature in our study area was about 15°C during the September test period. This may explain the relatively high concentration of stem starch. Subsequent hydrolysis of starch to sugar later in the fall is thought to be induced by lowering air temperatures. This hydrolysis may take place over a relatively short period of time. Marvin and others *(1971)* reported a 40-percent decrease in starch within maple callus tissue stored at 4°C, rather than 27°C, for 48 hours.

Diurnal Variations

Diurnal patterns of sugar concentrations found for sugar maple leaves (early morning minimum; late afternoon or early evening maximum) have also been reported for potato *(Watson 1936)* and barley *(Gauch and Eaton 1942)*. Apparently there are substantial diurnal changes in the difference between carbohydrate production (photosynthesis) and carbohydrate utilization (respiration, assimilation, and translocation) rather than just temperature-induced interconversions of starch and sugar, because total carbohydrates also fluctuated diurnally. Leaves produce more carbohydrates than the phloem can transport during daylight hours *(Zimmerman 1971)*. Translocation continues at night, so leaf carbohydrate concentrations decrease.

Surprisingly, alcohol-soluble sugar concentration rose during the period 1 to 6 am (before sunrise) on 22 June and 14 September (fig. 1). All leaves were mature in September and nearly so in June, so they probably did not import photosynthates. The increase in September may have been due, at least partially, to a temperature-dependent conversion of starch to sugar. Witherell *(1963)* has reported a net conversion of starch to sugar at temperatures between 3°C and 10°C. Air temperature in the study area was below 10°C at this time, and leaf starch dropped. But this would not explain the similar increase during predawn hours on 22 June, when air temperature did not drop below 18°C.

Leaf carbohydrate concentrations seemed quite responsive to current weather conditions. On 21 June, a warm, mostly sunny day, sugar and starch increased from 6 am to 4 pm, but not on the following cool, overcast, rainy day (fig. 1).

No definite diurnal patterns were found in the concentration of stem carbohydrates. Mason and Maskell *(1928)* found that sugar content did not vary diurnally in the wood of cotton plants, but diurnal changes in the bark resembled those in leaves. We did not analyze separately the bark and wood of our current-year maple stems.

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