INTRODUCTION

Biochemical research, particularly over the past 50 years or so, has revealed ever more clearly the underlying unity of living processes. And this possibly has obscured to some extent the fact that there are nevertheless important physiological differences between microbial cells and, say, the cells of higher animals. One of the most fundamental of these, and one which undoubtedly has considerable evolutionary significance, is evident in the ways in which the different cells accommodate to environmental change. Clearly, the cells of higher animals have evolved to spend the whole of their existence in a closely regulated environment, and this is a condition of life for them. But microbial cells are markedly different. They generally are exposed to environments that fluctuate extensively (and often rapidly) and, being free-living creatures, they do not possess the capacity to regulate their surroundings. Instead, they respond to environmental change by changing themselves—structurally and functionally—and seemingly have acquired in the course of evolution a whole armoury of sophisticated control mechanisms whereby to effect such change. As most people realize, it is this enormous versatility of microbial cells (their structural and functional plasticity) that makes them economically, as well as ecologically, of considerable importance; it also makes them fascinating objects for study.

One serious problem, however, faces persons attempting to study this so-called phenotypic variation; that is, that microorganisms interact with their environment in a way that causes it to change continuously. Consequently, if one grows microorganisms in a closed system (that is, the classical batch culture method) one cannot obtain prolonged steady state environmental conditions; and
one then must recognize that inevitably one will be dealing with populations whose properties are changing continuously with time. There is only one practical way around this problem and that is to grow organisms in an open system - that is, a continuous-flow culture system. Moreover, if one employs the chemostat mode of continuous culture then further benefits accrue in that not only can one obtain a wide range of controlled environments, but also a range of unique environments in which organisms may express properties that are not otherwise expressed, or expressed only transiently. And by relating these properties to the precise conditions provoking their expression, insight frequently may be gained into their functional significance. It is the purpose of this article to detail some of these properties and to place them in a rational physiological context.

Before proceeding to a detailed description of microbial response to nutrient-limited environments, however, it is useful to consider in a little more detail the question of cell-environment interaction as it may relate to the behaviour of organisms in natural ecosystems. For, as already indicated, it is logical to suppose that the physiological plasticity of microorganisms is related to their need to cope with the vicissitudes of life outside the laboratory culture. In this connection, it is relevant to draw attention to the enormous growth rate potential of most microorganisms which we study routinely. For example, in broth culture, *Escherichia coli* is able to double in mass within 20 min. Thus, if one *E. coli* organism (weighing about 0.2 pg) and its progeny were to grow at an unrestricted rate for as little as 3 days, then there would be produced a mass of organisms equal to about 1000-times the mass of the Earth. So why is it, one might reasonably ask, that the surface of this planet is not deep with *E. coli*? The simple answer must be that, in natural ecosystems, organisms rarely grow at their potentially maximum rate. Hence it is important to consider why this is so: or, to put it another way, to consider what may constrain the growth of organisms in natural ecosystems. Many factors, of course, may play a part; microorganisms may be limited in their growth by extremes of temperature, pH, salinity and/or water activity, as well as by the presence of noxious substances, predators and parasites. But over and above these, one factor that will consistently constrain the rate at which these populations grow must be the availability of nutrient substances. For what we know with certainly is that heterotrophic organisms require to consume at least 2 g of some carbon substrate (such as glucose) to synthesize 1 g of biomass. Consequently, irrespective of other considerations, the availability of nutrient substances always would ultimately limit the extent to which any population could grow - be it in the laboratory culture or in some natural ecosystem. On the basis of this argument, then, it is reasonable to conclude that nutrient insufficiency will be the most common environmental extreme to which microorganisms are routinely exposed and that, in consequence, such conditions will have exerted