concentrations have only slight, if any, effect on permeability.

Killing of the tissue results in a very slight increase in permeability. The smallness of the increase indicates that the cell wall rather than the cell membranes is the primary barrier to water movement.

Determination of tissue permeability by osmotic means yields rates of water movement essentially identical to those obtained by the isotopic method. The half-time of protoplast expansion or contraction of individual cells located near the surface is however 2 to 3 minutes and in cases in which the cells are very near to cut tissue edges, 1 minute or less. Cell permeability of Avena coleoptile section tissue is thus greater than the permeability of the tissue as a whole.

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A STATISTICAL EVALUATION OF SOME OF THE FACTORS RESPONSIBLE FOR THE FLOW OF SAP FROM THE SUGAR MAPLE[1,2]

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No adequate explanation has yet been proposed for the mechanism responsible for vessel sap pressures and sap flows from wounded stems in several species of Acer and some other genera during the dormant period. It is generally agreed that the pressures and flows are temperature-induced. Clark (1, 2) and Jones (5, 6) many years ago made extensive observations on soil, air and stem temperatures and the sap flows from trees in the field. More recently, similar observations on excised stems have been made by Stevens and Eggert (8) and on both stems and stumps by Johnson (4). On the basis of these field observations, a number of authors have proposed and discussed possible mechanisms responsible for the pressures and flows (1, 2, 4, 5, 8 and 9). Most of the observations have been made in the field, but Marvin and Greene (7) have reported on a series of experiments on excised stems under conditions of controlled temperature in the laboratory. Some of these investigators have observed that sap pressures and flows occur only following a rise in the temperature of the stem tissues and also that the pressures and rates of flow decrease when the temperatures fall.

Temperature and flow rate or flow volume data have not heretofore been given a critical analysis to evaluate the possible relationship between these variables. In the experiments reported here temperature and flow rate data have been collected for several trees for four seasons. A multiple regression analysis of these data has demonstrated a quantitative relationship between the daily total volume of sap flow and four independent variables derived from the temperature and flow data.

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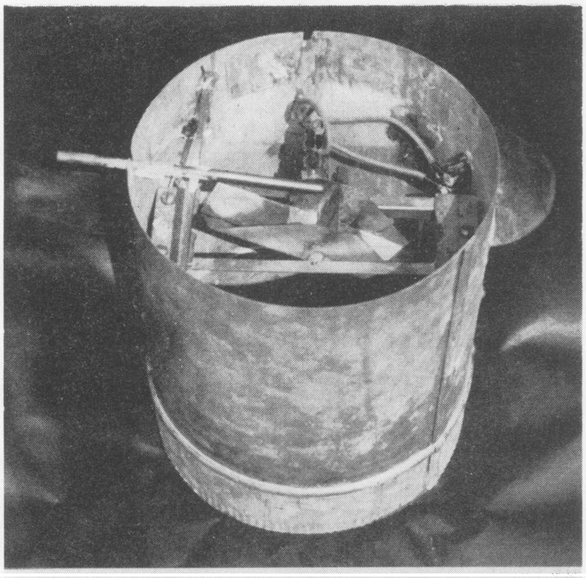
MATERIALS AND METHODS

The data presented here were collected during the months of March and April for the years of 1950, 1951, 1952 and 1953 at the Proctor Maple Research Farm of the College of Agriculture, University of Vermont. The temperature and sap flow data were recorded from mature trees of *Acer saccharum* Marsh. Using copper-constantan thermocouples, a continuous record through each season was made of air temperatures in the shade at 6 ft (1.8 m) and at 30 ft (9.1 m) in the crown. Temperatures of the xylem were recorded 6 cm inside the stem surface as well as temperatures of the inner bark. Twig temperatures were obtained by inserting the thermocouple into the cut end of a twig 6 mm in diameter, 30 ft from the ground in the center of the crown. The thermocouple junctions were inserted at least 5 cm into the tissues and were sealed with plastic wood. These and other temperatures were recorded by two 16-point Leeds and Northrup Micromax recording potentiometers.



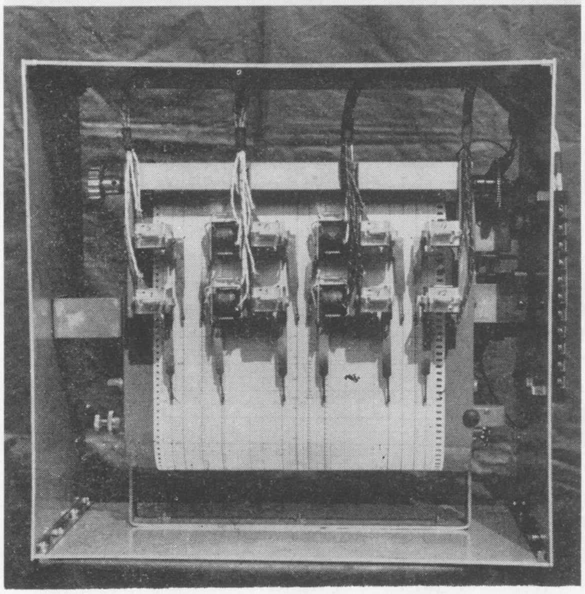


FIG. 1 (*above*). Tipping bucket measuring element.
FIG. 2 (*below*). Multiple recorder for the tipping buckets.

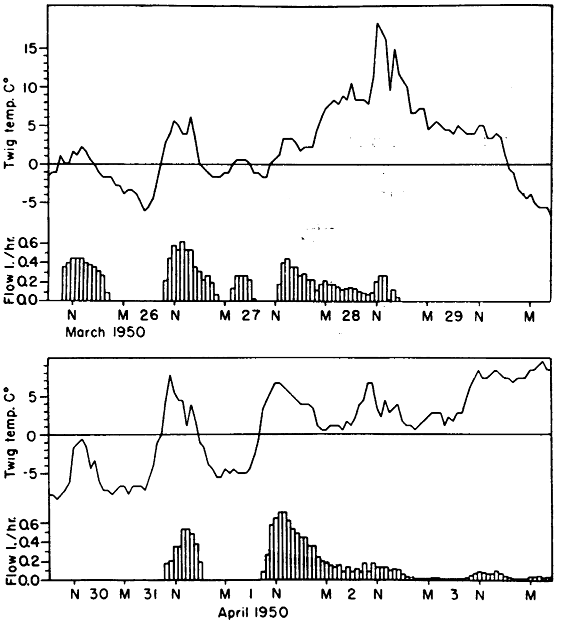


FIG. 3. Twig temperatures and sap flow rates for tree 500 for nine days plotted at hourly intervals.

Sap flow rates and volumes were continuously recorded by devices constructed for the purpose, shown in figures 1 and 2. The sap flowed from a standard tap hole (7/16 in × 2 in) through a rubber tube to a tipping bucket unit mounted on a large reservoir. The measuring unit was similar to that of a rain gauge. The capacity of each bucket was 15 ml. When the bucket tipped to empty, it momentarily closed a magnetically operated switch which sent an impulse to the recorder. The recorder consisted of a Leeds and Northrup chart frame to which 12 relays with pens mounted on the armatures were attached. The pens recorded on a chart which moved at the same rate of speed as the potentiometer charts. The rates of flow could then be compared with the temperatures for any given time or period of time.

RESULTS

The several temperatures and rates of sap flow were plotted at hourly intervals for each of the four seasons for three trees. A careful study of these graphs indicated that twig temperatures correlated best with flow rates. Frequently rapid flow rates were observed when there had been no change in the xylem and inner bark temperatures, although the temperature of the twig had increased. However, on some days with bright sun and a cold wind, the xylem and inner bark temperatures may have risen as much as 10° C, whereas a change of less than 1° C above 0° C was observed in the twig temperature and no flow occurred. Several trees were decapitated 20 ft (6.1 m) above the ground but below the first branches, and the cut surface was sealed with a rubber-faced cap. The rates and volumes of flow were much reduced following the treatment and were found to correlate with changes in the temperatures of the inner bark and xylem. It was concluded from these observations that twig temperatures correlated best with the flow rates and volumes, and were therefore used in the statistical analysis.

Twig temperatures and flow rates for one tree are plotted for hourly intervals in figure 3. Two characteristic temperature and flow relationships are apparent. When a flow occurs it follows a rise in temperature above 0° C and a decrease in temperature is followed by a decrease in the rate of flow and, in some cases, by a cessation of flow. It may also be observed that the rate of flow is not proportional to the magnitude of the rise in temperature, as, for example, in the flows recorded on March 26 and 27, April 1 and 3.

Experiments on stem sections previously reported (7) and the experiments of Stevens and Eggert (8) have demonstrated that during the cooling period preceding a flow, stems absorbed water or an aqueous solution. If the stems were not permitted to absorb, the flow following a cooling period was greatly reduced or did not occur at all. These observations suggested that an important relationship might be found between preceding temperatures and flows. A period of freezing temperatures (7) is not a necessary prerequisite for a flow. Figure 3 (March 28, April 2 and 3) shows that a rising temperature from a previous low above 0° C increases the rate of flow. However, it is apparent in figure 3 that when the preceding temperature was below 0° C the flow was greater both in rate and volume than when the lowest temperatures between the flows were above 0° C. On March 29 temperature rises comparable to those of March 27 did not cause a flow, and on April 2 and 3 temperature rises had only slight effects on the rate of flow.

An attempt has been made to formulate these relationships by the methods of regression analysis outlined by Ezekiel (3). Daily volumes of flow, Y, were related to varying numbers of independent variables, X_i, variously defined, and in various functional relationships, such as multiple linear, exponential and polynomial. In each trial, a least-squares solution of the regression was found, values of the predicted flow, Y', calculated, and the coefficient of multiple correlation, R, of Y and Y' values used to assess the goodness of fit. After a number of trials, the best fit of the flow data was obtained from a multiple linear regression on four independent variables, three of which were derived from the temperature data, and one from the flow data, as described below. It should be realized that the success of an analysis such as this is greatly dependent upon the insight and ingenuity of the analyst, and we have no doubt that it would be possible to improve considerably upon the prediction of flow rates which our analysis permits.

The equation finally adopted had the form

$$Y' = C(b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4)$$

where Y' is the predicted flow rate, b_i are constants, and X_i and C, the independent variables, as defined below. An example of observed flow rates, Y, appears in table I. X_1 is the number of hours during which twig temperatures were below 0° C, cumulated for the 24-hr period from 6:00 A.M. to 5:00 A.M. inclusive, preceding the flow in question. It may be termed the "conditioning" factor, and was suggested by the experiments of Stevens and Eggert (8), and Marvin and Greene (7) referred to above. For many years, farmers have observed that a storm with wet snow that adheres to the trees precedes the largest flow. Criteria for this weather condition were established from field notes and the temperature data and, where these criteria applied, the conditioning factor (X_1) was increased by a factor of 3. The factor was chosen after preliminary analyses showed that flows on days characterized by wet snows were exceptionally large. This condition occurred five times in the four years—for example, April 14, 1950, table I.

TABLE I

DAILY SAP FLOW (Y), AND THE INDEPENDENT VARIABLES (X_1 TO X_4) TO WHICH IT IS RELATED FOR TREE 500 IN 1950

$$Y = -3.491 + 2.135X_1 + 0.340X_2 + 0.026X_3 + 0.412X_4$$

DATE	Y	X_1	X_2	X_3	X_4
Mar. 20	8.8	0	0.0	74	0
21	13.2	13	8.8	133	1
22	36.8	11	13.2	189	2
23	9.4	5	36.8	60	3
24	10.7	0	0.0	0	0
25	43.8	24	10.7	15	5
26	65.4	18	43.8	65	6
27	47.8	16	65.4	147	7
28	17.5	6	47.8	97	8
29	0.0	0	17.5	7	9
30	0.0	0	0.0	0	0
31	36.3	24	0.0	60	11
Apr. 1	84.6	16	36.3	127	12
2	19.6	3	84.6	95	13
3	11.2	0	19.6	275	14
4	22.7	0	11.2	311	15
5	0.0	0	22.7	26	16
6	0.0	0	0.0	0	0
7	32.2	24	0.0	38	18
8	73.8	16	32.2	75	19
9	0.6	0	0.0	0	0
10	50.0	22	0.6	28	21
11	149.6	17	50.0	124	22
12	34.1	3	149.6	19	23
13	0.0	0	0.0	0	0
14	149.3	72	0.0	93	25
15	121.7	14	149.3	59	26
16	64.8	8	121.7	288	27
17	8.2	1	64.8	217	28
18	12.1	0	8.2	222	29

The temperatures initiating a flow and during a flow were quantized by cumulating degree-hours above 0° C, or the lowest temperature for the previous 24-hr period. They were tabulated for the day of each flow

TABLE II

TOTAL VOLUME (LITERS) OF SAP YIELDED BY THREE TREES IN FOUR YEARS

YEAR	TREE		
	457	499	500
1950	54	50	101
1951	57	98	129
1952	26	56	69
1953	..	52	82

For difference between trees 457 and 499 $t_2 = 2.28$; $P < 0.25$.

For difference between trees 457 and 500 $t_2 = 5.95$; $P < 0.05$.

For difference between trees 499 and 500 $t_3 = 4.02$; $P < 0.05$.

from 6:00 A.M. to 5:00 A.M. An example of these data appears in table I as X_3. An examination of the seasonal pattern of twig temperatures and flow rates indicated that in some years the mechanism was more responsive to temperature changes late in the season than earlier. The X_4 term, simply the serial number of the day of the flow, represents this seasonal effect, and in these analyses the use of this term improved the relationship. Its biological significance is not known.

It seemed reasonable to assume that the magnitude of a flow might be related to that of the preceding one. It was supposed that a large flow would deplete the system and tend to make the succeeding flow smaller. Accordingly, the flow volumes for the preceding 24 hrs were tabulated and are the X_2 term. The flow data Y and X_2 are in arbitrary units and may be converted into ml by multiplying each daily flow value by 90. The terms X_1 and X_3 are in Fahrenheit units, for convenience in calculating. They may be converted to Centigrade degree-hours by multiplying by 0.56. In nature, the temperature may rise above 0° C although neither high enough nor long enough to thaw the tissues and permit a flow. Therefore, the convention was adopted that when X_3 was less than 5, C is equal to zero, and otherwise has the value of 1.0.

TABLE III

COEFFICIENTS FOR THE MULTIPLE REGRESSION * FOR EACH TREE FOR EACH YEAR AND A SUMMARY FOR EACH TREE FOR THE YEARS COMBINED

TREE	b_0	b_1	b_2	b_3	b_4
			1950		
457	-2.388	+1.034	+0.168	+0.002	+0.699
499	-0.631	+1.158	+0.286	+0.008	+0.115
500	-3.491	+2.135	+0.340	+0.026	+0.412
			1951		
457	+2.403	+0.935	+0.098	+0.166	-0.352
499	+4.447	+2.019	+0.109	+0.290	-0.810
500	+5.933	+1.920	+0.068	+0.328	-0.479
			1952		
457	-4.585	+1.431	+0.310	-0.005	+0.314
499	-2.521	+2.725	+0.151	-0.006	+0.463
500	-5.219	+3.026	+0.127	+0.002	+0.774
			1953		
499	+5.307	+2.212	-0.014	+0.043	-0.297
500	+16.225	+3.131	-0.014	+0.059	-0.749
			Combined		
457	-1.106	+1.134	+0.295	+0.055	-0.050
499	+2.741	+1.778	+0.161	+0.079	-0.282
500	+3.780	+2.387	+0.171	+0.100	-0.210

* $Y^1 = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$.

The yields of sap for each tree for each year are shown in table II, as well as the statistical evidence that there are significant differences in the yields between the trees. The coefficients of the multiple regressions for each tree for each year, and for each tree for the years combined, are shown in table III. In comparing the yields of the three trees and the b-values, no consistent pattern is apparent from year to year. However, when the years are combined, the b_1 values are ranked in the same order as the total yield from the trees. In contrast, the b_3 values are essentially the same. The b_4 values are in some years positive and in some years negative, negative when the seasonal effect is large at first and diminishes during the season, positive when the seasonal effect increases during the season. Contrary to the supposition on which X_2 was defined, the coefficients b_2 are positive, except in 1953. That is to say, large flows tend to occur on successive days, and there is no evi-

TABLE IV

COEFFICIENTS OF SEPARATE DETERMINATION (d), COEFFICIENTS OF MULTIPLE CORRELATION (R^2) AND VARIANCE RATIOS (F = REGRESSION MEAN SQUARE/RESIDUAL MEAN SQUARE) FOR MULTIPLE REGRESSIONS FITTED TO THE DATA FOR EACH TREE EACH YEAR AND THE YEARS COMBINED

TREE	ΣY	d_1	d_2	d_3	d_4	R^2	F	VALUES OF F FOR $P = 0.001$
				1950				
457	600.8	.341	.063	.009	.125	.538	9.42	6.4
499	555.6	.439	.067	.002	.017	.525	8.85	6.4
500	1124.2	.477	.105	.006	.044	.632	14.90	6.4
				1951				
457	633.1	.198	.009	.257	.002	.466	8.69	6.1
499	1086.4	.296	.011	.247	.015	.568	13.70	6.1
500	1433.6	.229	.003	.276	-.006	.503	10.28	6.1
				1952				
457	289.3	.438	.107	-.002	-.005	.538	10.25	6.3
499	624.8	.528	.040	.000	-.016	.551	10.80	6.3
500	771.4	.465	.029	.001	.011	.505	8.84	6.3
				1953				
499	582.3	.733	.000	.028	.013	.774	46.80	5.3
500	908.2	.727	.000	.024	.050	.801	58.75	5.3
				Combined				
457	1523.2	.335	.079	.049	-.003	.459	21.74	5.0
499	2849.1	.406	.022	.045	.003	.476	32.80	5.0
500	4237.4	.454	.025	.048	-.001	.527	40.42	5.0

dence for the supposed depletion. Nevertheless, this term contributes somewhat to the regression and has been retained.

The numerical values of the coefficients of any one equation cannot be compared, since they depend on the units chosen to represent the variables. The importance of the separate terms of the regression can, however, be compared by use of the coefficients of separate determination (Ezekiel, 3), and these are shown in table IV, for the regressions of table III, together with multiple correlation coefficients squared, R^2, and ratios of residual to regression variance, F. It is apparent that the "conditioning" factor, X_1, has the greatest value in prediction of flows. This is apparent in the combined values.

Discussion

For many years it has been evident that a relationship exists between tissue temperatures and the sap flow in maples. There have been, however, no published data attempting to demonstrate a quantitative relationship between differing temperatures and the volumes of sap flow. It has been possible in this analysis to account for a statistically significant portion of the flow for each of three trees for four years.

Flow has been visualized in this analysis as dependent upon four independent variables derived from the temperature data. The two most interesting independent variables are the temperature terms X_1 and X_3. With the exception of 1951, the X_1 term, the conditioning factor, makes the largest single contribution. The coefficient of separate determination d_1 indicates that X_1 accounts for the major portion of the flow (table IV). This is shown when the years are combined, as well as in individual years. It would appear, therefore, that variations in flow are more closely related to the preceding temperatures than to the temperatures at the time of the flow. Data are not at hand to support adequately an hypothesis for the mechanism of flow, but these particular data do suggest that the X_3 term, that of the temperatures prevailing on the day of the flow, has an indirect rather than a direct thermal effect on the tissues producing the flow. This strongly suggests a trigger mechanism. The X_2 and X_4 terms do not show a consistent pattern through the four years and possibly could have been left out of the analysis without serious consequences.

Although the four independent variables considered here account for a significant portion of the flows observed, other factors undoubtedly influence the volume of flow. Soil temperature and soil moisture are probably both important, during the sap flow season and the preceding months. The rainfall and temperatures throughout the preceding months may also have an effect. Data on these factors would be required to establish such relationships.

Summary

Hourly data on the flow of sap from three sugar maple trees, *Acer saccharum* Marsh., during March and April of 1950, 1951, 1952 and 1953 have been obtained from an automatic recording device. Wood, bark, twig and air temperatures were recorded simultaneously for the same trees. Preliminary study of the data showed that the flows were more closely related to twig temperatures than to the other temperatures recorded, and twig temperatures have been used in a multiple regression analysis. A significant portion of the daily flow can be accounted for by a multiple linear regression of flow rate on 1) the number of hours during the day preceding the flow, when twig temperature was below 0° C; 2) the total volume of flow on the preceding day; 3) the number of degree-hours above a previous low, cumulated for the day of the flow; and 4) the serial number of the day of the flow. Of these 1) is of most importance, indicating that preceding temperatures are more important than current temperatures in determining the amount of a flow. The fact that flows characteristically begin after a rapid temperature rise above freezing suggests a "triggering" effect of temperature.

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