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Changes in Cell Diameter During the Division Cycle of *Escherichia coli*

FRANK J. TRUEBA* AND CONRAD L. WOLDRINGH

Department of Electron Microscopy and Molecular Cytology, University of Amsterdam, Amsterdam, The Netherlands

Extensive measurements of steady-state populations of several *Escherichia coli* strains have consistently indicated that cell diameter decreases with increasing cell length. This was observed both after electron microscopy of air-dried cells and after phase-contrast microscopy of living cells. The analysis was made by considering separately the unconstricted cells and three classes (slight, medium, and deep) of constricted cells in the population. During slow growth, cells with the average newborn length were up to 8% thicker than unconstricted cells twice as long. This decrease in diameter is less at higher growth rates. Despite the small changes and the large variation of the diameter in any particular length class, significant negative correlations between diameter and length were obtained. Cell diameter increases again at the end of the cell cycle as indicated by an increase of average diameter in the three consecutive classes of constriction.

In studies concerning the determination of cell dimensions in rod-shaped bacteria, cell diameter has usually been assumed to remain constant during the division cycle (1, 2, 8, 12, 14, 17, 18, 25, 26). To support this assumption, reference is generally made to the observations of Marr et al. (11) who measured from electron micrographs 214 *Escherichia coli* cells which did not show a correlation between diameter and length.

In contrast, the diameter of gram-negative cells does vary in response to changes in growth rate (2, 10, 19). Such changes in the diameter of *E. coli* cells could be attributed to the mechanical properties of the cell wall: to accommodate the decreased surface-to-volume ratio upon transition to a higher growth rate, the cell wall may become stretched in its short dimension (16, 17). Such a stretching by mechanical forces induced by a difference in the rates of surface and mass synthesis could also occur during the cell cycle. In many growth models, cell mass is assumed to increase exponentially, and cell surface is assumed to increase linearly during the cycle. As a result, small variations are to be expected in either cell density, cell diameter, or both.

Some experimental evidence (15) and theoretical arguments (18) have been presented to support cell density change during the cycle. In this study we present observations which show that *E. coli* cells gradually become thinner while elongating during most of the cycle and become wider again during the period of constriction and separation of the daughter cells.

MATERIALS AND METHODS

Bacterial strains. The bacterial strains used were *E. coli* B/r H266 (23), B/r A (ATCC 12407), and B/r K (5, 24), K-12 CR34 (27), PAT84 (7), W7 (22), and *Bacillus subtilis* Marburg (13).

Media and growth conditions. *E. coli* cells were grown in a minimal salts solution (4), supplemented with either 0.04 to 0.2% L-alanine, 0.04% L-aspartate; 0.04% L-alanine, 0.04% L-proline, and 0.4% glucose; 0.4% glucose and 1% Casamino Acids (Sigma Chemical Co., St. Louis, Mo.); or Luria broth and 0.5% glucose and, if required, L-amino acids (50 μg/ml) and thymine (20 μg/ml). *B. subtilis* cells were grown in Spizizen medium (21), supplemented with 0.5% glucose. The doubling time of 194 min (see Fig. 2) was obtained by using alanine as a source of both carbon and nitrogen in the minimal salts medium without NH_4Cl.

To start the experimental cultures, stationary-phase cells were diluted 500 to 1,000 times in growth medium aerated by vigorous shaking in a water bath at 37°C. In all growth experiments, the cells were cultured with a constant doubling time for about 10 generations. Samples were fixed by 0.25% formaldehyde for absorbance measurements (Gilford microsample spectrophotometer, at 450 nm wavelength) and for titration (Coulter Counter, model Z_B, with a 30-μm orifice). Unless otherwise noted, the establishment of steady-state growth was verified by obtaining either constancy of length distributions in consecutive samples (24) or obtaining a constant mass/cell ratio.

Preparation of cells for electron and light microscopy. Cells were fixed with 0.1% OsO_4 and air dried by a modification of the agar filtration technique as previously described (24). In the case of cells cultured in minimal salts medium, Bacto-tryptone (Difco Laboratories, Detroit, Mich.) was added to the fixed cells to promote spreading at a final concentration of

about 0.1%. Visibility of the nucleoplasm(s) in all cells is used as a criterion for homogeneous drying and flattening of the cells on the agar filter (Fig. 1).

Living cells were concentrated by centrifugation and immobilized by spreading on a thin layer of 1 to 2% agar on a microscope slide. They were then photographed under phase-contrast optics within 5 to 20 min after sampling from the culture medium. Micrographs were taken with a Wild microscope placed in a small chamber kept at 37°C.

Measurements of cell dimensions. Electron micrographs were projected through a transparent digitizing screen (Summagraphics Co.) or printed at a final magnification of between 9,000 and 15,000 and calibrated with a cross-grating replica (Ladd, Vermont). Light micrographs were printed at a final magnification of about 6,000 and calibrated with a graded microscope slide (Olympus, Tokyo). The reproducibility of determining the final magnification was better than 0.5%, but the accuracy of that determination was not as good, as we realized when we obtained two series of measurements of the same cell sample which occasionally differed as much as 3% systematically from each other (usually much less difference was found, however). We notice here that pooling of cell measurements at different magnifications increases the real correlation coefficient toward positive values.

Cell dimensions were measured by tipping with an electronic pen the poles and middle of each cell or cell half, as indicated in Fig. 1. In some cases the cell diameter in unconstricted cells was measured twice (as for constricting cells), at one-third of the cell length from each pole. Because the same results were obtained, we dropped this more laborious method.

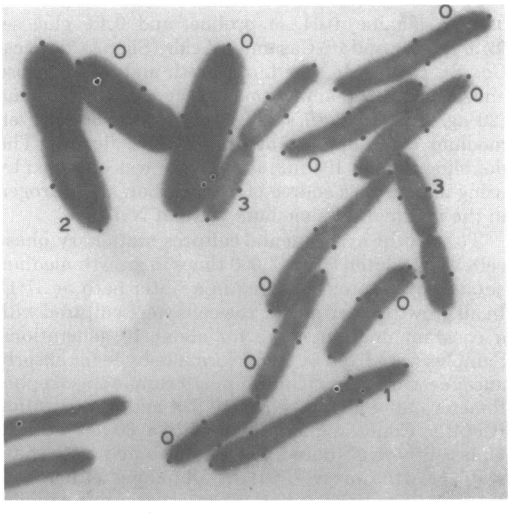

FIG. 1. *Measurement of the dimension of cells prepared by agar filtration. Dots indicate the places pointed with the electronic pen of the digitizer. Cells are divided into four subpopulations: unconstricted (0), slight-constricted (1), medium-constricted (2), and deep-constricted (3). The three big cells grew in broth with a doubling time of 20 min; the small ones grew in minimal salts medium with a doubling time of 78 min.*

A desk-top calculator (Hewlett-Packard model 9825 A) calculated and stored in its memory the two dimensions with a precision of 0.01 μm. The constricted cells were divided into three classes according to the degree of constriction; the length and width of each of the halves of a constricted cell were measured and stored apart, but together with a code number indicating their degree of constriction. Hence, we could analyze four subpopulations in each experiment: unconstricted cells and slight-, medium-, and deep-constricted cells.

Fifty measurements of the same cell (magnification 10,500×) gave a coefficient of variation of 2% for the length (mean, 2 μm) and 5% for the diameter (mean, 0.5 μm); 50 measurements of a bigger cell (magnification, 15,000×) gave 1.4% for the length (mean, 3.4 μm) and 3% for the width (mean, 0.9 μm). The greatest added variation due to measurement error is thus 5% for the diameter of thin cells.

RESULTS

Diameter as a function of length in cells prepared by agar filtration. Preparation of cells by the technique of agar filtration has been applied in this laboratory in several studies on the size and shape of individual cells in bacterial populations (2, 7, 8, 18, 24, 27). During these studies, we frequently observed that short cells were thicker and long, unconstricted cells were thinner than the average diameter of the population. To investigate whether cell diameter changes in a systematic way during the cell cycle, we carried out new growth experiments and measured again the electron micrographs from many old experiments. In some of these latter experiments, the stored data of cells measured for other purposes could be analyzed directly for a possible correlation between diameter and length.

Figure 2A shows a typical scatter diagram obtained from the dimensions of *E. coli* B/r H266 cells. From the diagram, a relationship between diameter and length is not apparent because of the large variation in diameter at any length. When the mean diameter of cells grouped according to length is plotted (Fig. 2B), a negative correlation becomes evident.

To obtain better insight into possible diameter changes during the cell cycle, we divided the cells into four separate subpopulations: (i) unconstricted cells, (ii) slight-constricted, (iii) medium-constricted, and (iv) deep-constricted cells. In Table 1 the parameters of the correlation between diameter and length of unconstricted cells in several *E. coli* B/r H266 and B/r A populations have been calculated. In most populations, the correlation coefficient between diameter and length (r in Table 1) is very low, the

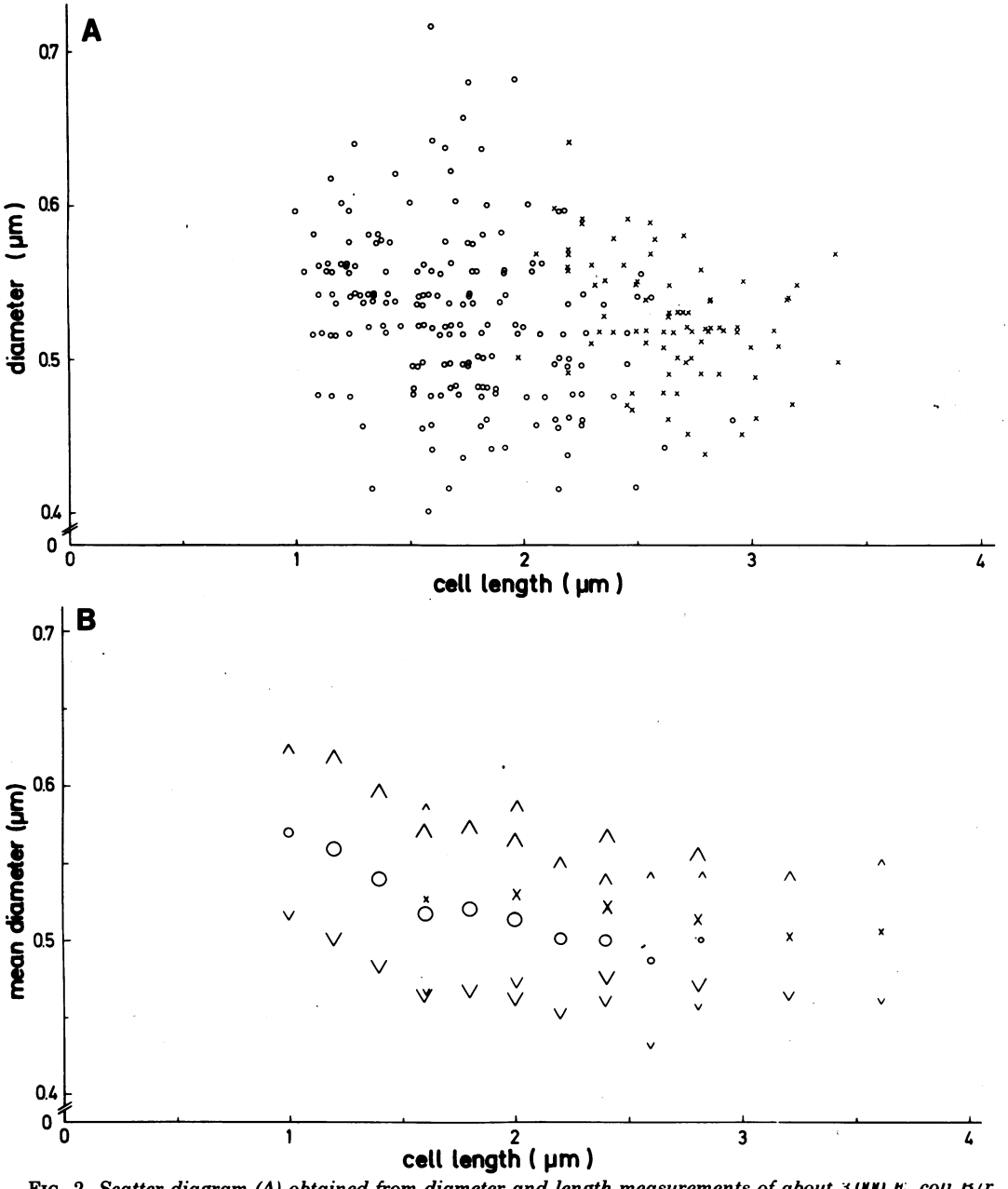

FIG. 2. *Scatter diagram (A) obtained from diameter and length measurements of about 3,000 E. coli B/r H266 cells, grown with a doubling time of 194 min and prepared by agar filtration. To avoid crowding of points, only a fraction of the cells has been plotted. (B) Mean diameter ($2\bar{R}$) per length class calculated from the same data as in A. Symbols: O, unconstricted cells; X, constricted cells (these are overrepresented to smooth the plot; in the original population only 13% of the cells are constricted); arrow tips indicate standard deviation. Note that the standard deviation is smaller for constricted cells because their diameter is calculated as the average of the two cell halves. The size of each symbol is proportional to the third root of the number of cells from which it is calculated, to show the different number of cells in each class.*

diameter at the end of the cell cycle being at most 8% less than that at L_0 μm (L_0, mean length of newborn cells). Nevertheless, statistical significance of the negative correlation as indicated by the upper 95% confidence limit was obtained in samples where enough cells could be meas-

ured. As can be seen from Fig. 2B, the negative correlation is most obvious at shorter cell lengths and levels off gradually with increasing length. As a result, higher correlation coefficients could be obtained for hyperbolical or quadratic relationships than for linear (data not shown).

In Fig. 3, the regression coefficients for unconstricted cells in all measured populations have been summarized. It can be seen that in almost every case the linear regression line between diameter and length was found to have a negative slope. Only in a few cases of rapidly growing cells was the slope positive. The results in Fig. 3 suggest that the negative correlation between diameter and length increases in absolute value with increasing doubling time.

Negative slopes for the diameter-to-length regression lines, similar to those found for unconstricted cells (Fig. 3), were also obtained for the three subpopulations of constricted cells (data not shown). However, as shown in Fig. 4, the average diameter of the deep-constricted cells was found to be larger than that of the slight-constricted cells or of the unconstricted cells of the same length. These observations are consistent with an increase in diameter during constriction and separation, i.e., at the end of the division cycle. This increase of the diameter of constricting cells is obscured by the thinner unconstricted cells if the diameter is calculated as the average of all four subpopulations in a length class.

E. coli cells divide approximately at their middle. The degree of symmetry of the cell halves depends on the strain (8) and on growth rate (unpublished data). In our experiments, the coefficient of variation of the ratio between length of cell half and length of mother cell (3) is 4 to 11%. In most constricting cells, we found that the shorter cell halves were thicker than

TABLE 1. *Parameters of correlation between diameter (2R) and length (L) of unconstricted E. coli B/r cells prepared by agar filtration*

Strain	Doubling time (min)	No. of cells measured	$\bar{L}$ (μm)	$2\bar{R}$ (μm)	CV^a (%)	b^b	r^c	Upper 95% confidence limit of r
B/r A	22.5	1,786	2.64	0.96	7.2	−0.006	−0.03	+0.06
B/r A	60	530	2.00	0.73	9.0	−0.039	−0.19	−0.10
B/r A	109	2,776	1.51	0.57	8.3	−0.033	−0.22	−0.15
B/r A	125	1,598	1.66	0.61	7.8	−0.033	−0.24	−0.19
B/r H266	194	2,098	1.68	0.53	10.7	−0.049	−0.33	−0.29

[a] *CV*, Coefficient of variation of the diameter.
[b] *b*, Regression coefficient of the least-squares regression line $2R = a + bL$.
[c] *r*, Linear correlation coefficient.

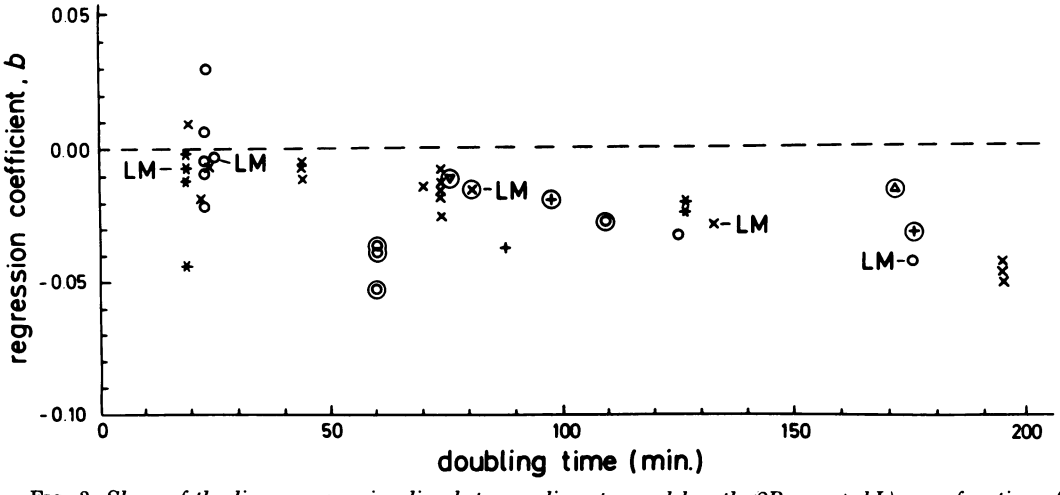

FIG. 3. *Slope of the linear regression line between diameter and length (2R = a + bL) as a function of doubling time. The slope b was calculated for the unconstricted cells in each population. Symbols: ○, B/rA; +, B/rK; X, B/r H266; *, K-12; △, PAT84; ▽, W7. The encircled symbols represent populations for which the steady-state condition was not ascertained. LM, light microscope observations (see Table 4).*

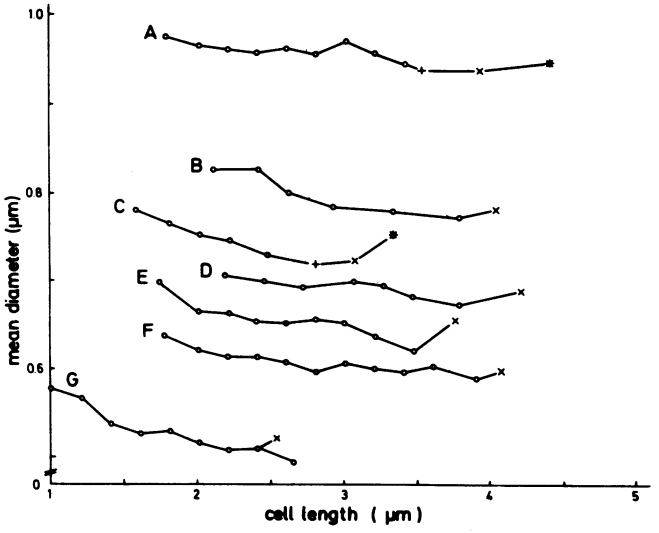

FIG. 4. *Changes in cell diameter during exponential growth of seven E. coli cultures. Each symbol represents the average diameter of at least 15 cells. The unconstricted cells* (O) *are grouped in length classes; the constricted cells are grouped all together (X) or, where enough cells were measured (A and C), according to their degree of constriction: slight-constricted* (+), *medium-constricted (X), and deep-constricted* (*). *A, strain B/r ATCC 12407, τ = 22.5 min; B, strain K-12 CR34; τ = 130 min; C, strain B/r ATCC 12407, τ = 60 min; D, F, and G, strain B/r H266, τ = 43, 72, and 194 min, respectively; E, strain B/r K, τ = 90 min.*

the longer halves. These observations, summarized in Table 2, show that variations in cell diameter can occur along the length of one constricting cell and therefore support our contention that cell diameter changes during the cell cycle (Fig. 6).

Diameter measurements in cells prepared by different methods. Cells prepared by agar filtration are dehydrated and have become flattened by surface tension during air drying. This flattening of the cells is indicated by the visibility of the nucleoplasms as electron transparent areas (Fig. 1) and is further evident from scanning electron microscopy of agar filters (24) and shadow-casting of air-dried cells (12). As a result of the drying process, a correlation between diameter and length of the cells could have been artificially induced or distorted. We therefore considered different methods of cell preparation to establish the diameter-length correlation in cells which have not become flattened.

The results summarized in Table 3 show that electron microscope techniques, such as thin-sectioning and critical-point drying, cause severe shrinkage of the cells as a result of dehydration with acetone or alcohol (see Fig. 4 in reference 24). The technique of freeze-drying also induces considerable cell shrinkage as compared to the light microscope measurements of living cells. The more laborious preparation of sacculi, recommended by Meacock et al. (12), did not, in our hands, result in the expected increase (57%) in diameter as a result of complete flattening of the cell perimeter, possibly because of the sensitivity of isolated sacculi to ionic strength and pH (R. W. H. Verwer, personal communication). Moreover, we have found that the necessary washing steps and the easy development of clumps of sacculi resulted in incomplete distributions, the smaller cells being left out. Table 3 also shows that, at three different growth rates,

TABLE 2. *Comparison of diameters of the cell halves of constricting E. coli (B. subtilis is included for contrast)*

Strain	Doubling time (min)	No. of cells	$2\bar{R}_s$ (nm)	$2\bar{R}_l$ (nm)	% Difference[a]
B/r A	22.5	697	941	937	0.43
B/r A	60	70	787	782	0.60
B/r A	125	1,195	615	612	0.49
B/r H266	20	241	951	936	1.59
B/r H266	45	55	638	631	1.10
B/r H266	69	80	675	667	1.19
B/r H266	72	139	587	584	0.51
B/r H266	194	491	479	477	0.42
CR 34	130	62	774	755	2.49
B. subtilis	65	909	812	811	0.12

[a] The percentage of difference between the diameter of the shorter ($2R_s$) and the diameter of the longer ($2R_l$) cell halves of each constricted cell is calculated from the averages with the formula $2(\bar{R}_s - \bar{R}_l)/(\bar{R}_s + \bar{R}_l) \times 100$.

TABLE 3. *Average cell diameter (μm ± standard deviation)[a] of E. coli B/r H266 grown at different doubling times and prepared by light and electron microscope techniques*

Cell prepn	Microscopy[b]	Doubling time (min)		
		20–24	42	72–78
Living cells	Ph.C.	1.02 ± 0.06[c] 0.94 ± 0.06 1.09 ± 0.07	0.74 ± 0.03	0.57 ± 0.07[c] 0.63 ± 0.07
Agar filtration[d]	EM	1.04 ± 0.04[c] 1.01 ± 0.08 1.19 ± 0.06	0.68 ± 0.05	0.55 ± 0.05[c] 0.56 ± 0.07 0.59 ± 0.04
Freeze-drying	EM	ND[e]	0.38 ± 0.02	ND
C.P.D.[f]	EM	0.66 ± 0.08	0.32 ± 0.03	ND
Thin-sectioning	EM	ND	0.51 ± 0.06	ND
Sacculi[g]	EM	1.08 ± 0.03[c] 0.89 ± 0.08	ND	0.39 ± 0.06

[a] Number of cells measured varied from 30 to 200.
[b] Ph.C., Phase-contrast microscopy; EM, transmission electron microscopy.
[c] Different values are from independent growth experiments.
[d] Cells prefixed with 0.1% OsO_4 and air-dried (see text).
[e] ND, Not determined.
[f] C.P.D., Critical point drying (reference 24).
[g] See for method of isolation reference 22.

the diameter of cells prefixed with 0.1% OsO_4 and air dried is well in agreement with that of living cells. Apparently the increase in diameter of flattening compensates for cell shrinkage as a result of dehydration.

On account of the above observations, light microscopy of living cells remained the only preparation technique comparable with agar filtration. In spite of the smaller number of cells measured, the results in Table 4 show that in living cells also, negative slopes were obtained for the regression lines. We therefore come to the conclusion that the correlation between diameter and length as observed in agar-filtered cells is not attributable to a drying artifact, but is a property of the growing cell.

B. subtilis. In contrast to *E. coli*, this organism is known to keep a constant diameter with changing growth rate (20). Within the division cycle also, the diameter can therefore be expected to remain constant. Figure 5 shows the diameter and length measurements of *B. subtilis* cells grown with a doubling time of 65 min and prepared by agar filtration (data obtained from reference 13). The analysis of correlation (r = +0.0011, with 95% confidence limits: +0.11 and −0.10) shows that in these cells the diameter is independent of length.

DISCUSSION

Our observations show that the diameter of *E. coli* cells decreases over most of the division cycle and rises again during the process of constriction and cell separation. Although the changes are small, the negative slopes of the regression lines are reproducible (Fig. 3) and even show statistically significant correlation in populations where enough cells have been measured (Table 1). That no such negative correlation has been observed by Marr et al. (11) might be attributed to (i) their preparation procedure, i.e., washing of the unfixed cells in distilled water before air-drying; (ii) the small number (214) of cells measured; and (iii) their pooling of both unconstricted and constricted cells. The observations on living cells (Table 4) support our contention that cell diameter changes during the cycle. Unexpectedly, we found in Henrici's classic book on the subject measurements of living cells that are in agreement with this conclusion (see p. 90–92 in reference 6).

TABLE 4. *Parameters of correlation between diameter and length of unconstricted living cells observed by phase-contrast microscopy*

Strain	Doubling time (min)	No. of cells measured	$2\bar{R}$ (μm)	CV[a] (%)	b[a]	r[a]	Upper 95% confidence limit of r
B/rA	22.5	262	0.85	9.2	−0.004	−0.024	0.10
B/rA	175	45	0.40	11.5	−0.043	−0.190	0.11
CR34	19	471	0.94	9.0	−0.007	−0.022	0.15
B/r H266	78	172	0.63	9.6	−0.016	−0.047	0.18
B/r H266	133	221	0.43	12.4	−0.029	−0.323	−0.15

[a] See footnotes *a*, *b*, and *c*, Table 1.

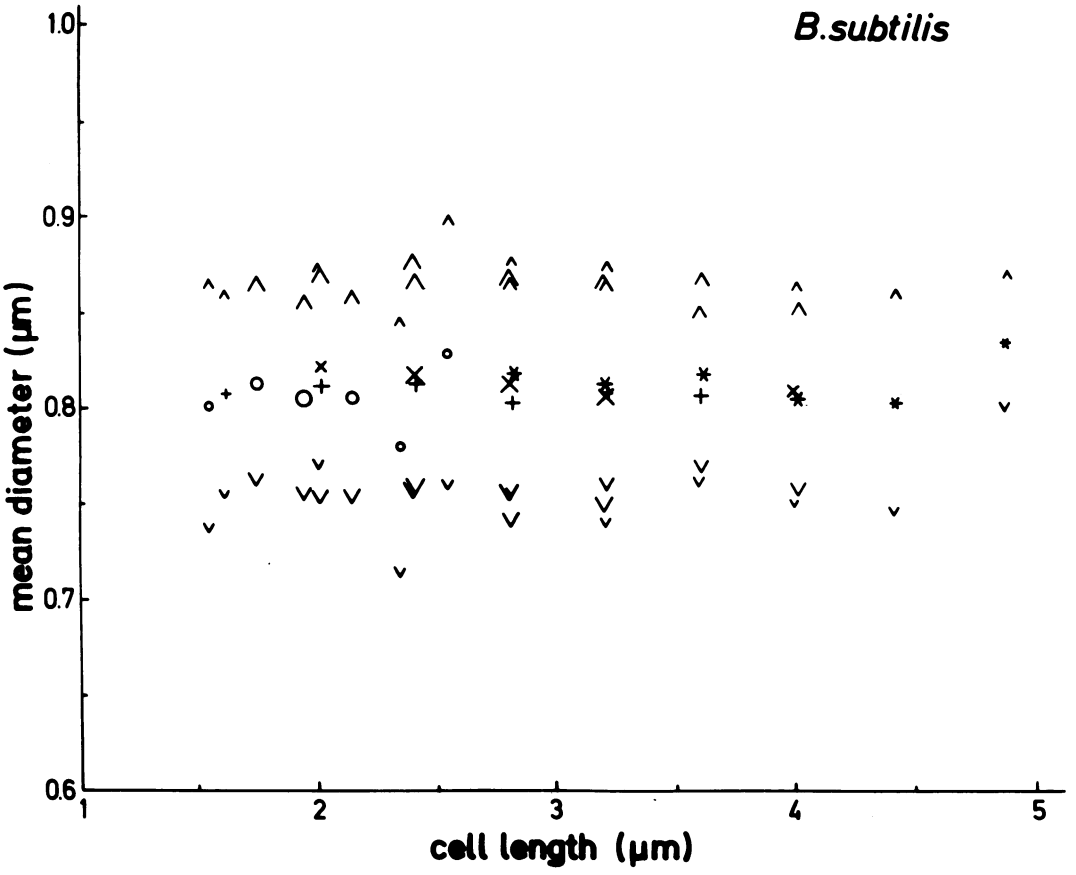

FIG. 5. *Average diameter per length class (2R) as a function of length in a population of 1,253 B. subtilis cells, grown with a doubling time of 65 min. Symbols: O, cells without septum or constriction; +, septated rods without constriction; x, slight-constricted and medium-constricted cells; *, deep-constricted cells. Compare this figure with Fig. 4.*

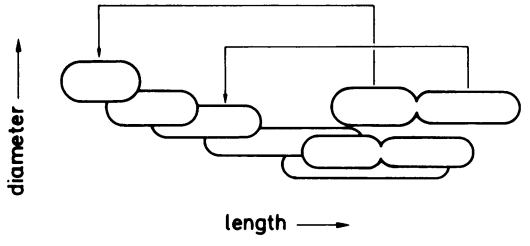

FIG. 6. *Diagrammatic representation of the change in cell dimensions during the life cycle of E. coli. Note the influence of the asymmetry of the constriction site on cell dimensions. The diameter and length scales are different.*

Nevertheless, the length-diameter relationship in agar-filtered cells may still have been influenced by the drying process. For instance, changes in cell composition during the cycle may result in different degrees of compression or shrinkage or both of the cells upon air-drying. That DNA concentration can influence cell diameter during air-drying is demonstrated by cells in which DNA synthesis has been inhibited for a short period. The small filaments thus obtained contain a centrally located spherical nucleoid and show, after air-drying, a local increase in diameter in the form of a central bulge (observations not shown). In a similar way can be explained the results of Meacock et al. (12), who observed that the degree of flattening of cells becomes less when the DNA concentration in the cell decreases. This explanation also seems applicable to asymmetrically constricting cells, where the two cell halves probably have a similar DNA content but different DNA concentrations. They may, therefore, become flattened differently although both cell halves will dry under identical microconditions on the agar filter.

To understand the diameter fluctuations in growing cells, different mechanisms have to be considered, such as changes in the rate of surface synthesis relative to that of cell mass increase.

Such a mechanism has been proposed (17) to explain the increase in average diameter with growth rate (2, 8, 14). In an analogous way, diameter changes in an individual cell could result from different rates of surface and mass increase during the cycle, as proposed in recent growth models (2, 18). These models predict a maximum for either cell density or cell diameter at a certain period before cell division, at which time the rate of elongation (2) or surface synthesis (18) doubles. According to these models, cell diameter may either increase or decrease during large parts of the cycle, depending on the growth rate. Because our results suggest that diameter decreases during most of the cell cycle at all doubling times (Fig. 3), the present models cannot help in explaining our observations.

In contrast to the above growth models, it can be assumed that surface area (A) and volume (V) increase at the same rate during the cell cycle, so that the ratio between surface and volume remains constant. If, in addition, the cell is assumed to be a cylinder with hemispherical caps, it can be shown (see Appendix) that, during elongation, cell diameter must decrease to prevent the otherwise occurring decrease in the surface-to-volume ratio. According to this model, the diameter will increase again to its original value during the constriction process. Although this prediction fits well with some of our observations (Fig. 7B-G), the predictions of the model are independent of growth rate and cannot explain why the negative correlation between diameter and length of the unconstricted cells (Fig. 3) decreases with increasing growth rate (Fig. 7A). A combination of periods in which the surface-to-volume ratio remains constant with others in which this ratio changes could explain the present results, but we feel that such an explanation would be too artificial and would have to be reviewed when more exact diameter-length relationships are found.

On the assumption that the cell wall is able to withstand considerable hydrostatic pressure, Rosenberger et al. (18) have proposed previously that cell density changes during the cycle. However, the density differences which can be expected for the individual cells in a population are much smaller than those predicted on theoretical grounds (18) or those claimed by Poole (15). This we deduce from observations with density gradients in which the average densities of *E. coli* populations grown at different growth rates were found to differ by less than 1% (9, and our unpublished observations with Percoll gradients); nevertheless, the mixed cells of two *E.*

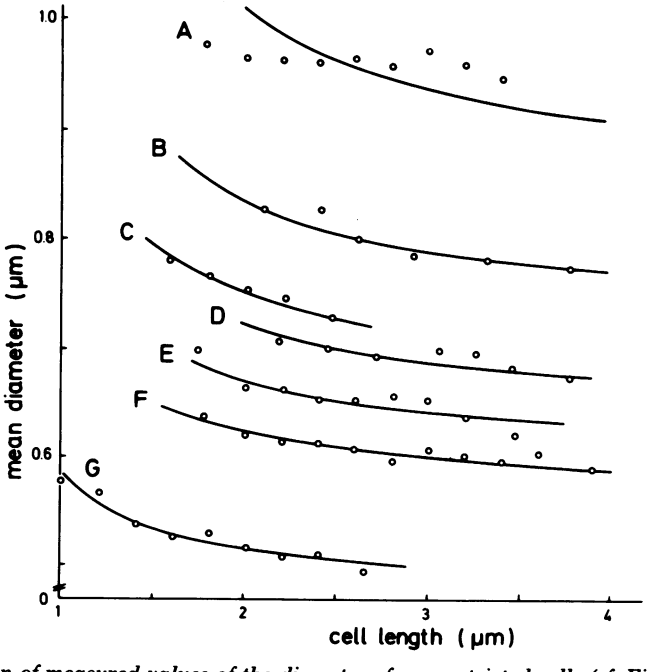

FIG. 7. *Comparison of measured values of the diameter of unconstricted cells (cf. Fig. 4) with theoretical values of the diameter as a function of length (see equation 5 in Appendix). The parameters R_1 have been approximated from the empirical $\bar{L}$ and $2\bar{R}$ of each population, with the formula $R_1 = 3/2 \cdot \bar{R} - \bar{R}^2/\bar{L}$, derived from equation (5). Symbols and labels as in Fig. 4.*

coli B/r H266 populations (doubling times 72 and 20 min) could be fully separated into two narrow bands (data not shown). This means that within one band, i.e., between individual cells of one steady-state population, the density differences are much less than 1%.

In conclusion, our observations show that the diameter of *E. coli* cells changes during the cell cycle in a systematic way, which is not predictable by the present growth models on mass and surface synthesis. The results, however, conform well to the observations of R. W. H. Verwer, C. G. van Eden, and N. Nanninga (manuscript submitted for publication) who found that the internal osmotic pressure of *E. coli* cells, as indicated by their susceptibility to plasmolysis, decreased during elongation and increased again during constriction. Whether the cell wall is able to contract or expand in response to the internal hydrostatic pressure of the cell is currently being investigated.

APPENDIX

Consider the geometry of an *E. coli* cell to be a cylinder with hemispherical polar caps. Its surface, A, is then given by

$$A = 2\pi R\,(L - 2R) + 4\pi R^2 = 2\pi RL \qquad (1)$$

where L is the length and R is the radius of the cell. The volume (V) of the cell is given by

$$V = \pi R^2\,(L - 2R) + 4/3\cdot\pi R^3 = \pi R^2\,(L - 2/3\cdot R) \qquad (2)$$

If surface area increases at the same rate as mass, then, at a constant density of the cell

$$A/V = 2L/R\,(L - 2/3\cdot R) = \text{constant} \qquad (3)$$

If for a cell L equals $2R_1$ (a sphere), we have:

$$A_1/V_1 = 2\cdot 2R_1/R_1\,(2R_1 - 2/3\cdot R_1) = 3/R_1 \qquad (4)$$

Equating (4) and (3), we obtain:

$$A/V = A_1/V_1 = 2L/R\,(L - 2/3\cdot R) = 3/R_1$$

from which we can resolve R as a variable of L:

$$R = (3L \pm \sqrt{9L^2 - 16R_1L})/4 = 3/4\cdot L - \sqrt{9/16\cdot L^2 - R_1L} \qquad (5)$$

Equation (5) implies that if $L \to \infty$ (filamentation), $R \to 2/3\cdot R_1$, i.e., very long cells have a constant diameter. Figure 7 shows how this equation fits to our experimental data. We emphasize that equation (5) holds only if the shape of the cell is of the idealized kind that has been assumed and as long as A/V is constant. The relationship (5) is independent of other variables, like growth rate or size of the cells.

That the diameter decreases during elongation can also be envisaged in the following way: if elongation would proceed at a constant diameter, the volume of a cell at division without new polar caps, will be larger than that of the two newborn cells after its division (i.e., A/V decreases). To keep A/V constant, the diameter must decrease during elongation. On the other hand, during constriction and cell division, the diameter will increase again to compensate for the otherwise occurring increase of A/V.

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