

## COMPOSITION OF FRUITS AND PHLOEM EXUDATE OF CUCURBITS

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Phloem exudate has been used in many studies on solute transport in plants. As far as can be determined by microscopic observation, it comes from the sieve tubes and represents, therefore, an unmixed sap that moves rapidly within the plant.

If the exudate from cut peduncles of cucurbit fruits represents a true sample of a solution of food materials moving through the phloem by mass flow to nourish those fruits, there should exist a fairly constant proportionality between the various compounds present in the exudate and in the fruits. That the process of phloem exudation has been variously interpreted in the past is apparent from the following review of literature.

Since the researches of HARTIG and NÄGELI (6) it has been commonly assumed that the sieve tubes of the phloem tissue of plants are continuous elements interconnected by open pores through which substances in solution may pass more or less freely. Phloem exudation from cut cucurbit stems, described in detail by NÄGELI, was cited as confirming evidence for an open system; and many considered it a manifestation of the normal process of food transport.

ZACHARIAS and KRAUS (6), analyzing such exudate, showed that it contained sugar, organic nitrogen compounds, potassium, and phosphorus, all of which were presumably translocated in the phloem.

The works of FISCHER, STRASBURGER, and HILL (6) tended to confirm this early interpretation. The cucurbit sieve tube became the accepted type of food-conducting element, illustrated in elementary texts, and often cited as an example of adaptation of structure to function. To many botanists the structural aspects of the process of food transport in plants seemed clear.

In 1855, however, VON MOHL questioned the actual perforation of the sieve plate, contending that the middle lamella remained intact. LECOMTE described the protoplasm as penetrating into the striations of the callose plates in the form of filaments terminating at the swellings in knobs. Such structures are commonly found in the position of the middle lamella of the sieve plate. The researches of HILL, STRASBURGER, and other early workers (6) emphasized the extreme fineness of the sieve-tube connections in many plants, the gymnosperms in particular. KUHLA (16) denied the perforation of the protoplasmic connection of the sieve plate, and since then others have shared his view (6, 9, 26, 27).

If the sieve tubes are not perforate elements through which ready mass flow of solutions can take place, how are foods transported in plants? BIRCH-HIRSCHFELD (1), DIXON and BALL (12), and MASON and LEWIN (18) concluded that they move through the xylem. Later, DIXON (11) and

MASON (19) changed their views. In 1931, CRAFTS proposed that foods move through the highly hydrated wall of the phloem (5); in 1932 and 1936 (6, 7), reversing this opinion, he suggested that the sieve-tube protoplasm of the mature element is permeable, allowing the foods to move readily in solution along phloem strands.

In 1936, MASON and PHILLIS (21) confirmed the early analyses on phloem exudate from cucurbits, but retained MASON and MASKELL's interpretation (20) that food materials move by "activated diffusion" independent of the solvent.

In such a controversial field, what rôle can be assigned to phloem exudation, and of what value are studies on that subject? NÄGELI, FISCHER, LECOMTE, and STRASBURGER (6) had all regarded the conduction of slime—that is, the more proteinaceous food constituents—as a normal function of sieve tubes. In 1931, 1932, and 1936 CRAFTS experimented with phloem exudation from cucurbits (5, 6, 7). Though he recognized that the initial rate of outflow might be as high as ten times the normal rate, he maintained that phloem exudation was a manifestation of the normal process of food movement and that the exudate was a true sample of the solution of foods moving in the phloem.

In 1937, MASON and PHILLIS (22) questioned the complete permeability of the mature sieve tube, casting doubt on the mass-flow mechanism. Meanwhile, studies on phloem exudate from forest trees by PFEIFFER (24) and by HUBER, SCHMIDT, and JAHNEL (15) clearly pictured the concentration of solutes in this material; also the diurnal fluctuations in concentration resulting from changes in the processes of carbon assimilation. In a way, these changes followed the diurnal changes in sugar concentration found in the bark of cotton by MASON and MASKELL (19).

HUBER and ROUSCHAL (14) confirmed CRAFTS' observations on sieve-tube permeability, while the latter (8) suggested a newer technic for demonstrating phloem exudation in many plant species.

Thus, though workers in the field were still lacking agreement on the mechanism of phloem transport, evidence that seemed to support the mass-flow theory was rapidly accumulating. While STEWARD and PRIESTLEY (28) concluded that phloem exudation was of local origin and was due to turgor pressure or tissue tensions, and while CURTIS (10) considered it strictly abnormal, they provided no experimental proof for their contentions.

CLEMENTS (2) studying the growth and composition of the fruits of the sausage tree (*Kigelia africana*), deduced that the mass-flow mechanism was inadequate in this plant. His conclusions are weakened by several unwarranted assumptions: namely, that all water in the phloem is mobile; that a sugar analysis of the total phloem reveals the sugar content of the sieve tubes; and that because fruits are young, the sieve tubes leading into them are immature and therefore in a high state of metabolic activity. His work implies, nevertheless, that there should be a certain agreement between the composition of a growing structure and the solution moving in to nourish

its tissues. That such an agreement fails with respect to the composition of fruits and phloem exudate from cucurbits is evident from the work of COOL (4).

COLWELL (3) found no agreement between the composition of the fruits and exudate from peduncles of Connecticut Field pumpkin with respect to carbon and nitrogen. He found that the C/N ratio of the exudate varied from 3.7 to 4.4; while the ratio in the fruit varied from 7.5 in very young to as high as 18.5 in more mature fruits. In general, the C/N ratio averaged about three times higher in the fruit than in the exudate from peduncles supplying the fruit. As both the exudate and fruit approached a value of about 3 per cent. carbon on the basis of fresh weight, the disproportionality in the C/N ratio resulted from the much lower nitrogen content of the fruit than of the exudate. In other analyses, COLWELL found the exudate to be higher in dry weight than the fruit. Reducing sugars and total sugars were three to four times higher in the fruit than in the exudate. He was able to account for practically all of the carbon of the exudate as existing in the form of protein compounds and sugars.

The experimental work of this paper is concerned with further testing the proportionality between carbon and nitrogen compounds of the exudate and fruits of two cucurbit species.

### Methods

Two varieties of *Cucurbita pepo* were used: Connecticut Field pumpkin because of its vigorous growth, copious exudate, and because COLWELL's previous studies had been made upon it; and Early Prolific Straightneck summer squash because of rapid growth, uniform shape, and yellow color, apparently containing no chlorophyll.

The exudate was collected in the morning. Successive cuts from the stem tip or the peduncle were made until 3 to 10 milliliters of the exudate had been collected. Successive cuttings were necessary because only a few drops could be collected from any one cut, owing to the tendency of the exudate to coagulate. Ten or more stem tips or peduncles were used as a composite in obtaining material for any one sample. The exudate was collected in glass vials. Since it tended to coagulate on standing, it was usually dried, and analyses were then made on the dried material. Nitrogen was determined by the Kjeldahl method. Insoluble nitrogen was designated as that fraction insoluble in boiling 80 per cent. alcohol. Carbon was determined by the wet combustion described by MCCREARY and HASSID (17). In ashing, the samples were ignited at 450° C. for 48 hours. For the dry weights the samples were dried in a forced-draft oven at 70° C. for 48 hours. Sugars were determined by the ceric sulphate method described by HASSID (13). Except for some of the dry weights and ash, all determinations were made in triplicate.

### Results

The data presented in table I show the changes in carbon, nitrogen, and ash content of the exudates over a period of time. Successive cuts were made

TABLE I

NITROGEN, CARBON, AND ASH CONTENT OF PHLOEM EXUDATE FROM SUCCESSIVE CUTS OF THE SAME CONNECTICUT FIELD PUMPKIN STEMS; EXUDATE COLLECTED FROM STEM TIPS AUG. 25, 1942

CUTS*	TIME OF COLLECTION	PERCENTAGE OF DRY WEIGHT			C/N	DRY WEIGHT AS PERCENTAGE OF FRESH
		C	N	ASH		
		%	%	%		%
1-3	8:00-8:30 A.M.	59.03	16.22	7.49	3.63	6.81
4-7	8:30-9:00	45.85	14.73	7.86	3.11	7.28
8-12	9:00-9:30	46.36	13.84	8.80	3.35	6.32
13-18	9:40-10:35	40.05	11.50	9.06	3.48	6.58
19-24	10:40-11:10	40.05	11.73	8.97	3.41	5.93
25-44	11:15 A.M.-12:25 P.M.	32.77	11.39	7.98	2.88	6.18

\* Cuts 1-7 were made in 5-mm. sections, while for the remaining sections the cuts were of 2-mm. sections.

from the same stem tips until about 5 milliliters of exudate had been collected. The first column in the table shows the number of cuts made in obtaining the samples; the second column, the time consumed in gathering the exudate. Carbon concentration tended to decrease with time. The first sample, taken from 8 to 8:30 A.M., was considerably higher in carbon than the last sample, taken from 11:15 A.M. to 12:25 P.M. Nitrogen content showed a marked decrease in the samples taken at the intervals between 8:00 and 10:35 A.M. and apparently reached a constant value after that time. The C/N ratio was approximately constant except in the last collection, where the ratio was lower. The ash content remained almost constant.

Table II presents further evidence that there was no great change in carbon and nitrogen composition of the exudate collected over a period of time. In this instance a comparison was made between the composition of the first and second drops of exudate from the same stem tips. Individual first and second drops from each stem tip were collected and composited until about 5 milliliters of sap were available for analysis. There was a small increase in carbon content of the second drop of exudate as compared with the first drop; but no difference in the nitrogen content. The C/N ratio was approximately the same for both the first and second drops of exudate.

Efforts were made to determine the relation existing between the nitro-

TABLE II

CARBON AND NITROGEN CONTENT OF FIRST AND SECOND DROPS OF EXUDATE OF CONNECTICUT FIELD PUMPKIN; EXUDATE FROM STEM TIPS COLLECTED 1-3 P.M., AUG. 21, 1942

DROP TESTED	PERCENTAGE OF FRESH WEIGHT		C/N
	C	N	
	%	%	
First .....	7.38	2.61	2.83
Second .....	8.14	2.53	3.22

gen, carbon, and ash content of the fruit and the similar content of the exudate from peduncles of these same fruits. If the ratio of these constituents was the same in the exudate as in the fruit, one might conclude that the constituents observed in the exudate were a true measure of what was actually moving into the fruits. These analyses were made on small-immature, medium-sized, and mature fruits of each of the two varieties. As shown by the data in table III, carbon, nitrogen, and ash in the peduncle exudate of Early Prolific Straightneck were the same regardless of the size or age of the fruit. The C/N ratio was likewise a constant value. In the fruit the carbon, nitrogen, ash, and dry weight tended to decrease slightly as the fruit became larger. The C/N ratio was approximately the same for all the various-sized fruits. This ratio in the fruits was about 14 to 1, as compared with only 3.4 to 1 in the exudate of their peduncles. In other

TABLE III

CARBON, NITROGEN, AND ASH CONTENT OF PHLOEM EXUDATE AND FRUITS OF DIFFERENT-SIZED EARLY PROLIFIC STRAIGHTNECK PUMPKINS; EXUDATE FROM PEDUNCLES COLLECTED AND FRUITS HARVESTED 8-11 A.M., SEPT. 8, 1942

FRUIT* SIZE	PHLOEM EXUDATE					FRUIT				
	PERCENTAGE OF DRY WEIGHT			C/N	DRY WEIGHT AS PERCENTAGE OF FRESH	PERCENTAGE OF DRY WEIGHT			C/N	DRY WEIGHT AS PERCENTAGE OF FRESH
	C	N	ASH			C	N	ASH		
	%	%	%		%	%	%	%	%	%
1	44.69	13.21	9.70	3.38	9.40	42.71	3.50	10.95	12.20	6.90
2	44.07	13.13	8.74	3.36	9.70	38.49	2.46	10.07	15.65	5.51
3	44.30	13.19	9.07	3.36	10.54	36.92	2.62	10.09	14.09	5.12

\* Description of fruit sizes:

Size 1: Length 10.15 cm.; greatest diameter 2.66 cm.; weight 42.66 gm.; average of 44 fruits.

Size 2: Length 21.29 cm.; greatest diameter 5.72 cm.; weight 343.55 gm.; average of 19 fruits.

Size 3: Length 27.04 cm.; greatest diameter 7.64 cm.; weight 893.63 gm.; average of 12 fruits.

words, the C/N ratio in fruits was over three times as high as that found in the exudate.

As table IV shows, the results obtained with the Connecticut Field variety resembled those obtained with Early Prolific Straightneck. The carbon, nitrogen, and ash content of the exudate revealed no consistent differences between the fruits of different sizes or ages. The C/N ratio approached a constant in the exudate from all the fruit sizes. In the various-sized fruits the carbon content was relatively constant, whereas the nitrogen content fluctuated. There were indications of a decrease in nitrogen content as the fruits enlarged. In the young fruits the total nitrogen content was considerably higher than in any of the others. Differences between the ratios in the exudate and in the fruits were highly significant. The ratio

TABLE IV

CARBON, NITROGEN, AND ASH CONTENT OF PHLOEM EXUDATE AND FRUITS OF DIFFERENT-SIZED CONNECTICUT FIELD PUMPKINS; FRUITS HARVESTED AUG. 28, 1942; PHLOEM EXUDATE FROM PEDUNCLES COLLECTED AUG. 31, 1942

FRUIT* SIZE	PHLOEM EXUDATE†					FRUIT‡				
	PERCENTAGE OF DRY WEIGHT			C/N	DRY WEIGHT AS PERCENTAGE OF FRESH	PERCENTAGE OF DRY WEIGHT			C/N	DRY WEIGHT AS PERCENTAGE OF FRESH
	C	N	ASH			C	N	ASH		
	%	%	%		%	%	%	%		%
1	38.82	11.32	.....	3.43	.....	47.43	3.09	8.87	15.3	6.71
2	43.65	12.62	6.77	3.46	9.43	38.79	2.39	6.72	16.2	5.81
3	50.24	13.84	6.96	3.63	11.32	40.70	1.79	6.82	22.7	6.75
4	46.46	12.18	7.55	3.81	10.46	45.41	2.11	7.71	21.5	8.63

\* Description of fruit sizes:

Size 1: Diameter 7.8 cm.; weight 272 gm.; collected a day or two after pollination.

Size 2: Diameter 18.1 cm.; weight 2473 gm.

Size 3: Diameter 25.3 cm.; weight 5255 gm.; fruits still of green color.

Size 4: Diameter 29.2 cm.; weight 8816 gm.; fruits of yellow color.

† Average of 10 or more fruits each.

‡ Average of three each.

in the exudate averaged about 3.6 for all the different-sized fruits, as compared with 18.9 in the fruits.

Table V gives more complete information regarding the constituents present in the exudate. On the dry-weight basis the exudate of Connecticut Field pumpkin contained 41.5 per cent. carbon, 11.50 per cent. total nitrogen, 6.42 per cent. insoluble nitrogen, 2.55 per cent. reducing sugars, 0.79 per cent. sucrose, and 3.34 per cent. total sugar. The exudate of Early Prolific Straightneck was slightly higher in carbon, total nitrogen, reducing sugars, and total sugars. In both varieties the insoluble form of nitrogen

TABLE V

CARBON, NITROGEN, SUGAR, AND ASH CONTENT OF PHLOEM EXUDATE FROM CONNECTICUT FIELD\* AND EARLY PROLIFIC STRAIGHTNECK PUMPKINS; EXUDATE FROM PEDUNCLES OF CONNECTICUT FIELD COLLECTED 8-12 A.M. ON SEPT. 10, 1942, AND FROM EARLY PROLIFIC STRAIGHTNECK 8-12 A.M. ON SEPT. 22, 1942

VARIETY	PERCENTAGE OF DRY WEIGHT							C/N	DRY WEIGHT AS PERCENTAGE OF FRESH
	C	TOTAL N	INSOLUBLE N	REDUCING SUBSTANCES AS GLUCOSE	SUCROSE	TOTAL SUGARS	ASH		
	%	%	%	%	%	%	%		%
Connecticut Field .....	41.46	11.50	6.42	2.55	0.79	3.34	7.49	3.60	11.35
Early Prolific Straightneck	52.92	13.20	6.32	4.61	0.58	5.19	7.66	4.01	8.65

\* The Connecticut Field pumpkin exudate had a freezing-point depression of 0.74° C. and a refractometer reading of 12.2.

accounted for about half of the total nitrogen. The carbon present in the form of sugars accounted for only about 3 per cent. of the total carbon present, leaving much carbon to be associated with nitrogen in the form of proteins or other compounds.

### Discussion

As has long been recognized, the exudate of cucurbits is a slimy coagulable material that gives typical protein reactions with microchemical reagents. The possibility of very high protein composition of the exudate is manifest in data from table VI. Here an attempt has been made to show the relation between the carbon present and the protein content. The nitrogen of the exudate of the two varieties was converted to protein by the conventional factor, and the possible carbon content of the protein

TABLE VI

CARBON CONTENT OF EXUDATE BY ANALYSIS AND BY CALCULATION. RESULTS GIVEN AS PERCENTAGE OF DRY WEIGHT

VARIETY AND FRUIT SIZE	CARBON CALCULATED FROM PROTEINS*	CARBON DETERMINED IN SUGARS	TOTAL CARBON	
			CALCULATED FROM PRO- TEINS AND SUGARS	DETERMINED
	%	%	%	%
Connecticut Field				
Size 1 .....	37.4	1.4	38.8	38.8
2 .....	41.8	1.4	42.8	43.6
3 .....	45.8	1.4	47.2	50.2
4 .....	40.3	1.4	41.7	46.4
Early Prolific				
Size 1 .....	43.7	2.1	45.8	44.7
2 .....	43.5	2.1	45.6	44.1
3 .....	43.6	2.1	45.7	44.3

\*  $N \times 6.25 = \text{protein} \times 0.53 = C$ .

calculated by the average value of 53 per cent. as suggested by PLIMMER (25). The carbon content as thus calculated, in addition to the carbon present in the form of sugars, has proved to be very nearly equal to the actual carbon observed. In the Early Prolific variety the value is even slightly higher than the observed, suggesting that the proteins present contain an average value of about 51 per cent. carbon. COLWELL (3) found essentially the same relation in his work on Connecticut Field pumpkin.

There is no ready way of explaining why over three times as much carbon per unit of nitrogen was found in the fruit as in the exudate. The more evident possibility is that materials were moving into the fruit by independent diffusion. As determined by COLWELL, this situation would necessitate the diffusion of sugars into the fruit at more than three times the rate of nitrogen compounds, even though the latter are several times as concentrated in the sieve tubes and even though the sugar gradient is in the wrong direction.

If mass flow is operative, there are several possibilities. Since some water from the xylem would be required over and above that delivered by the phloem, possibly the excess carbon might enter in this way. Xylem sap of cucurbits is known, however, to be extremely dilute (7) and analyses have indicated that it contains more nitrogen than carbon.

On the basis of the dry-weight measurements the apparent difference in the C/N ratio of about 13:1 in the exudate and 3:1 in the fruit results from differences in the nitrogen content, since the carbon content of the exudate was not much different from that of the fruit (tables III and IV). In the Connecticut Field pumpkin some carbon may have been provided by photosynthesis of the fruits, which are very green at first and turn yellow on ripening; but such could not have been the case with the Early Prolific variety, which is yellow and lacks chlorophyll.

The data presented disregards the effect of respiration on the carbon content of the fruit. This carbon loss, however, would tend to make the C/N ratio of the fruit narrower than the ratio of the exudate; correction for such loss would tend to increase the discrepancy rather than eliminate it.

If mass flow is operative and if the end walls of the sieve tubes with their parietal protoplasm act as filters, as the formation of particulate slime plugs would indicate (8), the proteinaceous compounds in the phloem might be restrained, the sugars or other carbonaceous compounds might pass more freely just as fine particles pass a filter more rapidly than coarse ones. A sample of sieve-tube sap might represent the composition of the contents without giving an index to the rates at which the various constituents are delivered. And if, when the phloem was cut, the sieve plates of many elements were disrupted by the rapid flow of contents, then the first sap to exude would represent a more reliable sample of sieve-tube contents; whereas later samples, collected after the gradient of flow had lowered, with no disruption of sieve plates, would reflect the rates of delivery, but not the composition of the sieve tubes. In other words, the first drop or two might approximate in composition the sieve-tube content, whereas the later collections would approach the composition of the fruits. This does not seem to be the case; actual measurements between the first and second drops of exudate, although in the direction expected by this possible theory, indicated little if any significant difference in composition. A similar conclusion emerges from comparative data on successive collections from the same stem.

Apparently the discrepancy in C/N ratio between phloem exudate and fruit of cucurbits cannot be explained by forcing through the sieve plates of highly proteinaceous vacuolar contents as a result of cutting. If such were the action, the ratio of succeeding samples should broaden radically as the pressure is relieved and as the flow approaches that of normal phloem transport. The ratio was found either to remain constant or to change only slightly in the exudate collected from successive cuts from the same stem.

Just as clearly, the discrepancy in C/N ratio cannot result from the emptying of cut cells; the volume is entirely too great from a single cut



to have come from the sieve tubes that are opened (6, 7), and microscopic examination proves that the tubes are not empty after cutting. Nor can the discrepancy be caused by photosynthesis, for the fruits of Early Prolific Straightneck contain little or no chlorophyll.

One further possibility is that the ectocyclic, entocyclic, and commissural sieve tubes of the cucurbit stem constitute a latex system and that the latex varies in composition from the phloem exudate sufficiently to account for the difference. Latex flows much more rapidly from tubes of a given size than does phloem exudate; if the latex were high in protein in comparison with exudate, it might come from a cut fast enough to provide the excess nitrogen of the samples that were collected and analysed.

Several arguments oppose this view. According to careful anatomical studies by FISCHER, STRASBURGER, and CRAFTS (6), and others, though this cortical sieve-tube system differs from that of the main vascular bundles in both structure and content, the specialized elements are true sieve tubes with typical sieve plates, and not latex vessels.

When a latex system is cut, it usually flows for a longer period than does the cut phloem. If this occurred, and if the latex were higher in nitrogen than phloem exudate, the C/N ratio of successive samples should narrow. In the one case, where successive drops were analysed (table II), the C/N ratio of the second was broader than that of the first. In the results reported in table I, where a significant narrowing might have been expected between the first and succeeding samples, there is no major difference—except possibly in the last sample, where it would have no significance for the situation under examination.

With these various possibilities eliminated, what explanation remains for phloem exudation in the cucurbits? There seems little chance that the exudation can be a manifestation of normal food movement. Rather, it appears to result from some secretory process in the phloem. By this process, apparently, a large amount of proteinaceous material is emptied into the sieve tubes, whence, by following the channel of least resistance, it flows to the cut surface.

And what bearing has this situation on the mode of normal food transport? Because of the constancy of C/N ratio of the exudate cited above, and because the exudate contains largely proteinaceous material, whereas the particulate contents of the sieve tubes remain filtered out behind the sieve plates, it seems evident still that the sieve tubes constitute a permeable system through which liquid may flow rapidly. Further than this, the phloem exudation from cucurbits can have little significance, for the composition of the exudate and the rate of flow seem unrelated to normal processes of food movement.

And of what significance is phloem exudation to the protoplasmic and mass flow theories of phloem function? It is of little import to either, for it provides no positive evidence. It suggests either that materials do not move into the fruit by a unidirectional mass flow, or that phloem exudate

is not a true sample of substances actually moving in the phloem. It does, however, emphasize that cucurbits may constitute a special group of plants with respect to both structure and function of their phloem. Obviously they should no longer be used as type material for teaching phloem anatomy. In fact, all plants exhibiting excessive exudation from the phloem should be viewed with suspicion, since sieve-tube structure and calculated transport both indicate that these rapid movements are not necessary nor normal in most plants.

Some physiologists may consider the evidence presented by these studies to be damaging enough to justify abandonment of the mass-flow hypothesis. Judging, however, from the work of MOOSE (23) and that of HUBER and his associates (14), phloem exudate from many species is relatively high in sugars and might therefore be a true sample of the assimilate stream of these species. Furthermore, as indicated above, COLWELL (3) pointed out that the concentration relations of exudate and fruit of cucurbits do not support a diffusional mechanism. These studies indicate the need for chemical analyses of unmixed tissue saps and extracts, in contrast to the mass analyses of whole stem or root regions as commonly practiced in the past.

### Summary

The nitrogen content of the phloem exudate of Connecticut Field pumpkin and Early Prolific Straightneck summer squash is much higher than is the nitrogen content of their fruits; the carbon contents are essentially the same. Thus the carbon/nitrogen ratio of the exudate is consistently lower than is that of the fruits. Furthermore, this ratio does not change significantly between the first and second drops of exudate nor between successive exudate samples collected by repeatedly cutting the same stems. It is concluded that phloem exudate from cucurbits can no longer be considered a true sample of the assimilate stream.

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