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GROWTH AND ACID TOLERANCE OF HUMAN DENTAL PLAQUE BACTERIA

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Summary—Pure cultures of representative strains of cariogenic and non-cariogenic plaque bacteria were assessed for their ability to initiate and maintain growth in broths, adjusted to initial pH levels of 7.0, 5.5 or 5.0, and to produce lactic acid from sucrose or glucose in resting-cell suspensions at pH 6.5, 5.0, 4.5 and 4.0. *Streptococcus mutans*, *Lactobacillus casei* and *Streptococcus faecalis* showed greater acid tolerance than strains of *Streptococcus sanguis*, *Streptococcus salivarius*, *Streptococcus mitis* and *Actinomyces viscosus*. For all species, growth initiation in broth was more acid sensitive than lactic-acid production in resting-cell suspensions. These data confirm and extend previous observations that the species of plaque bacteria most closely associated with the initiation or progression of dental caries are more aciduric than non-cariogenic species.

INTRODUCTION

Streptococcus mutans is statistically associated with human dental decay (Krasse *et al.*, 1968; Loesche, 1982) and shows a significant numerical increase with the initiation of dental decay in man (Ikeda and Sandham, 1971; Ikeda, Sandham and Bradley, 1973; Loesche and Straffon, 1979). *Strep. mutans* also produces high levels of multisurface caries in animals, in contrast with other species of dental bacteria which are less cariogenic (Dummer and Green, 1980; Hamada and Slade, 1980). Explanations for the high cariogenicity of *Strep. mutans* have been based upon its production from sucrose of extracellular polysaccharides which mediate its adherence to tooth surfaces (Gibbons and Nygaard, 1968; Hamada and Slade, 1980); its formation of intracellular polysaccharide energy reserves (Gibbons, 1968; Hamilton, 1967); and the rapid metabolism of sugars to organic acids, particularly lactic acid (Minah and Loesche, 1977a,b). Acid tolerance (reviewed by van Houte, 1980; Loesche, 1982) has been proposed as another factor in the specific cariogenicity of *Strep. mutans* and *Lactobacillus* species, and could account for high levels of these bacteria in fissure plaque (Ikeda and Sandham, 1971; Ikeda *et al.*, 1973; Theilade *et al.*, 1978) and carious lesions (Loesche and Syed, 1973; Loesche *et al.*, 1975). The pH of plaque in sites prone to caries drops rapidly upon ingestion of fermentable carbohydrates and can remain below pH 5.0 for substantial periods of time (Graf and Muhlemann, 1966; Schachtele and Jensen, 1982).

Aciduricity, as it has been applied to oral bacteria, has been defined as the ability to lower the terminal pH of carbohydrate-containing broths to a pH of 4.5 to 4.0, the ability to initiate growth at pH levels of pH 5.5 or below, or the possession of a pH-lowering potential at low pH levels (van Houte, 1980). Many studies have not distinguished between falls in pH and specific acid production, or have not related aciduricity to growth rates at low pH levels. Our object was to compare the pH-lowering potential and growth capacity of 30 strains of cariogenic and noncariogenic oral bacteria and the rate of lactic-acid production by resting-cell suspensions of selected strains.

MATERIALS AND METHODS

Bacterial strains

The bacterial strains used were obtained from frozen and lyophilized stocks maintained by Dr Loesche. Several strains (designated as recent isolates) were obtained from caries active children Loesche and Straffon, 1979) and used after a minimal number of *in-vitro* passages. Biotypes of all *Strep. mutans* isolates were confirmed using the metabolic assay of Shklair and Keene (1974).

All isolates were subcultured in Trypticase Soy Broth, (BBL, Cockeysville, Maryland, U.S.A.), concentrated by centrifugation and stored frozen in suspension with blood on glass beads (Nagel and Kunz, 1972). These glass beads, containing about 10^7 colony-forming units (c.f.u.), then served as inocula for the tests to be described.

Growth in pH-adjusted media

The ability of 30 strains (Table 1) to establish growth in Trypticase Soy Broth (TSB) with 1 per cent additional glucose was determined at pH 7.0, 5.5 and 5.0 (initial pH adjusted with lactic acid). Broths were inoculated with 0.1 ml of 18 h TSB cultures of streptococci or 24-h cultures of *Actinomyces* and *Lactobacillus* and incubated anaerobically (85 per cent N_2, 10 per cent CO_2 and 5 per cent H_2) for 48 h at 5°C.

Terminal optical density (O.D.) was measured at 540 nm in a Spectronic 20 spectrophotometer (Bausch & Lomb, Rochester, New York, U.S.A.), and terminal pH was determined with a combination glass electrode (Model MI410, Microelectrodes, Inc. Londonderry, New Hampshire, U.S.A.). Selected

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Table 1. Terminal pH and growth density of plaque bacteria initiated in TSB broths at pH 7.0, 5.5 or 5.0

	Terminal O.D.			Terminal pH			pH drop		
	7.0	5.5	5.0	7.0	5.5	5.0	7.0	5.5	5.0
Strep. mutans:									
AHT (a)*	1.42	0.66	0.30	4.6	4.8	4.6	2.4	0.7	0.4
E49 (a)	1.67	0.98	0.22	4.2	4.3	4.7	2.8	1.2	0.3
FA1 (b)	2.06	1.17	0.21	4.2	4.4	4.8	2.8	1.2	0.2
BHT (b)	1.42	0.96	0.32	4.2	4.3	4.6	2.8	1.2	0.4
Ingbritt (c)	1.46	0.77	0.27	4.3	4.3	4.6	2.7	1.2	0.4
S (c)	1.33	0.99	0.49	4.3	4.2	4.4	2.7	1.2	0.6
GS 5 (c)	1.12	0.58	0.23	4.5	4.4	4.6	2.5	1.0	0.4
OMZ-175 (c)	0.95	0.48	0.14	4.5	4.6	4.8	2.7	0.9	0.2
MI-33† (c)	1.20	0.46	0.29	4.3	4.4	4.5	2.6	1.0	0.4
MI-76† (c)	1.00	0.33	0.18	4.4	4.5	4.6	2.5	0.9	0.3
MI-186† (d)	1.17	0.87	0.48	4.3	4.2	4.4	2.7	1.2	0.5
OMZ-176 (d)	1.10	0.56	0.39	4.4	4.6	4.6	2.5	0.8	0.3
TH (d)	0.78	0.39	0.20	4.7	4.5	4.6	2.2	0.9	0.3
BHR (d)	0.96	0.36	0.34	4.7	4.7	4.6	2.2	0.7	0.3
MI-83† (d)	0.94	0.51	0.31	4.5	4.4	4.5	2.4	1.0	0.4
B2 (e)	1.32	0.69	0.31	4.4	4.5	4.6	2.5	0.9	0.3
LM7 (e)	0.80	0.46	0.24	4.5	4.5	4.6	2.4	0.9	0.3
MI-158† (e)	1.19	0.62	0.41	4.3	4.3	4.4	2.6	1.1	0.5
6715 (g)	1.00	0.68	0.41	4.4	4.7	4.5			
Average:	1.20	0.68	0.30	4.4	4.4	4.6	2.6	1.0	0.3
L. casei 49L	1.37	1.2	1.02	4.2	4.0	4.0	2.8	1.42	0.95
Strep. faecalis DS27	1.59	0.78	0.65	4.5	4.4	4.4	2.4	1.0	0.5
Strep. sanguis:									
10558	1.56	0.36	0.01	4.4	4.7	5.0	2.5	0.7	0.0
167N	1.03	0.27	0.01	4.4	4.7	5.0	2.5	0.7	0.0
S1-25†	1.13	0.26	0.01	4.4	4.7	5.0	2.5	0.7	0.0
S1-26†	1.13	0.12	0.01	4.5	5.1	5.0	2.4	0.3	0.0
Strep salivarius:									
HHT	1.21	0.30	0.01	4.5	4.8	5.0	2.4	0.7	0.0
SS2	1.12	0.17	0.01	4.6	4.8	5.0	2.3	0.7	0.0
A. viscosus:									
No. 21	1.49	0.20	0.01	4.6	5.0	5.0	2.3	0.4	0.0
GA	1.02	0.16	0.01	4.6	5.1	5.0	2.3	0.4	0.0
Strep. mitis 2S	0.93	0.14	0.01	4.7	5.1	5.0	2.24	0.37	0.0
Average:	1.24	0.33	0.01	4.6	4.9	5.0	2.4	0.5	0.0

**Strep. mutans* strains followed by serotype in parentheses. †Recent clinical isolate.

strains (Table 2) were incubated under similar conditions with O.D. measurements taken at hourly intervals up to 18 h, then at 1, 2 and 7 days.

Carbohydrate catabolism assay

Sucrose and glucose catabolism by resting cell suspensions of selected pure cultures was evaluated using a modification of the technique developed by Minah and Loesche (1976, 1977a). All streptococcal cultures were inoculated directly from glass-bead stocks into 5 ml of TSB, and slower-growing *Lactobacillus* and *Actinomyces* strains were inoculated from 24-h broth cultures. As TSB contains sufficient trace sucrose to induce sucrose-inducible enzyme systems (Hamada and Slade, 1980), additional sucrose was not added to the broth. All cultures were incubated anaerobically under an atmosphere of 85 per cent N_2, 10 per cent CO_2 and 5 per cent H_2 at 35°C for 16 to 18 h. Cultures were centrifuged, washed once with reduced transport fluid (RTF, Syed and Loesche, 1972) and resuspended in RTF. Cell concentrations of the suspensions were determined turbimetrically, and adjusted to make all suspensions approximately equal in colony-forming unit concentration.

The cell suspensions were transported into an anaerobic chamber kept at 35°C (Aranki *et al.*, 1969) and dispersed by 20 s of mild sonication (Cell Disruptor, Kontes Glass Co., Vineland, New Jersey, U.S.A.). Fifteen-microlitre samples were removed and diluted in RTF for later determination of viable counts. The RTF buffers used for washing and suspending the cells were adjusted to pH 6.5, 5.0, 4.5 or 4.0 by mixing appropriate proportions of acidic and basic RTF stocks containing 9.96 mM lactic acid and 5.17 mM K_2HPO_4, respectively.

The assay was started by adding 100 μl of the cell suspensions to 150 μl of RTF containing 1 μCi of [U-^{14}C]-sucrose or 1 μCi of [U-^{14}C]-glucose (New England Nuclear, Boston, Massachusetts, U.S.A.). Additional cold sucrose or glucose was added to

bring the final concentration of sugar in the reaction mixture to 0.1 per cent.

At 2, 5, 10, 20 and 30 min, 1 μl samples of the assay suspensions were spotted on thin-layer chromatography sheets. The sheets were dried, and developed using a solvent mixture of 88 per cent formic acid–2-butanone–t-butanol–water (15:30:40:15) (Minah and Loesche, 1976). Spots corresponding to lactic acid, which migrated separately from the other organic acids (Minah and Loesche, 1976), were removed, and their radioactivity determined in a liquid scintillation counter. Volatile acid production, although present in *Actinomyces viscosus* and *Streptococcus sanguis*, and to a lesser extent in *Strep. mutans* (Minah and Loesche, 1976), was not quantitated. At the conclusion of the experiment, all reaction mixtures were immediately frozen and stored until total protein content of each reaction mixture could be assayed by the microfluorometric technique of Undenfriend *et al.* (1972).

Data analysis

Data obtained from the resting cell metabolism assays were corrected for quenching, normalized in terms of suspension-protein concentration, and analysed using computer programs in the Michigan Inte active Data Analysis System (MIDAS). Significant differences among groups were evaluated using Student's t-test or the non-parametric Mann–Whitney U-test.

RESULTS

The terminal (53 h) pH and turbidity of cultures incubated in TSB-glucose broths with initial pH levels of 7.0, 5.5 or 5.0 are presented in Table 1. All 19 *Strep. mutans* strains established growth at the three pH levels, as did the *Lactobacillus casei* and *Streptococcus faecalis* strains. The terminal growth of the *Strep. mutans* and *Strep. faecalis* strains in the pH 5.5 medium was about 50 per cent and in the pH 5.0 medium about 20 per cent of that observed in the pH 7.0 broth. The *L. casei* strain exhibited a slight reduction in terminal growth in the pH 5.5 and pH 5.0 medium. Growth of all 9 strains of *Strep. sanguis*, *Streptococcus salivarius*, *A. viscosus*, and *Streptococcus mitis* (non-cariogenic strains) inoculated at pH 5.5 was considerably less than the majority of *Strep. mutans* strains, and was completely inhibited at pH 5.0. The differences in terminal O.D. between the *Strep. mutans* strains, taken as a group, and the non-cariogenic strains were statistically significant ($p < 0.05$; Student's t-test) for cultures inoculated in the pH 5.5 and 5.0 broths.

The terminal pH levels of all cultures initiated at pH 7.0 were below 5.0 (Table 1); the average terminal pH of the *Strep. mutans* cultures was 0.2 pH units lower than the average for the non-cariogenic bacteria ($p < 0.05$). The difference in average terminal pH between these two groups was significantly greater in cultures initiated at pH 5.5 (4.46, compared to 4.91; $p < 0.01$). The *Strep. mutans* strains reduced the pH in the pH 5.0 broth by about 0.4 pH units whereas the less cariogenic strains did not grow. The terminal pH of the *Strep. faecalis* culture was similar to the *Strep. mutans* cultures, while that of the *L. casei* cultures was lower, especially in those initiated at pH 5.5 and 5.0.

A summary of growth-curve data for 12 selected strains (Table 2) shows that the streptococci inoculated at pH 7.0 had similar lag phases, with the exception of *Strep. mutans* OMZ-176, which had 4 h, as opposed to 2 h, lag time. The median log-phase growth rate for the streptococci inoculated at pH 7.0 was 0.108 O.D. units/hour, with *Strep. mutans* strains FA1, E49 and 10558 growing appreciably (>0.05 units) faster than the median, and *Strep. mitis* 2S growing appreciably slower than the median value. *A. viscosus* had the longest lag phase of the strains inoculated at pH 7.0, and the *A. viscosus* and *L. casei* strains grew at slower rates than many of the streptococci. Initiation in pH 5.5 broth increased the lag phase of all strains except *Strep. sanguis* SI-25 and *Strep. mutans* Ingbritt, and decreased the growth rates of all strains except *L. casei* 49/L. *Strep. mutans* strains FA1 and OMZ-176 had log-phase growth rates approx. 50 per cent lower than those of strains E49, Ingbritt, and FA1. *L. casei* and *Strep. faecalis* had growth rates that were similar to the faster-growing *Strep. mutans* strains. All the less cariogenic bacteria initiated at pH 5.5, except *Strep. sanguis* strain SI-25, had lower growth rates during log phase

Table 2. Growth curve summary for plaque bacteria grown in TSB initiated at pH 7.0, 5.5 or 5.0

	Terminal O.D.			Duration of lag (h)			Growth rate (O.D. units/h)*		
Initial pH	7.0	5.5	5.0	7.0	5.5	5.0	7.0	5.5	5.0
Strain									
Strep. mutans E49	1.57	0.55	0.34	2	3	13	0.180	0.049	0.006
Strep. mutans FA1	1.67	0.77	0.10	2	3	9	0.230	0.022	0.021
Strep. mutans Ingbritt	1.07	0.50	0.24	2	2	12	0.081	0.044	0.024
Strep. mutans OMZ-176	1.18	0.58	0.27	4	5	12	0.086	0.044	0.008
Strep. mutans LM7	0.92	0.40	0.15	2	8	12	0.104	0.027	
Strep. faecalis DS2	1.17	0.50	0.33	2	3	8	0.115	0.048	0.012
L. casei 49L	0.84	0.68	0.58	2	4	3	0.063	0.062	0.034
Strep. sanguis 10558	1.57	0.30	NG	2	4	—	0.151	0.014	—
Strep. sanguis SI-25	0.88	0.40	NG	2	2	—	0.096	0.042	—
Strep. salivarius HHT	0.86	0.20	NG	2	4	—	0.122	0.014	—
Strep. mitis 2S	0.65	0.04	NG	2	7	—	0.045	0.003	—
A. viscosus No. 21	1.27	0.17	NG	6	15	—	0.072	0.003	
Escherichia coli HV	1.17	0.36	NG	2	7	—	0.098	0.034	

*Growth rates were determined during log-phase growth. NG = No growth.

than did the *Strep. mutans* strains. Cultures initiated at pH 7.0 and 5.5 appeared to enter resting phase at approximately the same time. The slowest growth rates were observed in the cultures initiated at pH 5.0.

In other experiments, the rates of lactic acid production by resting cell suspensions of selected cariogenic and less cariogenic strains were determined at pH 6.5, 5.0, 4.5 or 4.0. *Strep. mutans* strain Ingbritt produced more lactic acid from both glucose and sucrose at pH 5.0 than at pH 6.5, 4.5 or 4.0 (Fig. 1A). At pH 4.5, acid production from glucose but not sucrose was increased in relation to that at pH 6.5. At pH 4.0, acid production from sucrose was moderately inhibited compared to that at pH 6.5, but acid production from glucose was not inhibited.

L. casei strain 54/L showed a slow and variable production of lactic acid from sucrose, but lactic acid production from glucose proceeded rapidly (Fig. 1B). Unlike *Strep. mutans*, *L. casei* strain 54/L did not reveal a stimulation of lactic acid production at pH 5.0 compared to that at pH 6.5, but rather, in the case of glucose, showed an approx. 20 per cent decrease in lactic acid production. Lactic acid production at pH 4.5 and 4.0 was decreased 30 to 50 per cent compared to that at pH 6.5. However, the amount of lactic acid production from glucose at pH 4.0 by strain 54/L was higher than that of the other strains studied.

Lactic-acid production by resting-cell suspensions of *Actinomyces viscosus* strain No. 21 was more variable than was acid production by the streptococci. However, it was apparent that more lactic acid was produced from glucose than sucrose at pH 6.5, 5.0 or 4.5, with a pH optimum of 4.5 for glucose catabolism (Fig. 1C). Acid production from both sugars was almost completely inhibited at pH 4.0.

The pattern of lactic acid production from glucose and sucrose at the four pH levels by *Strep. sanguis* strains 10556, 10558, and SI-26 (Fig. 2) differed from that observed with *Strep. mutans* strain Ingbritt. At pH 6.5, acid production by *Strep. sanguis* strains 10556 and SI-26 was greater than that of Ingbritt. At pH 5.0, lactic-acid production from sucrose and glucose was less than, or approximately equal to, that at pH 6.5. This was in contrast to the marked stimulation of acid production at pH 5.0 by Ingbritt, although strain SI-26 did show enhanced lactic-acid production from glucose after 30 min. Acid production from sucrose at pH 4.5 and 4.0 was inhibited compared to that at pH 6.5. At pH 4.5 and 4.0, acid production from glucose was also inhibited in strains 10558 and SI-26, but acid production by strain 10556 was not inhibited until pH 4.0 was reached. The amount of acid produced at the lower pH levels by the *Strep. sanguis* strains was less than that produced by *Strep. mutans* Ingbritt.

DISCUSSION

Strep. mutans and various *Lactobacillus* species are clearly associated with coronal caries in man (Krasse *et al.*, 1968; Ikeda *et al.*, 1973; Loesche and Syed, 1973; Loesche *et al.*, 1975; Loesche and Straffon, 1979; Loesche, 1982). *L. casei* and *Strep. faecalis* can cause fissure caries, but not high levels of smooth-surface caries in rats (Fitzgerald, Jordan and Archard, 1966; Dummer and Green, 1980). *A. viscosus* is associated with root-surface caries but not coronal caries (Jordan and Sumey, 1973; Syed and Loesche, 1975). *Strep. sanguis*, *Strep. salivarius*, *Strep. mitis* and *A. viscosus* are less cariogenic in animal models than *Strep. mutans* (Dummer and Green, 1980; Hamada and Slade, 1980).

Our study confirms the greater acid tolerance of *Strep. mutans* and *L. casei* in comparison to a variety of other plaque species. This aciduricity was seen not only in their ability to initiate and maintain growth at low pH levels, as described by previous authors (reviewed by van Houte, 1980; Loesche, 1982) but also in the ability to produce lactic acid in lactate buffers below pH 5.0. Ingbritt cell suspensions incubated in acetate and phosphate-based buffer systems also exhibited increased lactate production at pH 5.0 as compared to pH 6.5 (Harper and Loesche, 1983), indicating that this phenomenon was related to pH rather than to the lactate concentration of the buffer. Both manifestations of aciduricity would be expected to contribute to the pathogenicity of these organisms in the caries process.

The pH ranges studied here were lower than those reported in most previous *in-vitro* studies, but represent pH levels that are achieved *in vivo* for considerable periods in those sites most prone to carious

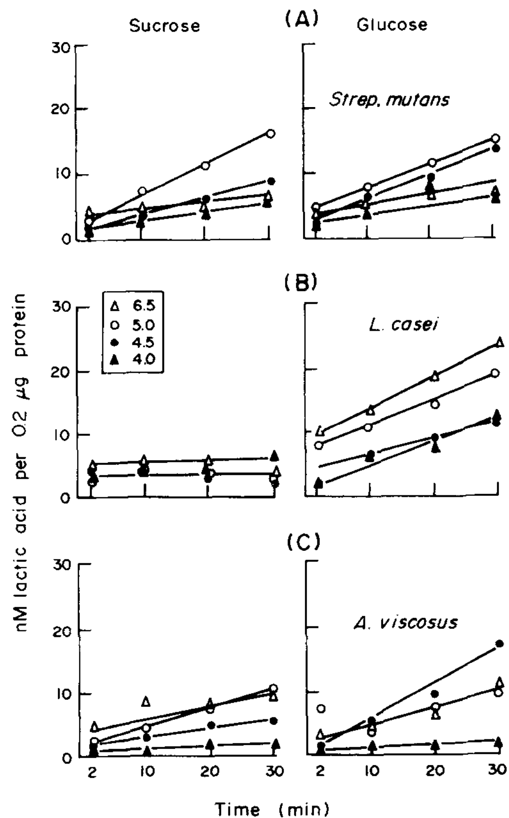

Fig. 1. Lactic-acid production from 0.1 per cent sucrose or glucose by resting-cell suspensions of *Strep. mutans* Ingbritt (A), *L. casei* 54/L (B) and *A. viscosus* strain 21 (C) incubated at pH 6.5, 5.0, 4.5 and 4.0. Points represent the mean of 4 to 8 repetitions.

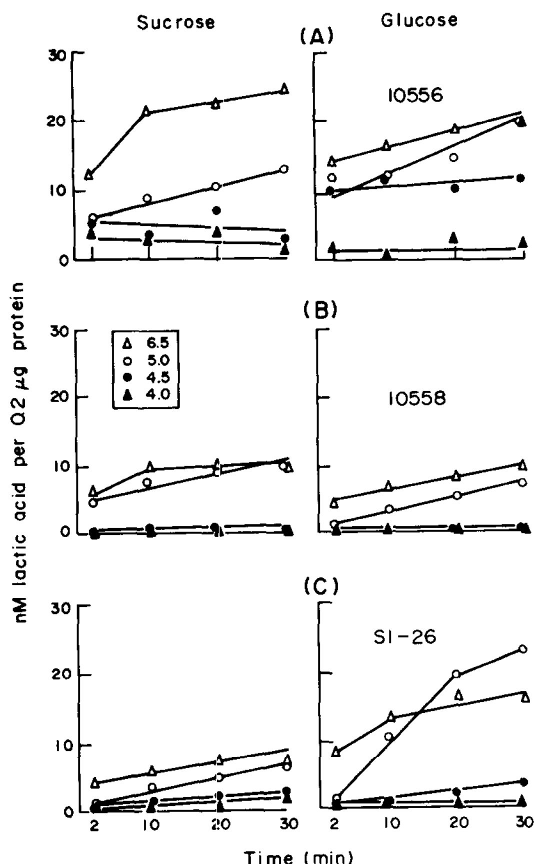

Fig. 2. Lactic-acid production from 0.1 per cent sucrose or glucose by resting-cell suspensions of *Strep. sanguis* strains 10556 (A), 10558 (B) and SI-26 (C) incubated at pH 6.5, 5.0, 4.5 and 4.0. Points represent the mean of 4 to 8 repetitions.

attack (Graf and Muhlemann, 1966; Schachtele and Jensen, 1982). The pattern of increased acidogenesis by *Strep. mutans* Ingbritt at pH 5.0 is shared by other serotypes with strains of *Strep. mutans* (Harper and Loesche, 1983), and is supportive of the observation of Hamilton and Ellwood (1978) that *Strep. mutans* Ingbritt cells grown in a chemostat at a constant pH of 5.5 were more metabolically active than cells grown at a constant pH of 6.5 and 6.0. However, these investigators did not find any increase in the metabolic rate of resting cells incubated at pH 5.5 in comparison to those incubated at pH 6.5 and 6.0. It may be that pH 5.5 falls above a threshold for acidogenic stimulation of *Strep. mutans*.

The differences in acid-forming ability of *Strep. mutans* and *Strep. sanguis* at low pH levels are in agreement with the results of Komiyama and Kleinberg (1974) and with the findings of Futakami, Sato and Iwami (1976), who reported that glucose uptake and acid production by *Strep. mutans* cells incubated at pH 5.0 or 4.5 were greater than that of *Strep. sanguis* strains. Our observations also complement those of Onose and Sandham (1976) and Ellen and Onose (1978), who reported that *Strep. mutans* colonies produced a greater local pH depression on agar media than did colonies of *A. viscosus* or *Strep. mitis*. The slow rate of sucrose metabolism demonstrated by *L. casei* 54/L is characteristic of many *L. casei* strains (Buchanan and Gibbons, 1974).

The inferior ability of the non-cariogenic bacteria to initiate growth at pH 5.5 and 5.0 when compared to *Strep. mutans*, *L. casei* and *Strep. faecalis* strains is in agreement with earlier studies, as is the observation of slightly different terminal pH values between the cariogenic and less cariogenic species (van Houte, 1980). The ability of the cariogenic bacteria to maintain growth at pH 5.0 may be more significant in terms of cariogenicity than the fact that the cariogenic strains, taken as a group, achieved a statistically significant lower terminal pH from all three initial pH levels than did the less cariogenic organisms. The additional ability of the *Strep. mutans* and *L. casei* resting-cell suspensions to maintain acid production at low pH levels in comparison with the less cariogenic *Strep. sanguis* strains (Figs 1 and 2) would also contribute to their cariogenicity, especially in fissures or carious lesions, where pH can remain below 4.5 for hours (Dirksen, Little and Bibby, 1963).

The greater acidogenicity of the cariogenic bacteria at low pH levels may be due to more acid-tolerant sugar-uptake systems than exist in the less cariogenic species such as *Strep. sanguis* (Komiyama and Kleinberg, 1974; Kashket, Rodriguez and Bunich, 1977). A detailed examination of the glycolytic pathway metabolism in *Strep. mutans* and *Strep. sanguis* (Iwami and Yamada, 1980), showed that *Strep. sanguis* produced less acid at low pH levels than did *Strep. mutans*. This difference was apparently caused by inhibition of ATP-dependent glucose phosphotransferase-mediated glucose transport. A similarly detailed study of *Actinomyces* and *Lactobacillus* strains has not yet been carried out. Another possible mechanism of aciduricity might be related to the ability of *Strep. mutans* to maintain a neural internal pH under conditions of increasing ambient acidity, as shown by Whitford *et al.* (1977), and Eisenberg, Bender and Marquis (1980). The ability of other oral bacteria to maintain such a pH gradient has not yet been studied.

No previous investigations have compared specific production of lactic acid from sucrose and glucose at the low pH levels reported here. At pH 6.5, lactic acid production from the two sugars proceeded at approximately equal rates in all species tested. However, at the lower pH levels, lactic acid production from sucrose was more inhibited than that from glucose. The reason for this difference in pH sensitivity of acid production from the two sugars is not known, but could reflect differences in pH optima of transport mechanisms for the two sugars. The differences underscore the importance of considering sucrose as well as glucose in metabolic activity studies, as sucrose is the predominant dietary sugar consumed by man.

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