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Why Do Sugars Taste Good?

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RAMIREZ, I. *Why do sugars taste good?* NEUROSCI BIOBEHAV REV **14**(2) 125–134, 1990.—The preference humans and animals show for sweet solutions has been the subject of hundreds of publications. Nevertheless, the evolutionary origin of sweet preference remains enigmatic because of the relatively low nutritional value of sugars and the absence of specific tastes for other, more essential, nutrients. Moderate concentrations of sugars are found in most plant foods because sugars play an important role in plant physiology. Widespread occurrence of sugars in plants is paralleled by widespread preference for sugar solutions in mammals. These observations suggest that preference for sugars evolved because they are common in plants and easy to detect rather than because of any special nutritional merits they offer. Perception of sweetness cannot be used to accurately meter the metabolizable energy or nutritive value of a food.

Evolution Comparative Carbohydrates Sucrose Fructose Glucose Preference

OF all the major energy sources (fats, proteins, starches, and sugars), sugar is the only one which has its own taste receptor system in humans. Starch is an equally important source of carbohydrate calories, yet starch is tasteless to humans. Similarly, there is no specific taste and no generalized preference for many essential minerals and vitamins. Many other species also act as if sugar solutions tasted good to them, although they may be able to taste other kinds of macronutrients as well (82).

A Darwinian outlook would lead one to expect that innate preferences should enhance the reproductive success, well-being or survival of organisms. Yet sugars are the least essential of all nutrients. Sugars contain less than or no more energy per gram than starch, protein, and fat (67). Indeed, osmotic factors make sugars retain water, causing sweet foods to have even fewer calories per gram. Elevated osmotic pressure in the gastrointestinal tract after meals containing sugars (47), can be stressful (38). In the laboratory, ingestion of high-sugar diets has many adverse health effects in animals (impaired glucose tolerance, increased cholesterol, hypertriglyceridemia, hypertension, etc.) (33). Excessive appetite for sweets can result in protein malnutrition (71) since the sweetest foods in nature (fruits, phloem, nectar, honey) are low in protein. There are no known advantages of sugars to offset these disadvantages.

This paper proposes that preference for sweet taste evolved in many animals because sugars are present in most plants and easy to detect, rather than because of any nutritional advantage they possess.

PREVIOUS VIEWS

The most commonly articulated explanation for sweet preference involves energy, e.g., "The sensitivity to sweet is biologically adaptive; it aids in recognition and selection of carbohydrates that are necessary as a source of energy." (94). This view seems to be widely held despite the paucity of evidence supporting it [see the Discussion section at the end of (13,83)].

A further refinement to this line of reasoning is the idea that taste preferences reflect the nature of the foods eaten by each species. Thus, "Each species has a sense of taste which was apparently evolved complementary to its survival. Unlike other physiological systems, which tend to have a universal functional character, diverse taste characteristics are encountered in closely related species or individuals" (58). Reasoning along these lines, Rozin has speculated that humans owe their "sweet tooth" to fruit-eating ancestors (80).

WAYS TO STUDY THE PROBLEM

It is proposed that there are four methods that may be used to understand the origin of sugar preference: 1) comparative, relating sugar preference in different species to their phylogeny or niche; 2) environmental, examining where and when sugars occur in the environment; 3) functional, examining how sweet taste performs and 4) genetic, characterizing differences among individuals in response to sugars. So little attention has been given to the genetics of sweet taste that it cannot be profitably discussed at present (75, 76, 87). Data pertaining to the first three sources of evidence will be examined below.

Technical Considerations

Many techniques for assessing behavioral response to sugars have been developed but they may be divided into four basic types; solution preference, solution acceptance, operant conditioning and introspection. Preference tests, in which animals are offered a choice of plain water and a sweet solution, is the most common technique. Acceptance tests measure intake when no choice is offered. Operant techniques examine how hard an animal will work for a chance to consume a solution. In introspective studies, human beings are usually tested by asking them to report how sweet or pleasant a solution tastes.

There is no way of knowing whether the subjective experience of sweetness is the same in animals and humans, therefore sweet taste is operationally defined as the taste of sugars. It is important

TABLE 1

COMPARATIVE STUDIES OF SUGAR PREFERENCE AND ACCEPTABILITY

Species	Sugar	Threshold	Acceptance	Reference
Armadillo *(Dasypus novemcinctus)*	Sucrose		0	(69)
Black-tailed deer *(Odocoilus hemionus)*	Sucrose	0.24%	+	(21)
	Glucose	0.53%	+	(21)
Bonnet macaque *(Macaca radiata)*	Sucrose	1.7%	+	(88)
Cat *(Felis catus)*	Sucrose	8.5%	+	(3)
			0	(5,17)
	Glucose		0	(5)
	Fructose		0	(5)
Cattle	Sucrose	0.85%	+	(19,35)
	Glucose	1.11%	+	(8)
Cotton rat *(Sigmodon hispidus)*	Sucrose	1.7%	+	(72)
	Glucose	0.9%	+	(72)
	Fructose	0.9%	+	(72)
Deer mice *(Peromyscus maniculatus)*	Sucrose	1.7%	+	(44)
	Glucose	0.09%*	+	(44,90)
	Fructose	0.09%*	+	(44)
Dog	Sucrose	0.036%	+	(27,36)
	Glucose	0.018%	+	(27)
	Fructose	0.018%	+	(27)
Egyptian spiny mice *(Acomys cahirinus)*	Sucrose	0.17%*	+	(40)
	Glucose	0.9%	+	(40)
	Fructose	0.9%	+	(40)
Florida mice *(Peromyscus floridanus)*	Glucose	5%*	+	(90)
Goats	Sucrose	1.13%	+	(35)
	Glucose	0.16%	+	(7)
Greater galago *(Galago crassicaudatus)*	Sucrose	5%*	+	(28)
Guinea pig *(Cavia porcellus)*	Glucose	3.6%	+	(4)
Hamster	Sucrose	0.034%	+	(17,26)
Hedgehog *(Erinaceus europaeus)*	Sucrose	10%	+	(30)
Horse	Sucrose	2.5%	+	(77)
House musk shrew *(Suncus murinus)*	Sucrose	6.8%	+	(49)
Jaguar *(Panthera onca)*	Sucrose		0	(5)
Kangaroo rats *(Dipodomys spectabilis)*	Glucose	5%*	+	(90)
Laboratory mouse	Sucrose	0.034–3.4%	+	(37, 75, 87)
	Glucose	2.7%	+	(87)
Laboratory rabbit	Sucrose	3.4%*	+	(17,31)
Laboratory rat	Sucrose	0.035%	+	(14, 16, 26, 78)
	Glucose	0.2%	+	(79)
	Fructose	7.2%	+	(14)
Leopard *(Panthera pardus)*	Sucrose		0	(5)
Lion *(Panthera leo)*	Sucrose		0	(5)
Meadow vole *(Microtus pennsylvanicus)*	Sucrose	3.4%*	+	(65)
Mongolian gerbil	Sucrose	0.034%*	+	(26, 39, 65)
	Glucose	3.6%	+	(39)
	Fructose	0.09%	+	(39)

TABLE 1
CONTINUED

Species	Sugar	Threshold	Acceptance	Reference
Northern grasshopper mice	Sucrose	1.7%	+	(41)
(Onychomys leucogaster)	Glucose	1.8%	+	(41)
	Fructose	1.8%	+	(41)
Ord's kangaroo rats	Sucrose	0.17%	+	(43)
(Dipodomys ordii)	Glucose	18%	+	(43)
	Fructose	0.09%*	+	(43)
Pig	Sucrose	0.34%	+	(59,61)
	Glucose	0.5%*	+	(59,61)
Porcupine	Sucrose	1.4%	+	(12)
(Erethizon dorsatum)	Glucose		0	(12)
	Fructose		0	(12)
Rhesus monkeys	Sucrose	0.25%*	+	(60,68)
	Glucose	3.6%*	+	(60)
	Fructose	3.6%*	+	(60)
Sheep	Sucrose	3.8%	+	(19, 21, 35)
			0	(34)
	Glucose	2.5%	+	(21)
			0	(34)
	Fructose		0	(34)
Slow loris	Sucrose	5%*	+	(28)
(Nycticebus ocucang)				
Southern plains wood rat	Sucrose	1.7%	+	(42)
(Neotoma micropus)	Glucose	0.9%	+	(42)
	Fructose	1.8%	+	(42)
Spiny mouse	Sucrose	3.4%	+	(26)
Squirrel monkeys	Sucrose	1.7%	+	(20,88)
(Saimiri sciureus)	Glucose	1.25%*	+	(20,23)
	Fructose	1.8%	+	(20)
Tiger	Sucrose		0	(5)
(Panthera tigris)				
Virginia opossum	Sucrose	1.8%	+	(74)
(Didelphus virginiana)				
Wild guinea pig	Glucose	0.45%	+	(52)
(Cavia aperea)				

Scientific names for species are given only if provided by the references. In most cases, threshold was the lowest concentration at which the sugar solution was significantly preferred over water, or the most dilute solution animals were willing to work to consume. If insufficient data for statistical tests were provided, the criterion used was 70% preference. An asterisk indicates that this was the lowest concentration used. As discussed in the text, most values are likely to be overestimates. Thresholds in these experiments should not be equated with detection thresholds which may be lower.

+ indicates that this species preferred some solutions containing this sugar over water, or was willing to work for solutions containing this sugar.

0 indicates that this species consumed the same amount of fluid regardless of the sugar concentration. Some species consumed less of concentrated sugars than of water, but this was interpreted as an appropriate response to the satiating effects of the sugar's calories rather than true aversion.

to distinguish between the ability to detect sugars and the motivational effects of sweet taste. It is easier to understand why many animals possess the ability to detect sugars than it is to understand why some animals will work for mere sensory stimulation. Since the present discussion pertains to natural history, only sugars that are plentiful in nature will be considered. The discussion will focus on terrestrial mammals.

Concentration of sugars is usually given in molar units; this is useful for biochemical purposes but completely obscures nutritional aspects of sugars. Caloric values for a mole of a sugar vary enormously depending upon the molecular weight of the sugar. Energy content per gram of sugar is nearly independent of the chemical structure for most common sugars (67).

The concept of nutritional value refers to the ability of a food to provide the nutrients needed by a mammal. The present discussion emphasizes food energy, protein, and toxins [see (15, 50, 56)].

Comparative Aspects of Sweet Taste

Preference for sugar solutions is only somewhat related to ecological niche. Table 1 summarizes the results of studies of sugar preference and acceptability tests in different species of terrestrial mammals. Most species, except felids and insectivores,

TABLE 2

SUGAR CONTENT OF RAW FOODS

Fruits	kcal/g	Sugar	Protein	Fat	% Sugar Calories
Apples	0.59	13.3%	0.2%	0.4%	82%
Apricot	0.48	8.5%	1.4%	0.4%	64%
Apricot	0.48	8.5%	1.4%	0.4%	64%
Avocado California	1.77	0.9%	2.1%	17.3%	2%
Avocado Florida	1.12	0.9%	1.6%	8.9%	3%
Banana	0.92	15.6%	1.0%	0.5%	61%
Blackberries	0.51	5.5%	0.7%	0.4%	39%
Blueberries	0.57	7.3%	0.7%	0.4%	47%
Boysenberries	0.43	6.2%	0.9%	0.2%	52%
Cherries sour	0.46	8.1%	0.9%	0.4%	63%
Cucumber	0.13	2.3%	0.5%	0.1%	64%
Gooseberries	0.45	8.4%	0.9%	0.6%	68%
Grape American	0.63	16.4%	0.6%	0.3%	94%
Grape European	0.71	16.4%	0.7%	0.6%	83%
Grapefruit pink	0.30	6.2%	0.5%	0.1%	75%
Grapefruit white	0.33	6.2%	0.7%	0.1%	67%
Kiwifruit	0.61	10.5%	1.0%	0.4%	62%
Lemon	0.29	2.5%	1.1%	0.3%	31%
Mellon Cantaloupe	0.36	8.1%	0.9%	0.3%	82%
Melon Casaba	0.26	6.3%	1.0%	0.1%	85%
Melon Honeydew	0.35	8.7%	0.5%	0.1%	89%
Nectarines	0.49	8.5%	0.9%	0.5%	62%
Orange	0.47	8.9%	0.9%	0.1%	68%
Peach	0.43	8.7%	0.7%	0.1%	74%
Pear Bartlett	0.59	10.5%	0.4%	0.4%	64%
Pear Bosc	0.59	10.5%	0.4%	0.4%	64%
Pear D'Anjou	0.59	10.5%	0.4%	0.4%	64%
Pineapple	0.50	11.9%	0.4%	0.4%	86%
Plum Japanese	0.55	7.0%	0.8%	0.6%	46%
Plum Prune type	0.71	7.5%	0.0%	0.0%	38%
Raspberries	0.50	5.4%	0.9%	0.6%	39%
Strawberry	0.30	5.8%	0.6%	0.4%	69%
Peppers sweet	0.24	2.5%	0.9%	0.4%	37%
Pumpkin	0.26	4.4%	1.0%	0.1%	61%
Tomato red	0.20	2.8%	0.9%	0.2%	51%
Squash zucchini	0.15	2.1%	1.2%	0.1%	52%
Means	0.51	7.6%	0.8%	1.0%	60%
SE	0.05	0.7%	0.1%	0.5%	4%
Vegetables					
Alfalfa seeds sprouted	0.30	0.4%	4.0%	0.7%	5%
Beans mung sprouted	0.31	3.0%	3.0%	0.2%	35%
Broccoli	0.30	0.9%	3.0%	0.2%	11%
Cabbage celery	0.16	1.4%	1.2%	0.2%	32%
Cabbage common	0.23	3.6%	1.2%	0.2%	57%
Cabbage red	0.27	5.4%	1.4%	0.3%	72%
Cabbage savoy	0.27	2.9%	2.0%	0.1%	38%
Carrot	0.43	6.6%	1.0%	0.2%	55%
Cauliflower	0.24	2.4%	2.0%	0.2%	36%
Celery	0.15	1.0%	0.7%	0.1%	24%
Chard swiss	0.17	1.5%	1.8%	0.2%	32%
Chicory greens	0.23	2.4%	1.7%	0.3%	36%
Chicory roots	0.73	2.4%	1.4%	0.2%	12%
Endive	0.16	1.1%	1.2%	0.2%	25%
Jerusalem artichokes	0.76	2.5%	2.0%	0.0%	12%

TABLE 2

CONTINUED

Fruits	kcal/g	Sugar	Protein	Fat	% Sugar Calories
Kohlrabi	0.27	3.9%	1.7%	0.1%	52%
Leeks	0.61	3.4%	1.5%	0.3%	20%
Lettuce butterhead	0.13	1.8%	1.3%	0.2%	50%
Lettuce iceberg	0.13	1.8%	1.0%	0.2%	50%
Lettuce looseleaf	0.18	1.8%	1.3%	0.3%	36%
Lettuce romaine	0.14	2.0%	1.6%	0.2%	50%
Mushrooms	0.30	1.5%	2.1%	0.4%	18%
Onions	0.34	6.2%	1.2%	0.3%	65%
Onions young green	0.25	3.2%	1.7%	0.1%	46%
Parsley	0.30	1.1%	2.2%	0.3%	13%
Peas podded	0.42	4.6%	2.8%	0.2%	39%
Radish	0.16	2.6%	0.6%	0.5%	60%
Spinach	0.22	0.4%	2.9%	0.4%	7%
Means	0.29	2.6%	1.8%	0.2%	35%
SE	0.03	0.3%	0.2%	0.03%	4%
Nuts and Seeds					
Almonds	5.89	5.4%	19.9%	52.2%	3%
Beechnuts	5.77	4.3%	6.2%	50.0%	3%
Brazil	6.56	2.6%	14.4%	66.2%	2%
Butternuts	6.13	7.0%	24.9%	57.0%	4%
Chinese chestnuts	2.25	11.0%	4.2%	1.1%	19%
Filbert	6.32	4.3%	13.0%	62.6%	3%
Macadamia	7.01	6.2%	8.3%	73.7%	3%
Peanuts spanish	5.66	4.3%	25.7%	49.2%	3%
Pecans	6.68	4.3%	7.8%	67.7%	2%
Pistachio	5.77	6.6%	20.5%	48.4%	4%
Pumpkin	5.41	1.0%	24.6%	45.9%	1%
Sesame	5.73	1.2%	17.7%	49.7%	1%
Sunflower	5.70	3.3%	22.8%	49.6%	2%
Walnut	6.07	2.1%	24.3%	56.6%	1%
Means	5.78	4.5%	16.7%	52.1%	4%
SE	0.31	0.7%	2.1%	4.7%	1%

This summary was extracted from USDA data compiled in the Nutritionist program (73). Only foods described as raw were used. The purpose of this table is to give the reader a concrete view of the abundance of sugars in edible plant material.

respond favorably to sugar solutions. Lack of strong sugar preference in felids is understandable in light of their carnivorous habits, although this has been disputed (3). Lack of strong sugar preference in insectivores (hedgehog, armadillo, shrew) is also easy to understand. Other findings in Table 1 are not so readily intelligible. Dogs prefer sugars despite being mainly carnivorous (27). Most ruminants tested prefer sugar solutions, but preference for sugar solutions by sheep is weak and can be eliminated by feeding certain diets (19).

TABLE 3

HUMAN SUGAR RECOGNITION THRESHOLDS

Sugar	Threshold Concentration	Heat of Combustion	Energy at Threshold
Sucrose	0.54%	3.94 kcal/g	21 kcal/l
Glucose	1.25%	3.72 kcal/g	46 kcal/l
Fructose	0.47%	3.73 kcal/g	18 kcal/l

Thresholds are taken from (24), heats of combustion from (67).

Threshold values for sugar acceptance are provided in order to show that most species seem to be able to detect 3.6% or less sugar. The values given probably underestimate true sensitivity because almost none of the tests were designed to accurately determine preference thresholds. In some cases, threshold values are the lowest concentration employed (see Table 1); and in most cases, insensitive techniques or small numbers of subjects probably have inflated thresholds.

Objective criteria seem to suggest that human beings show relatively weak responses to sugars. Human beings do not recognize sucrose solutions as sweet unless the concentration is at least 0.2–0.5%; the recognition threshold for glucose may be as high as 1.25% (24). In contrast, several species (e.g., dog, hamster, mongolian gerbil, pig, etc.) reliably prefer solutions that are insipid to humans. Furthermore, North American adults commonly rank sucrose solutions as being nearly neutral in hedonic tests, although variability among individuals is substantial (9, 26, 62). As an example, Kissileff asked over 200 people to rate pleasantness of various edibles on a nine point scale (62). Ratings for distilled water, 6.1% sucrose, and apple juice were 5.0 ± 1.23, 5.1 ± 1.23, and 7.3 ± 1.47 (means ± SD). Some evidence for sugar preference may, however, be found in children (6) and Chinese adults (9). Even in these cases, lowest effective concentrations are higher than for many animals. Instead of concluding that humans do not "like" sugar solutions, it may be appropriate to assume that hedonic tests with pure sugar solutions are not appropriate for humans.

It may be concluded that preference for sugars is common but not universal in terrestrial mammals. Evidence that some species show weak preferences for pure sugars (e.g., humans) may reflect inappropriate methods for testing preference rather than true indifference. Most species of mammals can apparently detect sugar levels of a few percent but this ability bears no obvious relationship to the species' ecological niche. This pattern suggests that the ability to detect and the propensity to consume sugars is adaptive for mammals having a wide variety of feeding habits.

Sugars in the Environment

Information on the natural abundance of sugars is generally not provided in most discussions of sweet taste. This section attempts to summarize current knowledge about where sugars are found and how sugar levels in foods might correlate with nutritional value to mammals. Several specific issues to be discussed include: basic physiological considerations, actual sugar levels in foods, the nutritional value of fruits, and the relationships between sugar level and other nutrients.

Plant physiology. Sugars are normally found at low to moderate levels in plants because they are the form in which energy is produced and transported from one part of a plant to another. Sucrose is the most widely used transport sugar, although some plants employ raffinose, stachyose, verbascose, or other sugars (1, 22, 32). The abundance of glucose and fructose is probably attributable to their being the components of sucrose. These sugars are indispensable constituents of living plants. Some other carbohydrates widely employed in behavioral studies (e.g., maltose, soluble glucose polymers, lactose) seem to be rare or absent in fresh plant material. However, it has been suggested that maltose and some other soluble carbohydrates may be present in decaying vegetation (89); this possibility is intriguing in light of the ability of some animals to taste very small amounts of such compounds (82).

In addition to their basic function as intermediaries of energy metabolism, sugars also perform other functions in plants by virtue of their ability to alter the osmotic and ionic milieu in plant cells (57). For example, sugars contribute to the ability of living cells in seeds to survive desiccation (63). Thus, sugar levels in plants would be expected to vary according to the needs of plants rather than simply reflect total energy level.

The reason sweet foods usually do not have high energy density is because of the substantial osmotic pressure exerted by sugars in solution. It follows that plants will accumulate substantial amounts of carbohydrates by either retaining large amounts of water, by expending enough energy to overcome osmotic pressure (45,93), or by transforming the sugars into insoluble substances such as starch and fats.

Sugar content of foods. In order to illustrate how abundant sugars are in plants, Table 2 gives sugar content and energy density for some fruits and vegetables commonly eaten by humans (U.S.A.) in the raw state (73). It may be seen that one third of the metabolizable energy in these vegetables comes from sugar. Most fruits contain more sugar than do vegetables, although most species contain less than 10% sugar. For both of these classes of foods, the amount of metabolizable energy per gram is very low (nearly always below 1 kcal/g). The third section of Table 2 shows that nuts and seeds contain 10–20 times as much energy as fruits and vegetables but only modest amounts of sugar. Comparable values for many root vegetables and grain are not available because these are usually processed (dried, cooked, etc.) before humans eat them. However, edible roots and grain typically contain more calories per gram than the fruits and vegetables listed in Table 2 but much less sugar per calorie (46, 63, 84, 86).

Additional data on the abundance of sugars in foods was obtained from the listing of 44 fresh vegetables and legumes (excluding fruits) compiled by Shallenberger (84) and 23 raw vegetables compiled by Southgate *et al.* (86). Average sugar concentration (sucrose + glucose + fructose) in these vegetables is 2.6±0.2% and 2.6±0.3% respectively (mean±SE), remarkably close to the value for vegetables in Table 2.

It could be argued that human foods might not be representative of foods used by animals. Published values of the sugar content of plants that are not used as human food (18, 25, 29, 55–57, 91, 92) give a range of values similar to that of Table 2, although wild fruits often have higher sugar contents (55, 91, 92). Such data are not easy to summarize here because the different articles report the values in different ways (e.g., percent dry weight, percent wet weight, percent of food energy, etc.). The most serious bias in Table 2 seems to be the under-representation of high-fat fruits and high-starch foods.

Nutritional value of fruits. Clearly, the highest levels of sugars are found in fruits. One could hypothesize that sweet taste evolved to increase fruit ingestion since they provide energy, vitamins and water. There are two obstacles facing any suggestion that sweet taste evolved to stimulate fruit intake: the existence of high-fat fruits and the low protein and energy content of fruits.

Table 2 overstates the correlation between sweetness and energy in fruits because high-fat fruits are under-represented. Fruits that are high in fat are moderately common in nature and tend to be high in energy (15, 50, 55, 92). Available data [Table 2 and (50,55)] suggest that fat and sugar or carbohydrate content are probably inversely related. Some animals [e.g., gorillas (15)] appear to favor high-fat fruits, presumably because of their greater nutritional value.

Table 2 shows that fruits are low in protein. This imbalance might be enhanced by the presence of substances that interfere with protein metabolism (50). The existence of such antimetabolites has been demonstrated for birds (50); whether they affect mammals is not known. Furthermore, the energy present in fruits may not be fully available; carbohydrate malabsorption is common in humans ingesting apple, grape or pear juice (48). Although the fruits in Table 2 have a higher energy content than most vegetables, they are very low in energy compared to seeds (grain and nuts).

Izhaki and Safriel (50) have argued that seed dispersal may be maximized if birds eat some fruit and then leave. If fruits provide too good a source of nutrients, birds would remain near the fruiting plant and hence reduce seed dispersal. If this theory applies to mammals, the development of a strong appetite for sweet foods would be limited by natural selection. Nevertheless, fruits are sufficiently common in nature that they probably played some role in the evolution of sweet taste.

Sugar content and other nutrients. The hypothesis that sugar levels might be correlated with some necessary nutrient, would be appealing if any evidence could be adduced for it. Unfortunately, the only available evidence seems to support the idea that sugar content is negatively correlated with nutritional value. It has already been noted that the foods highest in sugar, fruits, are also low in protein. In some species of plants (56) annual fluctuations in sugar level are negatively correlated with protein content.

Conversely, levels of toxic compounds (phenols and tannins) are sometimes positively correlated with sugar level (25,56). Whether these correlations are unusual or representative of general relationships cannot be determined at present. Therefore there is no reason to assume that sugar levels are correlated with other valuable nutrients.

Conclusions. Low to moderate concentrations of simple sugars (generally 0.4–10%) are found in most plant foods. Nevertheless, foods having the greatest amount of energy do not generally have the greatest amount of sugar. High-sugar foods do not possess any special properties that make them more nutritious than other foods. Thus, the presence of sugar in a substance implies that it may be edible, but the amount of sugar in food provides very limited information about its nutritional value.

Functional Analysis

By examining how organisms respond to different sugars under different conditions, one can learn something about what sweet taste was "designed" to do. The present discussion is limited to three issues: the relationship between sweetness and calories, lactose in milk, and the possibility of a starch taste.

Sweet and calories. In nature, the presence of sweet taste implies the presence of calories. However, degree of sweetness provides little information about the amount of energy in a food.

In order for sweet taste to function as an energy metering system, it is necessary for the sweet sensation to be proportional to the energy in the substances ingested. Thus, the sweetness of different sugars should be a function of the energy they provide. This is not the case. Table 3 gives the energy content and sweetness recognition thresholds of the three most abundant, readily digestible sugars. These three sugars have nearly identical energy content per gram but differ greatly in the concentration necessary for them to be perceived as sweet by humans. Thus, at threshold, a solution contains more than twice as many calories if the sweetener is glucose than if the sweetener is sucrose (Table 3). Similar results are obtained if one calculates the energy content of other supra-threshold solutions judged equal in sweetness. Table 3 overstates the correlation between sweetness and energy because it does not include naturally abundant but poorly utilized sugars such as the raffinose family of sugars (22). These sugars taste sweet to humans (70). It is not easy to calculate energy values for these sugars, however, because they tend to be fermented in the colon or caecum (in humans and rats) (22).

Another factor that disrupts any correlation between sweetness and energy is that nonsweet tastes suppress sweet taste (64,66). The bitter, sour, and salty tasting substances found in foods tend to reduce perceived sweetness.

It is more difficult to address this issue in animals. Nevertheless, solution preference and acceptance tests in animals suggest that there is no consistent relationship between the acceptability and energy content of glucose, fructose and sucrose [e.g., (14,79)].

It may be concluded that sweet taste does not provide quantitative nutritional information about food energy content.

Milk. It might be suggested that preference for sugars arises out of each animal's experience with the sweet taste of lactose in milk. If this were a simple conditioning process, one would expect that animals would prefer sweetness levels that approximate those of milk rather than weaker or greater sweetness levels. This does not seem to occur. After weaning rats gradually learn to avoid lactose and prefer sucrose, glucose and fructose (51,81). Some human ethnic groups avoid milk consumption after weaning (85) but still respond favorably to plant sugars [e.g., (9)]. If evolutionary processes shaped sugar receptors for detecting lactose, it seems odd that lactose is much less sweet to humans than the common plant sugars (70). This hypothesis also faces the problem of explaining why preverence for sugars persists well into adulthood. At present, there are no strong reasons to suppose that lactose in milk has been a major factor in the development of sweet preferences [see (81) for further discussion of lactose].

Starch taste. It has recently been proposed that some animals can taste starch (82). The ability to sense the amount of both starch and sugar in a food could improve the ability of animals to assess the energy content of foods, but it does not seem likely that the amount of starch in a food can be measured merely by tasting it. Understanding why, requires a brief consideration of molecular mechanisms of sweet taste.

Current theories about the mechanisms underlying sweet taste involve interactions between sweet molecules and one or more receptor sites on a taste cell (10). The overall shape of the molecule as well as the positions of hydrogen-bonding sites seem to influence sweetness (10). In order for this type of mechanism to work, it is necessary for sweet substances to be water soluble as well as to have functional groups capable of forming hydrogen bonds. Sugars are well suited for stimulating taste receptors because of their high solubility and many functional groups capable of forming hydrogen bonds. Furthermore, sugars are present at higher concentrations than other water soluble nutrients, such as vitamins and minerals in many plants.

On the other hand, insoluble substances such as starch and triglycerides cannot be sensed by similar mechanisms. Starches in uncooked plants are generally present in the form of tightly packed crystals (46). Although starch is not as hydrophobic as triglyceride, it is difficult to imagine how starch crystals could be brought close enough to receptors for hydrogen bonding to occur.

It might be suggested that some hydrolysis of starch occurs in the mouth, providing the animal with soluble polysaccharides that it could taste. Since the rate of starch hydrolysis varies with the physical form of the starch in a food (54), the amount of soluble polysaccharide released in the mouth would be highly dependent on the type of starch crystal in the plant species consumed and how thoroughly the food is chewed. This would make the amount of starch hydrolyzed in the mouth, a poor index of the amount of food energy available after thorough digestion. It is therefore unclear whether a starch or polysaccharide taste could function as a good energy metering system.

CONCLUSIONS AND OUTLOOK

Animals representing a very wide variety of ecological niches show preferences for sugar solutions. Most plants contain enough sugar to be detectable by many terrestrial mammals. Indeed, sugars are the most abundant class of solutes in plants. The water solubility of sugars combined with their ability to form hydrogen bonds and their abundance makes them easier to detect by taste receptors than other nutrients. The widespread occurrence of sugars in plants probably accounts for the preference for sweetened over plain water by many terrestrial mammals. The ability to detect and respond to sugars is potentially useful to any animal that consumes plants.

Fruits are probably the most abundant class of high-sugar food. However, it does not seem likely that sweet taste evolved solely to stimulate fruit ingestion because fruits are low in energy and protein, and because high-fat low-sugar fruits are fairly common in nature. A strong drive to consume sugar-rich fruits might not be beneficial unless countered by drives to consume high-protein energy rich foods.

The sweetness of foods is not strongly related to the nutritional value of foods. This is because: perceived sweetness is influenced by other taste stimuli present in foods, sweetness is not correlated with the energy value of different sugars, and other substances in foods contribute to nutritional values but not sweetness. Thus, perception of sweetness cannot be used to accurately assess the metabolizable energy of a food.

These findings suggest that sweet taste evolved because sugars are common and easier to detect than other nutrients, rather than because of any special nutritional significance sugars have. This line of reasoning may be applied to other tastes. Soft drink manufacturers commonly add sour and bitter flavors to sugar solutions. No satisfactory rationale for this practice has ever been offered. It may be that this practice makes soft drinks resemble natural plant foods.

If it is accepted that the primary function of sweet preference lies in its cue value for edibility, it may be necessary to revise current views that emphasize the strong pleasantness of sweet taste [e.g., (11)]. The idea that sugars have unique or special effects on behavior is difficult to reconcile with the very modest role proposed here. A considerable amount of research has been conducted based on the assumption of special effects of sugars [see (82)], yet critical reviews of the validity of this assumption have not been published.

Limitations. Several unresolved problems limit the confidence we can place on the answers proposed. In order to simplify the discussion, it was assumed that sweet preference is innate (i.e., genetic). If sweet preference is acquired as a result of experience, there is no need to invoke evolutionary processes. At present, evidence for genetic influence is strong for some rodents but not other species (75, 76, 87).

The argument presented here deals with herbivorous and omnivorous animals generally. Generalizations of this sort may not necessarily apply to every single species. It is possible that under some unusual circumstances (e.g., an animal specialized for honey), sweetness does correlate with nutritional value.

Another complicating factor is the observation that some animals may be able to discriminate different sweeteners [e.g., maltose and sucrose (82)]. This ability is probably mediated by different carbohydrate receptors (53,82). There is even some evidence that sweetness might not be unitary in humans (2). Sclafani (82,88) has speculated that having different kinds of carbohydrate receptors may allow animals to select high-starch or high-sugar foods when appropriate. If some species can detect starch in the mouth, as suggested by Sclafani (26, 82, 88), it becomes imperative to ask why humans lack this useful ability.

It should be recognized that the logic employed in the present paper applies only to situations in which the availability and abundance of sugar resembles that found in nature. What happens when organisms are presented with abundant sources of concentrated sugars cannot be predicted from what happens in nature. Nevertheless, an understanding of the evolutionary origins of sweet appetite is a first step towards understanding sugar intake by people in modern society.

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REFERENCES

1. Avigad, G. Sucrose and other disaccharides. In: Pirson, A.; Zimmermann, A.; Zimmermann, M. H., eds. Encyclopedia of plant physiology. New Series vol. 13A. Loewus, F. A.; Tanner, W., eds. Plant carbohydrates I. Intracellular carbohydrates. Berlin: Springer-Verlag; 1982:217–347.
2. Bartoshuk, L. M. Is sweetness unitary? An evaluation of the evidence for multiple sweets. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:33–47.
3. Bartoshuk, L. M.; Harned, M. A.; Parks, L. H. Taste of water in the cat: effects on sucrose preference. Science 171:699–701; 1971.
4. Bauer, F. S. Glucose preference in the guinea pig. Physiol. Behav. 6:75–76; 1971.
5. Beauchamp, G. K.; Maller, O.; Rogers, J. G., Jr. Flavor preference in cats (*Felis catus* and *Panthera* sp.). J. Comp. Physiol. Psychol. 91:1118–1127; 1977.
6. Beauchamp, G. K.; Cowart, B. J. Development of sweet taste. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:127–140.
7. Bell, F. R. Preference thresholds for taste discrimination in goats. J. Agric. Sci. 52:125–128; 1959.
8. Bell, F. R.; Williams, H. I. Threshold values for taste in monozygotic twin calves. Nature 183:345–346; 1959.
9. Bertino, M.; Chan, M. Taste perception and diet in individuals with Chinese and European ethnic backgrounds. Chem. Senses 11:229–241; 1986.
10. Birch, G. G. Chemical aspects of sweetness. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:3–13.
11. Blass, E. M. Opioids, sweets and a mechanism for positive affect: broad motivational implications. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:115–126.
12. Bloom, J. C.; Rogers, J. G.; Maller, O. Taste responses of the North American porcupine (*Erethizon dorsatum*). Physiol. Behav. 11:95–98; 1973.
13. Booth, D. A.; Conner, M. T.; Marie, S. Sweetness and food selection: measurement of sweetener's effects on acceptance. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:143–160.
14. Cagan, R. H.; Maller, O. Taste of sugars: Brief exposure single-stimulus behavioral method. J. Comp. Physiol. Psychol. 87:47–55; 1974.
15. Calvert, J. J. Food selection by western gorillas (G.g. gorilla) in relation to food chemistry. Oecologia 65:236–246; 1985.
16. Campbell, B. A. Absolute and relative sucrose preference thresholds for hungry and satiated rats. J. Comp. Physiol. Psychol. 51:795–800; 1958.
17. Carpenter, J. A. Species differences in taste preferences. J. Comp. Physiol. Psychol. 49:139–144; 1956.
18. Chatterton, N. J.; Thornley, W. R.; Harrison, P. A.; Bennett, J. H. Dynamics of fructan and sucrose biosynthesis in crested wheatgrass. Plant Cell Physiol. 29:1103–1108; 1988.
19. Church, D. C.; Randall, R. P. Effects of diet and feeding level on taste responses of sheep and calves to sucrose solutions. J. Anim. Sci. 48:1171–1181; 1979.
20. Clark, W. R.; Harriman, A. E. Acceptance of five common sugars by squirrel monkeys (*Saimiri sciurens*) in two bottle drinking preference tests. Am. Midland Naturalist 81:253–258; 1969.
21. Crawford, J. C.; Church, D. C. Response of black-tailed deer to various taste stimuli. J. Wildl. Management 35:210–215; 1971.
22. Cristofaro, E.; Mottu, F.; Wuhrmann, J. J. Involvement of the raffinose family of oligosaccharides in flatulence. In: Sipple, H. L.; McNutt, K. W., eds. Sugars in nutrition. New York: Academic Press; 1974:313–336.
23. Dua-Sharma, S.; Smutz, E. R. Taste acceptance in squirrel monkeys. Chem. Senses Flavor 2:341–352; 1977.
24. Faurion, A.; Saito, S.; MacLeod, P. Sweet taste involves several distinct receptor mechanisms. Chem. Senses 5:107–121; 1980.
25. Feeny, P. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581; 1970.
26. Feigin, M. B.; Sclafani, A.; Sunday, S. R. Species differences in polysaccharide and sugar taste preferences. Neurosci. Biobehav. Rev. 11:231–240; 1987.
27. Ferrell, F. Preference for sugars and nonnutritive sweeteners in young beagles. Neurosci. Biobehav. Rev. 8:199–203; 1984.
28. Fobes, J. L; Ehrlich, A.; Mukavetz, J.; Rodriguez-Sierra, J. Free operant measurement of taste preferences in prosimian primates.

Anim. Learn. Behav. 1:99–101; 1973.

29. Frossard, R.; Stadelmann, F. X.; Niederhauser, J. Effects of different heavy metals on fructan, sugar and starch content of ryegrass. J. Plant Physiol. 134:180–185; 1989.
30. Ganchrow, J. R. Consummatory responses to taste stimuli in the hedgehog (*Erinaceus europaeus*). Physiol. Behav. 18:447–453; 1977.
31. Ganchrow, J. R. Taste preferences in rabbits for acids, sucrose, saccharin and quinine. Physiol. Behav. 22:457–460; 1979.
32. Giaquinta, R. T. Translocation of sucrose and oligosaccharides. In: Stumpf, P. K.; Conn, E. E., eds. The biochemistry of plants. A comprehensive treatise. In: Preiss, J., vol. ed. vol. 3. Carbohydrates: Structure and function. New York: Academic Press; 1980:271–320.
33. Glinsmann, W. H.; Irausquin, H.; Park, Y. K. Evaluation of health aspects of sugars contained in carbohydrate sweeteners. J. Nutr. 116:S1–S216; 1986.
34. Goatcher, W. D.; Church, D. C. Taste response in ruminants: I. Reactions of sheep to sugars, saccharin, ethanol, and salts. J. Anim. Sci. 30:777–783; 1970.
35. Goatcher, W. D.; Church, D. C. Taste responses in ruminants. III. Reactions of pygmy goats, normal goats, sheep and cattle to sucrose and sodium chloride. J. Anim. Sci. 31:364–372; 1970.
36. Grace, J.; Russek, M. The influence of previous experience on the taste behavior of dogs toward sucrose and saccharin. Physiol. Behav. 4:553–558; 1965.
37. Harder, D. B.; Maggio, J. C.; Whitney, G. Assessing gustatory detection capabilities using preference procedures. Chem. Senses 14:547–564; 1989.
38. Harper, A. E.; Spivey, H. E. Relationship between food intake and osmotic effect of dietary carbohydrate. Am. J. Physiol. 193:483–487; 1958.
39. Harriman, A. E. Preferences by Mongolian gerbils for solutions of sugars, acids and salts in Richter-type drinking tests. J. Gen. Psychol. 83:79–86; 1970.
40. Harriman, A. E. Preferences by Egyptian spiny mice for solutions of sugars, salts, and acids in Richter-type drinking tests. Percept. Mot. Skill. 50:1075–1081; 1980.
41. Harriman, A. E. Preferences by northern grasshopper mice for solutions of sugars, acids, and salts in Richter-type drinking tests. J. Gen. Psychol. 95:85–92; 1976.
42. Harriman, A. E. Concordance of taste preferences by *Neotoma micropus* with those of other rodents in a grassland community. Percept. Mot. Skills 46:703–708; 1978.
43. Harriman, A. E.; Nevitt, J. R. Preferences for solutions of sugars, salts, and acids by Ord's kangaroo rats given Richter-type drinking tests. Psychol. Rep. 41:663–666; 1977.
44. Harriman, A. E.; Nevitt, J. R. Preferences by deer mice for solutions of sugars, salts, and acids in Richter-type drinking tests. J. Gen. Psychol. 98:207–214; 1978.
45. Ho, L. C. Metabolism and compartmentation of imported sugars in sink organs in relation to sink strength. Annu. Rev. Plant Physiol. Plant Mol. Biol. 39:355–378; 1988.
46. Hodge, J. E. Carbohydrates. In: Fennema, O. R., ed. Principles of food science. New York: Dekker; 1976:41–138.
47. Houpt, T. R.; Houpt, K. A.; Swan, A. A. Duodenal osmoconcentration and food intake in pigs after ingestion of hypertonic nutrients. Am. J. Physiol. 245:R181–R189; 1983.
48. Hyams, J. S.; Etienne, N. L.; Leichter, A. M.; Theuer, R. C. Carbohydrate malabsorption following fruit juice ingestion in young children. Pediatrics 82:64–68; 1988.
49. Iwasaki, K.; Sato, M. Taste preferences for amino acids in the house musk shrew, *Suncus murinus*. Physiol. Behav. 28:829–833; 1982.
50. Izhaki, I.; Safriel, U. N. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. Oikos 54:23–32; 1989.
51. Jacobs, H. L. Taste and the role of experience in the regulation of food intake. In: Kare, M. R.; Maller, O., eds. The chemical sense and nutrition. Baltimore: Johns Hopkins Press; 1967:187–200.
52. Jacobs, W. W. Taste responses in wild and domestic guinea pigs. Physiol. Behav. 20:579–588; 1978.
53. Jakinovich, W., Jr.; Sugarman, D. Sugar taste reception in mammals. Chem. Senses 13:13–31; 1988.
54. Jenkins, D. J. A.; Jenkins, A. L.; Wolever, T. M. S.; Thompson, L. H.; Rao, A. V. Simple and complex carbohydrates. Nutr. Rev. 44:44–49; 1986.
55. Johnson, R. A.; Willson, M. F.; Thompson, J. N.; Bertin, R. I. Nutritional values of wild fruits and consumption by migrant frugivorous birds. Ecology 66:819–827; 1985.
56. Jonasson, S.; Bryant, J. P.; Chapin, F. S., III; Andersson, M. Plant phenols and nutrients in relation to variations in climate and rodent grazing. Am. Nat. 128:394–408; 1986.
57. Jones, R. G. W. Salt tolerance. In: Johnson, C. B., ed. Physiological processes limiting plant productivity. London: Butterworths; 1981: 271–292.
58. Kare, M. R. Comparative study of taste. In: Beidler, L. M., ed. Handbook of sensory physiology. vol. IV. Berlin: Springer-Verlag; 1971:278–292.
59. Kare, M. R.; Pond, W. C.; Campbell, J. Observations on the taste reactions in pigs. Anim. Behav. 13:265–269; 1965.
60. Kemnitz, J. W.; Neu, M. M. Differential influence of various sweet solutions on caloric regulation by Rhesus monkeys. In: Else, J. G.; Lee, P. C., eds. Primate ecology and conservation. Cambridge: Cambridge University Press; 1986:67–74.
61. Kennedy, J. M.; Baldwin, B. A. Taste preferences in pigs for nutritive and non-nutritive sweet solutions. Anim. Behav. 20:265–269; 1972.
62. Kissileff, H. R. Quantitative relationship between palatability and food intake in man. In: Kare, M. R.; Brand, J. G., eds. Interaction of the chemical senses with nutrition. New York: Academic Press; 1986:293–317.
63. Koster, K. L.; Leopold, C. Sugars and desiccation tolerance in seeds. Plant Physiol. 88:829–832; 1988.
64. Lachmann, A. The role of sucrose in foods. The International Sugar Research Foundation, Inc.; 1975.
65. Laughlin, M. E.; Donovick, P. J.; Burright, R. G. Consummatory behavior in meadow voles (*Microtus pennsylvanicus*) and Mongolian gerbils (*Meriones unguiculatus*). Physiol. Behav. 15:185–189; 1975.
66. Lawless, H. T. Evidence for neural inhibition in bittersweet taste mixtures. J. Comp. Physiol. Psychol. 93:538–547; 1979.
67. Livesey, G.; Elia, M. Estimation of energy expenditure, net carbohydrate utilization, and net fat oxidation and synthesis by indirect calorimetry: evaluation of errors with special reference to the detailed composition of fuels. Am. J. Clin. Nutr. 47:608–628; 1988.
68. Maller, O.; Hamilton, C. L. Sucrose and caloric intake by normal and diabetic monkeys. J. Comp. Physiol. Psychol. 66:444–449; 1968.
69. Maller, O.; Kare, M. R. Observations on the sense of taste in the armadillo (*Dasypus novemcinctus*). J. Anim. Behav. 15:8–10; 1967.
70. Moskowitz, H. R. Ratio scales of sugar sweetness. Percept. Psychophys. 7:315–320; 1970.
71. Muto, S.; Miyahara, C. Eating behavior of young rats: experiments on selective feeding of diet and sugar solutions. Br. J. Nutr. 28:327–337; 1972.
72. Nevitt, J. R.; Harriman, A. E. Taste preferences in the cotton rat (*Sigmodon bispidus*). Percept. Mot. Skill 45:379–385; 1977.
73. N-Squared Computing, The N-squared nutritionist III: A program for analyzing and creating diets. Silverton, OR: N-Squared Computing; 1985.
74. Pressman, T. G.; Doolittle, J. H. Taste preferences in the Virginia opossum. Psychol. Rep. 18:875–878; 1966.
75. Ramirez, I.; Fuller, J. L. Genetic influence on water and sweetened water consumption in mice. Physiol. Behav. 16:163–168; 1976.
76. Ramirez, I.; Sprott, R. L. Genetic mechanisms of drinking and feeding. Neurosci. Biobehav. Rev. 2:15–26; 1978.
77. Randall, R. P.; Schurg, W. A.; Church, D. C. Responses of horses to sweet, salty, sour, and bitter solutions. J. Anim. Sci. 47:51–55; 1978.
78. Richter, C. P.; Campbell, K. H. Sucrose taste thresholds of rats and humans. Am. J. Physiol. 128:291–297; 1940.
79. Richter, C. P.; Campbell, K. H. Taste thresholds and taste preferences of rats for five common sugars. J. Nutr. 20:31–46; 1940.
80. Rozin, P. The selection of foods by rats, humans, and other animals. Adv. Stud. Behav. 6:21–76; 1976.
81. Rozin, P.; Pelchat, M. L. Memories of mammaries: adaptations to weaning from milk. Prog. Psychobiol. Physiol. Psychol. 13:1–29; 1988.
82. Sclafani, A. Carbohydrate taste, appetite, and obesity: An overview. Neurosci. Biobehav. Rev. 11:131–153; 1987.
83. Scott, T. R.; Giza, B. K. Neurophysiological aspects of sweetness. In: Dobbing, J., ed. Sweetness. London: Springer-Verlag; 1987:15–32.
84. Shallenberger, R. S. Occurrence of various sugars in foods. In:

Sipple, H. L.; McNutt, K. W., eds. Sugars in nutrition. New York: Academic Press; 1974:67–80.

85. Simoons, F. J. Geography and genetics as factors in the psychobiology of human food selection. In: Barker, L. M., ed. The psychobiology of human food selection. Westport, CT: Avi Publishing; 1982:205–224.
86. Southgate, D. A. T.; Paul, A. A.; Dean, A. C.; Christie, A. A.; Fric, C. Free sugars in foods. J. Hum. Nutr. 32:335–347; 1978.
87. Stockton, M. D.; Whitney, G. Effects of genotype, sugar, and concentration on sugar preference of laboratory mice (*Mus musculus*). J. Comp. Physiol. Psychol. 86:62–68; 1974.
88. Sunderland, G.; Sclafani, A. Taste preferences of squirrel monkeys and bonnet macaques for polycose, maltose and sucrose. Physiol. Behav. 43:685–690; 1988.
89. Thomas, J. D. The comparative ecological biochemistry of sugar chemoreception and transport in freshwater snails and other aquatic organisms. Comp. Biochem. Physiol. 93A:353–374; 1989.
90. Wagner, M. W. Studies in comparative sugar preference in rodents: 1. Methodology differences. Psychon. Sci. 11:160; 1968.
91. Wheelwright, N. T.; Haber, W. A.; Murray, K. G.; Guindon, C. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica 16:173–192; 1984.
92. White, D. W.; Stiles, E. The use of refractometry to estimate nutrient rewards in vertebrate-dispersed fruits. Ecology 66:303–307; 1985.
93. Willenbrink, J. Storage of sugars. In: Pirson, A.; Zimmermann, M. H., eds. Encyclopedia of plant physiology. New Series vol. 13A. Loewus, F. A.; Tanner, W., eds. Plant carbohydrates I. Intracellular carbohydrates. Berlin: Springer-Verlag; 1982:684–699.
94. Young, P. T. Role of hedonic processes in the development of sweet taste preferences. In: Weiffenbach, J. M., ed. Taste and development: The genesis of sweet preference. Bethesda, MD: U.S. Dept. of Health, Education, and Welfare; 1977:399–417.