TABLE 2 Macromolecular composition of exponentially growing *E. coli* B/r as a function of growth rate at 37°C[a]

Parameter	Symbol	Units	At τ (min) and μ (doublings per h): τ, 100 μ, 0.6	τ, 60 μ, 1.0	τ, 40 μ, 1.5	τ, 30 μ, 2.0	τ, 24 μ, 2.5	Observed parameter(s)	Footnote
Protein/mass	P_M	10^{17} aa/OD_{460}	6.5	5.8	5.2	5.1	5.0	*P*, *M*	*b*
RNA/mass	R_M	10^{16} nucl./OD_{460}	4.3	4.9	5.7	6.6	7.8	*R*, *M*	*c*
DNA/mass	G_M	10^{8} genomes/OD_{460}	18.3	12.4	9.3	8.0	7.6	*G*, *M*	*d*
Cell no./mass	C_M	10^{8} cells/OD_{460}	11.7	6.7	4.0	2.7	2.0	Cells/OD_{460}	*e*
$(P + R + G)/M$	PRD_M	μg/OD_{460}	149	137	129	131	136		*f*
Protein/genome	P_G	10^{8} aa residues	3.5	4.7	5.6	6.3	6.6	P_M, G_M	
RNA/genome	R_G	10^{7} nucl. residues	2.3	4.0	6.1	8.2	10.3	R_M, G_M	
Origins/genome	O_G	Dimensionless	1.25	1.32	1.44	1.58	1.73	*C*	*g*
Protein/origin	P_O	10^{8} aa residues	2.8	3.6	3.9	4.0	3.8	P_G, O_G	*g*
Protein/cell	P_C	10^{8} aa residues	5.6	8.7	13.0	18.9	25.0	P_M, C_M	
	P_C (μg)	μg/10^{9} cells	100	156	234	340	450		*h*
RNA/cell	R_C	10^{7} nucl. residues	3.7	7.3	14.3	24.4	39.0	R_M, C_M	
	R_C (μg)	μg/10^{9} cells	20	39	77	132	211		*h*
DNA/cell	G_C	genome equiv./cell	1.6	1.8	2.3	3.0	3.8	*C*, *D*	*i*
	G_C (μg)	μg/10^{9} cells	7.6	9.0	11.3	14.4	18.3		*h*
Mass/cell	M_C	OD_{460} units/10^{9}cells	0.85	1.49	2.5	3.7	5.0	C_M	*j*
	M_C (μg)	μg dry weight/10^{9} cells	148	258	433	641	865	μg/OD_{460}	*k*
Sum $P + R + G$	PRD_C	μg/10^{9} cells	127	204	322	486	679	P_C, R_C, G_C (in μg)	*k*
Origins/cell	O_C	no./cell	1.96	2.43	3.36	4.70	6.54	*C*, *D*	*l*
Termini/cell	T_C	no./cell	1.23	1.37	1.54	1.74	1.94	*D*	*l*
Replication forks/cell	F_C	no./cell	1.46	2.14	3.64	5.92	9.19	*C*, *D*	*l*

[a]Data are representative for the growth rates indicated, with an accuracy of ±10% or better. In compiling the data in this table and Table 3, we have been guided by the principle that, on average, parameters like protein, RNA, DNA, and cell number per mass, and their quotients, i.e., protein and RNA per genome, or the per-cell values, should have smooth functions of growth rate. (If two primary data were 5% off the true average, their quotient might contain a 10% error and thus make it impossible to draw a smooth line through the points.) In addition, we have checked for consistency if measurements were available from independent methods or involved theoretical relationships between different parameters. The data in our tables closely meet these criteria. For example, RNA, measured as absorption at 260 nm (A_{260}) of RNA hydrolysates, does not require a calibration standard; therefore, the RNA values are assumed to be quite accurate. Since the RNA-to-protein ratios from this table generated the same α_r curve as that determined from purified ribosomal particles (Table 3), we have confidence in both RNA and protein values. The amount of DNA per mass was measured independently with a colorimetric assay calibrated with purified *E. coli* DNA and by radioactive pyrimidine labeling of nucleic acids. The latter method gives the RNA-to-DNA nucleotide ratio which, combined with the absolute (presumably reliable) value for RNA per mass, gives DNA per mass (45). Again both methods gave essentially the same values. Thus, all three macromolecular concentrations (per mass) in this table have consistent values which are presumably accurate to better than 10% and representative for that growth rate. Representative per-cell values were more difficult to obtain, in part because the duration of the (average) *D* period, which affects the cell size and per-cell values, fluctuates considerably from culture to culture; this fluctuation is independent of and in addition to the variation in *D* from cell to cell within one culture (24). The DNA per cell values have been determined directly from DNA and cell numbers per mass and indirectly from the *C* and *D* periods. Both methods gave essentially the same DNA content of the average cell. Abbreviations: aa, amino acid; nucl., nucleotide; equiv., equivalent.

[b]Cell mass density was determined as OD_{460} using a 1-cm light path (27). Protein was determined by a modification of the method of Lowry et al. (20, 92), using (weighted) bovine serum albumin as a calibration standard and assuming 5.6×10^{15} amino acid residues per μg of protein. The values shown are from Fig. 3 of Churchward et al. (29).

[c]RNA was determined as A_{260} of acid-insoluble, alkali-labile cell mass (20). One A_{260} unit at pH 2 corresponds to 5.6×10^{16} nucleotides, assuming the mole fractions of A, U, G, and C in *E. coli* stable RNA to be 0.248, 0.210, 0.324, and 0.218, respectively (102). The RNA values shown are from Churchward et al. (28).

[d]DNA per mass was calculated from DNA per cell and cells per mass: $G_M = G_C \cdot C_M$. These calculated values closely agree with direct measurements of DNA per mass (Fig. 1 of reference 29), using the colorimetric diphenylamine reaction with *E. coli* DNA as a calibration standard and assuming 1 A_{260} unit of *E. coli* DNA at pH 12 to correspond to 2.86×10^{13} kbp (for a GC content of 0.50) and the *E. coli* genome to be 4,700 kbp (4).

[e]Cell numbers were determined using a Coulter Counter with a 20-μm orifice. The values shown are from Fig. 6 of Shepherd et al. (125).

[f]The sum of the weights of protein, RNA, and DNA per mass was calculated from the sum of the weights per cell (see footnote *h*, this Table) and cells per mass: $PRD_M = PRD_C \cdot C_M$.

[g]The number of replication origins per genome was determined from the value of the *C* period (Table 3), using equation 11 in Table 5 below.

[h]The weights of protein, RNA, and DNA were calculated, assuming the average molecular weight of an amino acid residue in *E. coli* protein to be 108 (composition of *E. coli* protein from reference 133), that of an RNA nucleotide residue to be 324 (composition of *E. coli* stable RNA from reference 102), and that of a DNA base pair to be 618 (for a GC content of 0.50), respectively.

[i]The average amount of DNA per cell, in genome equivalents, was calculated from the values of *C* and *D* (Table 3), using equation 3 in Table 5 below. These calculated values agree with direct (colorimetric) measurements of DNA and cell numbers per mass (reference 28; see footnote *d* in this Table).

[j]The average cell mass in OD_{460} units is the reciprocal of the cell number per OD_{460}, i.e., $M_C = 1/C_M$.

[k]The cell mass in micrograms dry weight was calculated, using the value of 173 μg per OD_{460} unit of culture mass (20).

[l]The average numbers of replication origins, termini, and replication forks were determined from the values of *C* and *D* (Table 3), using equations 7, 8, and 10, respectively, of Table 5 below.