FRUIT GROWTH AND FOOD TRANSPORT IN CUCURBITS

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Recently the writers reported that phloem exudation from cucurbits can no longer be considered a manifestation of normal food movement by mass flow. This does not mean that the growth of cucurbit fruits will not serve as an index of normal food movements, for only upon cutting the plant are these processes disturbed. The cultivated cucurbits are convenient to work with and grow very rapidly, so that the rates noted should represent the upper limits occurring in plants.

In 1941, Colwell (1) collected fruits of Connecticut Field pumpkins of five different sizes. From measurements and records he calculated the time required to grow from one size class to another. Table I gives the sizes of these fruits.

Colwell (1) secured further data on these fruits. In his own words: "For each size of fruit, measurements were made of the total cross-sectional area of the fruit stalk, of its total phloem, and of its total sieve tubes. The first two values were determined by mounting a fresh cross-section of the fruit stalk in water on a slide and projecting its image onto a large piece of white cardboard at a magnification of 25 diameters by means of a micro-projector. The outline of the phloem groups and of the entire section was lightly traced on the cardboard in pencil. The traced image of the whole fruit stalk was cut out of the cardboard and weighed, after which the same thing was done for the individual phloem groups. A 100-sq. cm. area of cardboard was also weighed, permitting a calculation of the actual area represented by these groups.

"The total cross-sectional area of the sieve tubes of the fruit stalk was similarly determined by tracing all the sieve tubes from portions of phloem tissue of the fruit stalk onto white cardboard by means of camera-lucida and calculating from weights of cardboard the percentage of phloem tissue occupied by sieve tubes. The average of 10 such determinations indicated that 20.6 ± 5.2 per cent. of the total phloem is occupied by sieve tubes."

Reference here is to sieve-tube lumina. Table I includes the results of these measurements.

Knowing the dry weight increments and time periods between the size classes and having the measurements recorded in table I, rates of food transport required for the observed rates of growth may be calculated. Since the phloem exudate is not characteristic of the assimilate stream in cucurbits (4) and since there is no other basis on which to calculate concentrations more rationally, rates are given in terms of the total volume of sieve-tube lumina that would be occupied by the increment of dry weight being moved per unit of time. Because the sieve tubes are obviously never filled with dry food materials, these values must be multiplied by some factor representing the proportion of the sieve-tube-lumina volume occupied by foods in transport. Table II presents the data and calculations.

TABLE I

CROSS-SECTIONAL AREAS OF TOTAL PHLOEM AND OF SIEVE TUBES IN SINGLE FRUIT STALKS OF CONNECTICUT FIELD PUMPKIN (COLWELL'S DATA)

	FRUIT SIZE (ARBITRARY)				
	1	2	3*	4	5
Average fresh weight, grams	40	450	1,600	6,000	10,000
Total cross-sectional area of fruit stalk, sq. cm.	2.40	4.81	3.46	4.88	5.00
Total cross-sectional area of phloem groups, sq. cm.	0.125	0.154	0.128	0.255	0.499
Total cross-sectional area of sieve-tube lumina, sq. cm.	0.025	0.031	0.026	0.051	0.100

* The fruit stalk used for size 3 was small for the size class; the other values seem typical.

Judging from these calculations of COLWELL's data, the fruits studied grew rapidly and food transport must have proceeded at speeds difficult to conceive in view of the known structure of the phloem. For instance, during growth from size 1 to 5, foods moving by mass flow as a 20 per cent. solution would have to traverse the sieve tubes at a linear rate of around 80 cm. per hour; as a 10 per cent. solution, at 160 cm. per hour. If the foods move by diffusion on or along the parietal protoplasmic layer and through the sieve pores via the protoplasmic strands that traverse them, the rates would necessarily lie between 800 and 1600 cm. per hour.

To obtain more reliable data on growth rates and food transport, fruits of Connecticut Field pumpkin and Early Prolific Straightneck summer squash were measured while small, then marked and remeasured at intervals during the summer of 1942 by the writers. Finally they were harvested and weighed, and the areas of phloem in the fruit stalks were measured by the method described above. Table III presents the resulting data.

TABLE II

CALCULATED RATES OF FOOD TRANSPORT THROUGH THE SIEVE TUBES OF CONNECTICUT FIELD PUMPKIN (COLWELL'S DATA. CALCULATIONS BY THE WRITERS)

GROWTH PERIOD—FROM	SIZE 1 TO 2	SIZE 2 TO 3	SIZE 3 TO 4	SIZE 4 TO 5	SIZE 1 TO 5
Length of growth period, hours	96.0	120.0	168.0	288.0	672.0
Total dry weight increment, grams	22.8	65.5	287.0	432.0	807.3
Dry weight increment, grams per hour	0.237	0.546	1.71	1.50	1.20
Dry weight increment ml. per hour*	0.158	0.364	1.14	1.00	0.80
Average area of sieve-tube lumina, sq. cm.	0.028	0.026	0.036	0.075	0.050
Linear rate of displacement, cm. per hour	5.64	14.00	31.67	13.33	16.00

* Based on the assumpton that the average specific gravity of the pure dry food materials is 1.5.

In order to use the values in table III for calculating rates, one must establish the relation between the linear dimensions of the fruits and their

TABLE III

DIMENSIONS, FRESH WEIGHT, AND FRUIT-STALK PHLOEM AREA OF CONNECTICUT FIELD PUMPKINS, 1942

FRUIT NUMBER	AUGUST 5		AUGUST 25		SEPTEMBER 7, HARVESTED				
	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH	WEIGHT	PEDUNCLE AREA	PHLOEM AREA
	cm.	*cm.*	*cm.*	*cm.*	*cm.*	*cm.*	*kgm.*	*sq. cm.*	*sq. cm.*
1	5.3	4.8	17	21	17	22	2.61	1.52	0.129
2	2.6	2.4	......	......	19	25	3.96	2.28	0.266
3	5.1	4.2	22	24	24	26	5.88	1.69	0.142
4	2.9	2.3	......	......	21	24	4.07	2.79	0.279
5	5.0	4.5	24	28	25	37	7.84	2.58	0.246
6	11.4	10.1	28	29	28	30	8.17	2.44	0.358
7	10.4	9.8	19	23	21	27	4.99	1.95	0.231
8	2.8	2.3	20	27	22	28	6.68	1.52	0.097
9	3.5	3.1	21	25	21	25	4.54	2.02	0.149
10	2.9	2.4	......	......	36	38	7.49	2.30	0.218
11	2.2	2.1	......	......	24	34	9.85	2.66	0.159
12	3.4	2.7	......	......	15	16	1.59	1.61	0.124
13	4.2	3.3	16	17	16	17	1.70	1.87	0.226
14	6.3	5.5	......	......	23	33	8.51	1.84	0.137
15	3.6	2.7	......	......	34	32	4.76	1.72	0.089
16	6.9	5.8	25	29	26	29	7.93	2.66	0.289
17	2.6	2.3	21	20	25	27	6.90	1.81	0.113
18	5.2	3.6	23	23	24	23	4.65	3.07	0.227
19	3.6	2.5	28	26	34	30	9.75	2.19	0.187
20	5.4	5.1	22	28	22	29	5.90	2.11	0.143
21	5.3	4.9	19	23	19	24	3.63	1.56	0.161
22	2.0	2.0	19	22	20	26	4.31	1.22	0.080
23	4.8	4.8	14	19	16	22	3.17	1.57	0.122
24	6.0	5.7	......	......	21	29	6.80	1.80	0.306
25	6.8	6.8	20	29	21	29	6.35	1.84	0.186
26	6.2	6.1	20	27	21	30	6.68	1.99	0.163
27	3.6	3.4	......	......	19	25	3.85	1.67	0.143
28	5.7	4.3	......	......	28	30	7.93	2.36	0.159
29	3.9	3.4	......	......	21	24	4.08	1.39	0.154
30	6.0	5.5	......	......	18	23	3.40	1.44	0.167
31	6.2	5.7	19	24	21	25	5.89	2.36	0.292
32	7.6	7.0	24	32	26	33	7.48	1.75	0.153
33	6.8	6.1	19	25	20	27	4.65	1.53	0.188
34	5.1	4.3	20	24	20	27	5.10	1.48	0.150
35	5.4	5.4	......	......	11	15	1.13	1.36	0.118
36	5.9	5.7	......	......	20	27	5.21	3.09	0.359
37	2.5	2.4	......	......	21	29	6.12	2.24	0.173
38	4.3	3.0	......	......	30	36	7.02	3.33	0.150
39	4.7	3.4	......	......	31	28	9.30	2.42	0.216
Total	194.1	171.4	460.0	545.0	881.0	1061.0	219.87	79.03	7.249
Average	4.98	4.40	20.9	24.8	22.6	27.2	5.64	2.03	0.186

fresh weights. For this purpose 28 small fruits of Connecticut Field pumpkin, covering the range in size represented by the August 5 measurements in table III, were measured and weighed.

Some of these small fruits were spherical; others somewhat cylindrical with hemispherical ends. Their approximate volumes can be calculated by the following formula:

$$V = 4/3\pi r^3 + \pi r^2 \ (l - d) \qquad (1)$$

where V = volume
r = radius
l = length
d = diameter

By use of this formula approximate volumes of the 28 fruits were calculated and a graph drawn representing the relation between volume and weight. Employing this graph and using approximate volumes calculated from linear dimensions one may determine the weight of any fruit, the dimensions of which come within the limits of those used in making the graph.

Fruit volumes so calculated have proved to be somewhat higher than actual volumes, measured by displacement. Since, however, the calculated volume is used only as a function of the linear dimensions and not in the determination of rates, the errors tend to compensate and they affect the rate values little, if any.

From table III, the fruits measured on August 5 averaged 4.98 cm. in length and 4.40 cm. in diameter. The average volume was 53.5 ml. Checking this volume against the curve mentioned above, the average fruit weighed about 51.5 gm. at the time of marking. The average weight at harvest time was $219.87 \div 39 \times 1000 = 5637.7$ gm. The gain therefore was $5637.7 - 51.5$ or 5586.2 gm. in the 33-day growth period. At the time of collecting, the average transverse phloem area was 0.186 sq. cm. per fruit stalk.

The fruits of table III were at about the same stage of maturity on September 7 as those reported to be size 4 in table V of our previous paper (**4**). On an average, they were somewhat smaller because they had undergone no selection, whereas those mentioned in table V had been selected for uniformity at a definite size.

Fruits of size 4 [table V (**4**)], had a dry-weight composition of 8.65 per cent. Applying this figure to the average fresh-weight increment, the average dry weight should have been 5586.2×0.0865, or 482 gm. This weight divided by 792, the number of hours in the growth period, gives the average hourly dry weight increment that moved into these fruits. This value, 0.61 gm., is the average amount of dry material that moved into the fruit each hour between August 5 and September 7. Based on a specific gravity of 1.5, this hourly dry weight increment would occupy 0.41 ml.

According to several studies (**1, 2, 3, 6**), an average value for the proportion of the total phloem occupied by the sieve-tube lumina is 20 per cent. Using this figure, the average phloem value for the peduncles of fruits of table III would be $0.186 \times 0.2 = 0.0372$ sq. cm. Dividing this area into the volume representing the hourly dry increment of food transported into the pumpkin fruits, the linear displacement rate would be $0.41 \div 0.0372$, or 11.0 cm. per hour. This is reasonably close to the value of 16.0 found in table II from COLWELL's data.

The value given above is an average. Calculating similar values for the three largest fruits and for the three smallest, we obtain the following values: for the largest fruits 21, 17, and 14 cm. per hour; for the three smallest 4, 3, and 3 cm. per hour.

These are, of course, lower than any possible real values: they represent rates at which pure dry food materials would have to move in order to provide for the observed rates of growth. If this food material were moving as a 20 per cent. solution, the rates would necessarily be five times the values given above; if it moved as a 10 per cent. solution, they would be ten times as great; and if it moved as individual molecules, independent of water but associated with the cytoplasm, the values must be multiplied by a factor between 50 and 100. The rates given above represent, furthermore, averages for the total growth period. According to COLWELL's data as given in table II, the rate during the most active growth period may be approximately twice the average rate for the whole period of growth. And even this rate does not take into account the diurnal fluctuations, which may be appreciable.

All the fruits reported so far were green during most of their period of growth. Photosynthesis is an unknown factor in these calculations, as is respiration. To avoid the error from photosynthesis, measurements were made on Early Prolific Straightneck squash, whose fruits are cream-colored when very young and yellow when mature. Respiration was not measured, but the error from it results in underestimation of rates rather than overestimation. Values given in the following pages are, accordingly, on the conservative side.

Following the previous experiment, fruits of Early Prolific Straightneck squash were tagged and measured periodically and were finally harvested, measured, and weighed. To evaluate the dimension measurements it was again necessary to establish the weight-volume relation. This was done by collecting 75 squashes, ranging in size from those of recently pollinated flowers to mature fruits, measuring and weighing them, and plotting volume against weight.

Thirty-six small fruits were measured and tagged on September 7, measured on September 10 and 15, and harvested on September 18, 1942. The final harvested weights were obtained directly by weighing; the others were taken from the graph mentioned above, using the volumes calculated by equation 1. Areas of fruit stalks and phloem were obtained by projecting sections and weighing the outlined areas, as described earlier.

Averages for growth during the three measured periods were obtained by subtracting the initial from the final weight values for the periods. These averages were 204.6, 477.8, and 186.8 gm. for the three periods, and 869.3 gm. for the total growth period. Dividing each by the number of days in the period, the average daily growth rates were 68.2, 95.5, and 62.2 gm. for the three periods, and 79.0 gm. for the total period.

To give a clearer view of the growth rates of the individual fruits, table IV lists the increments for the three periods measured and for the total growth period, both on the period basis and on the daily basis. Finally, it gives a series of values for rate of transport that were obtained by dividing the average daily growth increment for the total period by 24 (to put it on an hourly basis) and by the area of the sieve-tube lumina or one-fifth of the phloem area. These values represent the linear rate, in centimeters per

TABLE IV

GROWTH INCREMENTS OF EARLY PROLIFIC STRAIGHTNECK SUMMER SQUASH FOR THREE GROWTH PERIODS

	SEPT. 7–10 INCREMENT		SEPT. 10–15 INCREMENT		SEPT. 15–18 INCREMENT		TOTAL PERIOD INCREMENT		TRANSPORT RATE
	TOTAL	DAILY	TOTAL	DAILY	TOTAL	DAILY	TOTAL	DAILY	
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*	*cm./hr.*
1	248	82.8	295	59.0	23	7.8	567	51.6	186.5
2	350	116.7	208	41.6	77	25.7	635	57.7	148.5
3	346	115.5	605	121.0	67	22.3	1018	92.6	268.0
4	295	98.3	379	75.8	108	36.0	782	71.1	214.5
5	361	120.3	167	33.4	48	16.2	576	52.4	147.5
6	376	125.3	598	119.6	141	47.0	1115	101.4	306.0
7	248	82.7	368	73.6	47	15.8	663	60.3	157.5
8	144	48.0	215	43.0	32	10.7	381	34.6	85.0
9	414	104.8	624	124.8	86	28.8	1125	102.3	339.0
10	308	102.8	521	104.2	137	45.8	958	87.2	204.0
11	175	58.3	371	74.2	134	44.7	680	61.8	176.5
12	229	76.3	456	91.2	167	55.7	854	77.6	294.0
13	83	27.9	377	75.4	203	67.8	664	60.4	163.5
14	162	54.0	389	77.8	129	43.0	680	61.8	149.5
15	63	21.2	493	98.6	151	50.5	708	64.4	206.5
16	55	18.6	431	86.2	206	68.8	693	63.0	193.0
17	104	34.8	670	134.0	498	166.0	1272	115.7	238.5
18	67	22.3	519	103.8	452	150.7	1038	94.4	293.5
19	128	42.9	510	102.0	189	63.0	827	75.2	245.0
20	64	21.4	585	117.0	196	65.3	687	62.5	200.5
21	227	75.7	569	113.8	270	90.2	1066	97.0	243.5
22	194	64.7	806	161.2	228	76.2	1228	111.7	280.5
23	422	107.3	717	143.4	74	24.8	1213	110.3	377.0
24	375	125.0	415	83.0	96	32.0	886	80.5	207.0
25	348	116.1	883	176.6	117	39.0	1348	122.6	327.5
26	252	84.0	529	105.8	306	102.0	1087	98.8	260.5
27	66	22.1	384	77.0	292	97.5	743	67.6	168.0
28	140	46.9	510	102.0	283	94.5	934	84.9	203.5
29	117	39.0	589	117.8	231	77.0	937	85.2	219.0
30	108	36.0	673	134.6	424	108.2	1205	109.6	251.0
31	214	71.5	427	85.4	64	21.5	706	64.2	239.0
32	143	47.8	351	70.2	29	9.8	523	47.6	171.0
33	264	88.3	457	91.4	142	47.5	864	78.6	202.5
34	79	26.5	408	81.6	320	106.8	808	73.5	194.0
35	123	41.2	379	75.8	284	94.7	786	71.5	204.0
36	64	21.3	488	97.6	467	155.7	1019	92.6	182.0

hour, at which a solution equivalent in dry-weight concentration to the larger fruits [table III, (**4**)] must flow through the sieve-tube lumina to provide for the observed rates of growth. They range from 85.0 to 377.0 cm. and average 268.5 cm. These rates are based on a dry-weight composition of about 5 per cent. On a pure dry-weight basis this average value would be 13.4 cm. as compared with our figure of 11.0 for Connecticut Field pumpkin and COLWELL's figure of 16.0 for the same species. If this food were moving as a 10 per cent. solution, the rate would be around 130 cm. per hour. If it moved by diffusion along the protoplasm, the rate would be in the range of 650 to 1300 cm. per hour.

Discussion

Many rates of food movement in plants have been given in the literature. Since the mechanism of movement is as yet unknown, all such values are calculated or estimated by methods like those used above or by measurements on viruses, radioactive elements, fluorescent dyes, or other compounds assumed to be moving in the phloem but not serving as foods in the plant. Though chemical analyses on growing fruits provide reliable data on the daily or hourly amounts of dry weight added, the bases for transforming these to linear rates are only hypothetical: no one has yet determined whether the foods are moving through the total phloem, through the sieve-tube lumina, or along the protoplasm.

If foods move in plants by a mass flow of solution, the rate values found in this work must all be multiplied by a factor representing the quotient of the solution volume divided by the solute volume. The smallest probable value for such a quotient would be around 5, actual values might range to 10 or more. Using such factors on the rate values found, actual linear transport rates for foods in solution would lie between 55 and 160 cm. per hour for these species.

If foods move by an activated diffusion process, they must of necessity be closely associated with the cytoplasm of the sieve tubes. According to present day concepts of sieve-tube anatomy (**5**), the cytoplasm of the mature element occupies a very small portion of the space within the walls; it is a thin parietal layer lining the walls and surrounding the large central lumen. Providing this picture of sieve-tube structure is accurate, then the rate values found in this work must all be multiplied by a factor made up of the reciprocal of the proportion of the sieve tube occupied by cytoplasm times the reciprocal of the proportion of the cytoplasm occupied by food materials. Estimates of cytoplasmic volume of mature sieve tubes lie between 1 and 2 per cent. of the transverse area; it does not seem probable that foods would occupy over 20 per cent. of the cytoplasm during their movement through or along it. Such estimates indicate that the factor to be applied to the rates calculated in this work should be of the order of 100 or more. Such being the case, actual linear rates of movement must lie around or above 1000 cm. per hour during rapid transport of foods.

The above calculations are only approximate and are designed to provide some idea of the order of magnitude of transport rates required to account for growth and storage in highly active plants. Though the measurements leave much to be desired, they do provide a fairly reliable basis for arriving at approximate values for translocation rates. Enough fruits were measured to give dependable average values; measurements were taken often enough to catch the high rates that occur only for short periods; and analyses were made to show the amounts of the principal food constituents that were being moved [tables III and IV (**4**)].

The rates calculated from the measurements are obviously high, for the material used was chosen to indicate the upper limits of transport velocity. Such studies yield little evidence of the type of mechanism involved. But any mechanism proposed to account for food transport must be compatible with the observed velocities if it is to care adequately for normal growth rates in vigorous plants.

Summary

Calculations based on COLWELL's data prove that dry food materials would have to pass through the sieve-tube lumina of Connecticut Field pumpkin peduncles at an average rate of 16 cm. per hour in order to account for fruit growth. For a seven-day period the rate was over 31 cm. per hour.

Similar calculations based upon many measurements of fruit and phloem areas indicate transport rates of 11.0 and 13.4 cm. per hour for Connecticut Field pumpkin and Early Prolific Straightneck squash respectively.

Such rate values, when converted to linear displacement values for solutions, indicate movement at rates of 55 to 160 cm. per hour for transport by mass flow. By activated diffusion along the cytoplasm the above rate values indicate diffusion rates of 1000 cm. per hour or above.

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