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A theoretical study of pure and simple competition between two microbial species in configurations of two interconnected chemostat

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ABSTRACT

Title of Thesis: A Theoretical Study of Pure and Simple Competition between two Microbial Species in Configurations of two Interconnected Chemostats

Cheng-Ming Kung, Master of Science in Chemical Engineering, 1986

Thesis directed by: Dr. Basil C. Baltzis

It is known that two microbial populations competing purely and simply for a common substrate cannot coexist in a steady state in an environment which is spatially homogeneous. Hence they cannot coexist in a chemostat something which implies that a mixed culture of two pure and simple competitors cannot be maintained in a single ideal reactor in a steady state. The present study investigates theoretically pure and simple competition between two populations in two interconnected chemostats. Three reactor configurations are considered and analyzed. It is proved that two pure and simple competitors can coexist in a steady state in both reactors in cases where the conditions are such that they favor the growth of one species in one reactor and the growth of its competitor in the other vessel. It is then concluded that spatial inhomogeneities can lead to steady state coexistence of pure and simple competitors. The results of this study have been derived analytically and numerically. The dynamic behavior of the system at all possible steady states has been studied analytically. A number of conditions sufficient and/or necessary for the existence of each one of the possible steady states have been derived also analytically. The numerical studies have shown that one can always find a range in the operating parameters space where coexistence occurs, that the steady states are mutually exclusive and that no steady state exhibits multiplicity. The results are presented in series of two-dimensional operating diagrams and the effect of all parameters on the behavior of the system is studied and discussed in detail. It has been also proved that it is not necessary for coexistence to externally feed both vessels with nutrient medium and that there is a design configuration which makes the environment always homogeneous in which case coexistence is impossible.

A THEORETICAL STUDY OF PURE AND SIMPLE COMPETITION BETWEEN TWO MICROBIAL SPECIES IN CONFIGURATIONS OF TWO INTERCONNECTED CHEMOSTATS

BY
CHENG-MING KUNG

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of
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INTRODUCTION

Microorganisms may be most well known as agents that cause disease and spoil food. Nevertheless they are presently employed by man in quite a number of significant industrial operations. Fermentation technology—the most established branch of biochemical engineering—refers to those situations in which the technologist uses the activities of microorganisms to increase the value of raw materials. Sanitary or environmental engineering refers to those situations in which the technologist uses the activities of microorganisms in order to decrease the negative value of aqueous waste materials discharged to the environment. The activities of microorganisms can be also employed by the mining industry on a large scale to leach certain elements from their ores. Still another area where man might eventually utilize microbial activities on a very large scale is that of the capture and conversion of solar energy [1], an idea that enjoyed a lot of support in the period of oil crisis.

The fermentation industry uses mainly pure culture techniques. Probably the main reason for doing so is that in most cases the product is a complicated, valuable organic molecule which can be made by a single microbial population, and when such a population has been isolated and improved one does not want to introduce other microorganisms which might compete with or be antagonistic to the product yielding population. Nevertheless, there are reasons for studying the behavior of populations in mixed cultures. First, certain industrial operations, notably waste disposals, do utilize mixed populations. Second, invasion by contaminants or formation of mutants turn a pure culture into a mixed one. Third, mixed cultures offer some potential advantages, such as (i) ability to perform sequences of chemical transformations which no pure culture can do, (ii) ability to grow on simpler and hence cheaper media, (iii) ability to continue functioning over a wider range of environmental conditions, (iv) ability to resist invasion by contaminants. Finally, a fourth reason for studying mixed cultures is that natural systems always involve the activities of mixed cultures [2].

The main thing which makes pure culture techniques fundamentally different from those of mixed culture is that populations of microbial species interact between one another when they find themselves in a common environment. There are many types of microbial interactions and they have been classified [2] into two categories: direct and indirect. Parasitism and feeding are two examples of direct interactions. Competition, antagonism, commensalism and mutualism are some examples of indirect interactions. The present study deals with some aspects of microbial competition, an interaction which is discussed in the following.

Microorganisms in order to grow and proliferate need chemicals and available energy. The chemicals are used to supply elements such as carbon, oxygen, nitrogen, sulfur while available energy is used to synthesize molecules and to maintain life. These common needs give rise to competition, which occurs in all but the simplest ecosystems [3].

Osmotrophic organisms—such as bacteria, yeasts molds and microalgae—obtain chemicals by molecule-by-molecule or ion-by-ion transfer of the chemicals across their cell membranes. Phagotrophic organisms, such as many protozoan populations, obtain chemicals by ingesting and digesting particular matter and then absorbing the products of digestion. Evidently, phagotrophic microorganisms are more likely to prey on osmotrophic microorganisms than to compete with them. However, populations of phagotrophic microorganisms are likely to compete with one another for resources of particular matter, and populations of osmotrophic microorganisms are likely to compete for resources of chemicals [3].

The different ways microorganisms satisfy their needs for carbon divide them into two main categories. Heterotrophic microorganisms obtain carbon by uptaking organic compounds, phagotrophically or osmotrophically, whereas autotrophic microorganisms obtain carbon by uptaking carbon dioxide. Synthesis of organic compounds from carbon dioxide requires a supply of available energy. Photoautotrophs obtain this energy by absorbing light, whereas chemoautotrophs or chemolithotrophs obtain it by oxidizing certain inorganic compounds. Evidently, heterotrophs that are also osmotrophs will compete for organic compounds present in their environment, but they will not compete for such compounds with chemolithotrophs that are present. Photoautotrophs will compete similarly for light. Although heterotrophs do not have to compete with autotrophs for organic compounds, they may compete with autotrophs for other chemicals such as nitrogen or phosphorus [3].

Some microbial populations, called generalists, use several to many different chemical compounds to satisfy the same need in their subcellular economy (e.g. carbon), whereas other populations, called specialists, are obligately dependent on one compound or perhaps a few compounds to satisfy such a need. Some things that a generalist population uses will be most likely exempt from competition with a specialist population and this can have important effects to the outcome of competition [3].

From the discussion above it follows that there are many different patterns of competition that need to be classified. But first one needs to give the exact definition for competition. Populations P_1 and P_2 compete for resource ρ if and only of (i) both P_1 and P_2 use, but do not necessarily require, ρ and (ii) resource ρ has a dynamical effect on at least one of the populations, and possibly on both of them. Resource ρ has a dynamical effect on a population if its availability at any time has a significant effect on the net growth rate of that population [3]. It is emphasized that populations P_1 and P_2 are not said to compete for ρ when neither is dynamically affected by it, even though both use it.

One way to classify the patterns of competition is by counting the number of resources competed for: if one resource is competed for, competition is single, and if two are competed for it is double and so on. If competition is the only interaction between two populations, it is called pure.

Pure and simple competition which is the topic of the present thesis, arises in the case where the availability of a single nutrient affects the growth rate of at least two populations. A detailed classification of all patterns of competition has been offered by some researchers [3,4] with definitions based on the set theory.

Continuous culture techniques are based on the use of a chemostat. This is a vessel fed at a constant rate with sterile nutrient medium of constant composition and from which culture is removed at the same volumetric rate at which fresh medium is added. The culture is kept spatially homogeneous by mixing.

Most of the existing studies on competition, reviewed in the following section, are done for spatially homogeneous environments and they have concluded that pure and simple competitors cannot coexist in a steady state.

The present study entails finding if the same conclusion holds when the environment is spatially heterogeneous.

LITERATURE REVIEW

Several researchers have examined the dynamics of a chemostat in which two populations of microorganisms grow competing for the same rate-limiting nutrient. Their analysis showed that competition of two populations for a single rate-limiting nutrient leads to extinction of one of the populations if they are grown in a spatially uniform environment that is subject to time-invariant external influences. The above statement, or rather a less cautiously worded version of it, is known as the competitive exclusion principle [5], and its validity and applicability have been the subjects of much discussion among ecologists. This nonexistence of a coexistence steady state has been amply demonstrated both on microbial and nonmicrobial competitors [6-12]. However, it is commonly observed that populations which compete with one another do coexist in natural ecosystems; this apparent contradiction to the competitive exclusion principle has been called the paradox of the plankton by Hutchinson [13]. The paradox may be resolved in various ways, among which the most common are (i) the environment is not spatially homogeneous and (ii) the external conditions influencing the environment are not time-invariant. In such a case one population here or now has the competitive advantage, whereas the other population there or then has this advantage [14].

The paradox of the plankton is that the examination of a small volume of water (e.g. 10ml) usually yields a list of some tens of species while the competitive exclusion principle might lead one to expect only one or a few species. Hutchinson [13] believes that the main answer to the paradox of the plankton lies in the false assumption of the plankton being in an equilibrium state. Since conditions change in the plankton habitat, perhaps one, and then another, organism is the superior competitor, the succession of conditions being so rapid that no one organism has the advantage long enough to cause the extinction of the others.

Riley [15] offers another explanation to the paradox. He believes that natural selection has caused phytoplankton to approach asymptotically some upper limit of efficiency which makes differences between species so small that extinction, even in an equilibrium state, would proceed at a very slow rate.

After examining a series of samples from Castle lake, California and Tahoe, California-Nevada, Richerson et al [16] proposed the contemporaneous disequilibrium model to explain the paradox of the plankton. According to their hypothesis, at any instant of time, many patches of water exist in every one of which one species is at a competitive advantage relative to the others. These water masses are stable enough to permit a considerable degree of patchiness to occur in phytoplankton, but are obliterated frequently enough to prevent the exclusive occupation of each niche by a single species. This hypothesis differs from Hutchinson's by stressing the contemporaneous, rather than temporal, heterogeneity of the plankton habitat. Yet, these two nonequilibrium hypotheses are not contradictory, but they rather reinforce one another.

Grenney et al [17] developed a mathematical model to represent phytoplankton growth dynamics. The model which incorporates intracellular nutrient storage is used to demonstrate the succession of blooms and coexistence of species in phytoplankton communities as influenced by temporal changes in environmental conditions. Thus, an organism's ability to compete at any instant of time is based not only on current environmental conditions, but also on the past history of nutrient uptake (e.g. storage).

Based on the idea of repeated alteration of density dependent (competition phase) and density independent growth (unrestricted growth phase) Koch [18] used computer simulation to show that coexistence of two populations was possible if one had the advantage on density dependent periods while the other had the advantage on density independent periods. This predicted coexistence though, does not occur at a steady state but in an oscillatory mode.

Peterson [19] suggested that an assemblage of coexisting phytoplankton may be limited by several, not a single, nutrients each species being principally limited by the availability of a different nutrient. The principal assumption of the model is that each species is less effective at obtaining the nutrient of which it requires larger amounts when this nutrient is present at low concentration. The model offered an explanation for the coexistence of associated phytoplanktons in a stable equilibrium in continuous culture. This approach implied that competition is not single (i.e. for one nutrient only).

Titman [20] ran a series of experiments using mixed cultures of Asterionella formosa and Cyclotella meneghiniana which are potentially rate-limited by phosphate (PO_4) and silicate (SiO_2) in order to confirm that coexistence occurred only when the growth rate of each species was limited by a different resource. There were seventy-three experiments performed at different flow rates, and at various ratios of SiO_2 to PO_4 concentration so that both or either of them was rate-limiting. The results showed that if both species were grown together under PO_4 limitation A. formosa was the dominant species, while under SiO_2-limited growth conditions C. meneghiniana was the superior competitor. Under conditions of both PO_4 and SiO_2 limitation, in most cases both species coexisted indefinitely. These experiments support the ecological concept that as many competing species coexist as there are limiting resources, a hypothesis also used to explain the paradox [13].

Harder and Veldkamp [12] studied the maximum specific growth rates of obligate and facultative psychrophiles from low to high temperatures. At low temperatures obligate psychrophiles have a maximum specific growth rate higher than the facultative ones while the opposite is true at high temperatures. As a consequence, in a chemostat mixed culture obligate psychrophilic Pseudomonas species (L12) prevailed at low temperature (-2°C), while facultative psychrophilic Spirillum species (L5) always won the competition at high temperature (16°C). At intermediate temperatures (4 & 10°C), obligates won at high dilution rates, while facultatives prevailed at low dilution rates. These experiments prove that temperature also plays an important role on population dynamics, something which is sometimes ignored. In fact if the temperature is cycled between high and low values for the system described above the result can be coexistence of the two competitors in a state of sustained oscillations. In order for this to happen the cycling must be done in such a fashion so that one population has the advantage over a temperature range while the other population grows faster over another temperature range.

Powell [21] studied the growth of contaminants and mutants in a chemostat having a constant input. The interaction between the organism and the contaminant (or mutant) was assumed to be pure and simple competition. He claimed that either population could survive alone at either high or low dilution rates. In mixed culture though, if the growth rate of one of the organisms was always less than that of its competitor, it never established itself. As a result, contaminant organisms or mutants which appear in a continuous culture can grow successfully only when their maximum specific growth rate and saturation constants stand in a certain relation to the constants of the native organisms and to the rate of flow through the culture vessel. This study then provided answers to the following two questions: can the chemostat be operated so that two competitors coexist in a steady state? If the chemostat is operated in such a way that one competitor is excluded, what is it that determines which population is excluded? The aforementioned questions have been addressed both experimentally and theoretically by many other researchers as well.

Jannasch [10] concluded from his experiments that a chemostat inoculated with a mixed population would select for the organism that exhibits the fastest growth rate under the specific conditions (composition of medium, temperature, etc.). In his experiments, 0.1 to 10 mg/liter of lactate, glycerol, or glucose were added to filter-sterilized offshore seawater; ammonium and phosphate were added in sufficient concentrations to ascertain growth limitation by the carbon and energy source.

Meers [11] grew Bacillus subtilis var. niger and Torula utilis under magnesium-limited conditions in a chemostat. The dilution rate used was either 0.005 or 0.08 h^{-1}, both dilution rates being well below those at which the organisms would be washed out from the culture (i.e. 0.7 and 0.5 h^{-1}, respectively). Bacillus subtilis replaced the yeast at the higher dilution rate, but the reverse was true at the lower dilution rate. Coexistence was not observed.

Megee et al [8] worked with a mixed culture of Saccharomyces cerevisiae and Lactobacillus casei grown anaerobically in a chemostat under conditions of relatively low glucose concentration. Although the yeast has a slightly greater growth rate than L. casei, this advantage of the yeast is more than cancelled by its susceptibility to death by starvation and by its relatively high Michaelis constant

(K_s), which does not allow the yeast to develop its maximum specific growth rate except at relatively high substrate concentrations. Hence it was observed that the bacteria eventually prevailed in the chemostat.

Jost et al [9] studied the competition between E. coli and A. vinelandii for glucose in continuous culture. In about two days, Azotobacter got washed out to less than 10% of its initial density, and the glucose level dropped to a point where it was no longer measurable. Similar data were obtained at holding times from 5.6 to 23 hrs. In all cases, E. coli displaced Azotobacter. Both species followed Monod's model for the specific growth rate. The maximum specific growth rates for E. coli and Azotobacter were 0.32 hr^{-1} and $0.23hr^{-1}$ while the values for the saturation constant (K_s) were $1x10^{-7}$ mg/ml and $1.2x10^{-2}$ mg/ml, respectively. These values imply a tremendous competitive advantage for E. coli in the medium used.

Taylor and Williams [22] studied competition between two species for two substrates in a chemostat. This is a case of competition which is not simple. They used a multiplicative (interactive) model in order to express the specific growth rate of each competitor. They showed that coexistence in a steady state is possible provided that certain conditions on the yield coefficients are satisfied.

Aris and Humphrey [23] studied the dynamics of a chemostat where pure and simple competition occurs for the case where the resource competed for has an inhibitory effect on the growth of the competitors especially when its concentration is high [24]; in this case, coexistence occurs only for discrete values of the chemostat dilution rate something which cannot be achieved in practice.

Hsu et al [25] studied in a mathematically rigorous fashion the case where n species growing according to Monod's model compete for a single resource in a chemostat. They showed that only one species will eventually survive under given conditions of operation.

From the experimental and theoretical studies discussed above it becomes clear that pure and simple competition under conditions of spatial homogeneity and time-invariant external influences never leads to coexistence of the competing species. Furthermore, the winning species is always that which grows faster than all others.

The constraint of temporally invariant inputs to a chemostat has been relaxed in some studies.

The operation of a periodically forced chemostat in which two microbial populations compete for the same nutrient was studied by Stephanopoulos et al [26]. It was found that the cycling of the concentration of the substrate in the feed and/or the dilution rate between two values one of which is very large resulting in washout of both populations, cannot give stable cycles. On the contrary, the cycling of the dilution rate between two values each one of which favors the growth of a different population, the periodic harvesting of a certain amount of biomass and growing medium and refilling of the chemostat with fresh medium and the simultaneous cycling of the dilution rate and the concentration of the substrate in the feed, can give stable periodic trajectories of coexistence.

Smith [27] has presented some mathematically rigorous proofs for the existence of coexistence limit cycles when two species compete for a single nutrient in an environment having periodically varying inputs. The results of his analysis are local in character and they do not necessarily describe the global behavior of the system.

It becomes now clear that when the constraint of temporally invariable inputs to the chemostat is relaxed, there are conditions under which pure and simple competitors can coexist. It must be emphasized though that this coexistence is in a state of sustained oscillations and not in a steady state.

The question now about the outcome of pure and simple competition is modified as following: can pure and simple competitors coexist in an environment having temporally invariant inputs? The answer is negative if the environment is spatially homogeneous and thus one has to relax this constraint in order to give the final answer to the question.

PURE AND SIMPLE COMPETITION IN A SPATIALLY HETEROGENEOUS ENVIRONMENT AND THE SCOPE OF THE PRESENT STUDY

An environment is spatially heterogeneous when it consists of a number of subenvironments communicating between one another and having different characteristics that may imply different growth conditions for any population which finds itself in them.

In the case of biological reactors spatial heterogeneity may arise due to a number of reasons e.g. incomplete mixing, non-ideality of flow, attachment of cells on the walls of the reactor etc., all of which can be viewed as deviations from the notion of the ideal chemostat.

Baltzis and Fredrickson [28] studied the case where two populations compete for a single resource in a perfectly mixed chemostat having constant inputs with one of the competitors having the ability to attach on the walls of the vessel. The attachment of cells on the wall created two subenvironments, the suspended culture and the solid surface. Their analysis showed that if the population which does not attach on the walls has the competitive advantage in the liquid the overall result is that the two populations always coexist in a stable steady state if the attachment of cells on the solid is irreversible while when it is reversible there is again a wide range of the operating parameters space where stable coexistence occurs in a steady state. It must be noted that in this study competition occurs only in one of the two subenvironments.

Stephanopoulos and Fredrickson [14] in a short communication indicated that if pure and simple competition occurs in two interconnected vessels both of them fed by the rate-limiting nutrient at the same concentration level coexistence in a stable steady state is possible provided that the conditions are such that one population has the competitive advantage in one vessel while its competitor has the advantage in the other. This condition implies that the conditions prevailing in the two vessels must be different and as a consequence the system viewed as a whole is a spatially inhomogeneous one.

The idea for the present thesis came from the aforementioned short communication. The following questions were addressed:

For the system proposed by Stephanopoulos and Fredrickson, how large is the domain in the operating parameters space where coexistence occurs? If it is a very narrow domain then one could not in reality operate in it at least without controlling the system. What is the effect of parameters such as the recycle ratio, the splitting ratio of the external feed, the ratio of the volumes of the reactors, to the domain of coexistence?

Furthermore, a basic question is whether the external feed to both reactors is a necessary condition for coexistence or not. If not, then the effect of various parameters (mentioned also above) on the range of the domain of coexistence should be studied, in order to provide an answer to the question of which one (splitting or non-splitting of the feed) system is better in order to maximize the domain of coexistence?

Finally, suppose that both reactors are externally fed with medium containing the rate-limiting substrate at two different concentration levels. Does this system lead also to coexistence? Is it better or worse than the two previously mentioned ones, if the objective is to increase the domain of coexistence in the operating parameters space?

I MATHEMATICAL DESCRIPTION OF THE PROBLEM AND PRELIMINARY MANIPULATIONS

CONFIGURATION OF THE SYSTEM

According to the so-called competitive exclusion principle, competition of two populations for a single rate-limiting non-renewable nutrient always leads to extinction of one of the populations if they are grown in a spatially uniform environment that is subject to time-invariant external influences. In order to investigate if spatial heterogeneities of the environment lead to coexistence of the two competitors the present thesis studies all aspects of pure and simple competition between two populations in two interconnected chemostats.

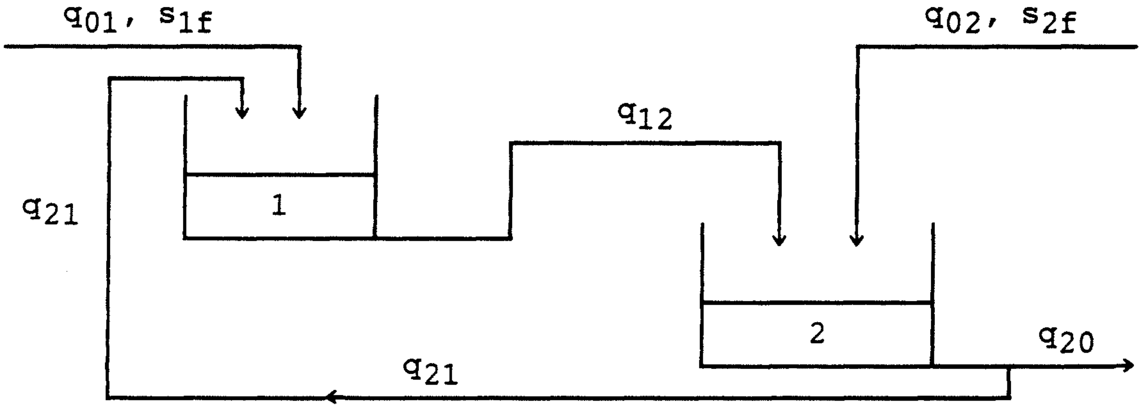


Figure 1: The General system

The most general configuration of the system is shown in Figure 1. Both chemostats are supplied with nutrients and the substrate competed for, from two different sources. The effluent of the first vessel is fed to the second one while the effluent of the latter is partially recycled to the first. Note that it is easy to show that without the recycle coexistence in both vessels is impossible.

The three systems mentioned in the previous section arise from the general configuration as following:

--$S_{1f}=S_{2f}$, $q_{01}\neq 0$, and $q_{02}\neq 0$ system proposed by Stephanopoulos and Fredrickson. It will be referred to as the splitting system.

—$q_{02}=0$, the simplest case. It will be referred to as the non-splitting system.

—$S_{1f}\neq S_{2f}$, $q_{01}\neq 0$, $q_{02}\neq 0$. The most general and complex system.

All three systems will be analyzed in later sections of this thesis.

MODEL EQUATIONS

Two populations A and B with biomass concentration a and b, respectively, competing for a rate-limiting substrate S the concentration of which is s, are considered. The specific growth rate of A is μ_1, while that of B is μ_2. When Monod's model is adopted, the expressions of μ_1 and μ_2 are the following:

$$\mu_1 = \frac{\mu_{m1} s}{k_1 + s}$$

$$\mu_2 = \frac{\mu_{m2} s}{k_2 + s}$$

where,

μ_{mi}: maximum specific growth rate of species i

k_i: saturation constant of species i

The equations describing the system for the general case are the following:

For reactor 1:

$$V_1 \frac{da_1}{dt} = q_{21} a_2 - q_{12} a_1 + \mu_1(s_1) a_1 V_1 \tag{1.1}$$

$$V_1 \frac{db_1}{dt} = q_{21} b_2 - q_{12} b_1 + \mu_2(s_1) b_1 V_1 \tag{1.2}$$

$$V_1 \frac{ds_1}{dt} = q_{01} s_{1f} + q_{21} s_2 - q_{12} s_1 - [\frac{1}{Y_a} \mu_1(s_1) a_1$$

$$+ \frac{1}{Y_b} \mu_2(s1) b_1] V_1 \tag{1.3}$$

For reactor 2:

$$V_2 \frac{da_2}{dt} = q_{12} a_1 - (q_{21}+q_{20}) a_2 + \mu_1(s_2) a_2 V_2 \tag{1.4}$$

$$V_2 \frac{db_2}{dt} = q_{12} b_1 - (q_{21}+q_{20}) b_2 + \mu_2(s_2) b_2 V_2 \tag{1.5}$$

$$V_2 \frac{ds_2}{dt} = q_{02} s_{2f} + q_{12} s_1 - (q_{21}+q_{20}) s_2 - [\frac{1}{Y_a} \mu_1(s_2) a_2$$

$$+ \frac{1}{Y_b}\mu_2(s_2)b_2]V_2 \tag{1.6}$$

where,

V_i: volume of the reactor i

Y_a: yield coefficient of species A on the rate-limiting substrate, assumed to be constant

Y_b: yield coefficient of species B on the rate-limiting substrate, assumed to be constant

The operating parameters for the system, in dimensionless form are the following:

$$R=\frac{q_{21}}{q_{20}} \qquad \beta=\frac{V_1}{V_2} \qquad \gamma=\frac{q_{02}}{q_{01}}$$

$$\eta=\frac{s_{2f}}{s_{1f}} \qquad D_{01}=\frac{q_{01}}{V_1}$$

where, R is the recycle ratio, β is the volume ratio of the reactors, γ is the ratio of external input flow rates (or splitting ratio, in the case where $S_{1f}=S_{2f}$), η is the ratio of rate-limiting substrate concentration while D_{01} is like a dilution rate. Using the quantities introduced above, one can write the following relationships:

$q_{20} = (\gamma+1)q_{01}$

$q_{21} = Rq_{20} = R(\gamma+1)q_{01}$

$q_{12} = [R(\gamma+1)+1]q_{01}$

$q_{21} + q_{20} = (R+1)(\gamma+1)q_{01}$

$s_{2f} = \eta s_{1f}$

And by introducing the following dimensionless quantities:

$$x_1=\frac{a_1}{Y_a k_1} \qquad x_2=\frac{a_2}{Y_a k_1} \qquad y_1=\frac{b_1}{Y_b k_1} \qquad y_2=\frac{b_2}{Y_b k_1}$$

$$u_1=\frac{s_1}{k_1} \qquad u_2=\frac{s_2}{k_1} \qquad \omega=\frac{k_2}{k_1} \qquad \varphi=\frac{\mu_{m2}}{\mu_{m1}}$$

$$\alpha=\frac{D_{01}}{\mu_{m1}} \qquad u_f=\frac{s_{1f}}{k_1} \qquad \vartheta=t\mu_{m1}$$

equations (1.1) to (1.6) can be written in dimensionless form as:

$$\frac{dx_1}{d\vartheta} = R(\gamma+1)\alpha x_2 - [R(\gamma+1)+1]\alpha x_1 + f(u_1)x_1 \tag{1.7}$$

$$\frac{dy_1}{d\vartheta} = R(\gamma+1)\alpha y_2 - [R(\gamma+1)+1]\alpha y_1 + g(u_1)y_1 \tag{1.8}$$

$$\frac{du_1}{d\vartheta} = \alpha u_f + R(\gamma+1)\alpha u_2 - [R(\gamma+1)+1]\alpha u_1 - f(u_1)x_1 - g(u_1)y_1 \tag{1.9}$$

$$\frac{dx_2}{d\vartheta} = \beta[R(\gamma+1)+1]\alpha x_1 - \beta(R+1)(\gamma+1)\alpha x_2 + f(u_2)x_2 \tag{1.10}$$

$$\frac{dy_2}{d\vartheta} = \beta[R(\gamma+1)+1]\alpha y_1 - \beta(R+1)(\gamma+1)\alpha y_2 + g(u_2)y_2 \tag{1.11}$$

$$\frac{du_2}{d\vartheta} = \alpha\beta\gamma\eta u_f + \beta[R(\gamma+1)+1]\alpha u_1 - \beta(R+1)(\gamma+1)\alpha u_2 - f(u_2)x_2 - g(u_2)y_2 \tag{1.12}$$

with,

$$f(u_i)=\frac{u_i}{1 + u_i}\,, \qquad g(u_i)=\frac{\varphi u_i}{\omega + u_i} \qquad i = 1,\ 2$$

DIMENSIONAL REDUCTION OF THE MODEL

Adding equations (1.7) through (1.9) one gets

$$\frac{d(x_1+y_1+u_1)}{d\vartheta} = \alpha u_f+R(\gamma+1)\alpha(x_2+y_2+u_2) - [R(\gamma+1)+1]\alpha(x_1+y_1+z_1)$$

while adding equations (1.10) through (1.12) one gets

$$\frac{d(x_2+y_2+u_2)}{d\vartheta} = \alpha\beta\gamma\eta u_f+\beta[R(\gamma+1)+1]\alpha(x_1+y_1+u_1) - \beta(R+1)(\gamma+1)\alpha(x_2+y_2+u_2)$$

The above two equations can be also brought to the form

$$\frac{dZ_1}{d\vartheta} = -[R(\gamma+1)+1]\alpha Z_1 + R(\gamma+1)Z_2 \qquad (1.13)$$

$$\frac{dZ_2}{d\vartheta} = \beta[R(\gamma+1)+1]\alpha Z_1 - \beta(R+1)(\gamma+1)\alpha Z_2 \qquad (1.14)$$

with,

$$Z_1 = x_1 + y_1 + u_1 - \frac{R(1+\eta\gamma)+1}{[R(\gamma+1)+1]}u_f$$

$$Z_2 = x_2 + y_2 + u_2 - \frac{1+\eta\gamma}{\gamma+1}u_f$$

The Jacobian matrix for the system of eqns.(1.13) & (1.14) is the following:

$$\underline{\underline{S}} = \begin{bmatrix} -[R(\gamma+1)+1]\alpha & R(\gamma+1)\alpha \\ \beta[R(\gamma+1)+1]\alpha & -\beta(R+1)(\gamma+1)\alpha \end{bmatrix}$$

The characteristic equation of the matrix above is:

$$\lambda^2 + \{[R(\gamma+1)+1]+\beta(R+1)(\gamma+1)\}\alpha\lambda + \beta[R(\gamma+1)+1](\gamma+1)\alpha^2 = 0$$

If λ_1 and λ_2 are the roots of the quadratic above, it is easy to see that

$$\lambda_1 + \lambda_2 < 0$$

and,

$$\lambda_1\lambda_2 > 0$$

Furthermore its discriminant Δ, is positive as it can be seen from the expression

$$\frac{\Delta}{\alpha^2} = \{[R(\gamma+1)+1]-\beta(\gamma+1)\}^2 + 2\beta[R(\gamma+1)+1]R(\gamma+1) + \beta^2(\gamma+1)^2(R^2+2R)$$

Thus, λ_1 and λ_2 are real and negative. Using now arguments similar to those of Aris and Humphrey [23], one can use at all times the following stoichiometric equations

$$x_1 + y_1 + u_1 - \frac{R(1+\eta\gamma)+1}{[R(\gamma+1)+1]}u_f = 0 \qquad (1.15)$$

$$x_2 + y_2 + u_2 - \frac{1+\eta\gamma}{\gamma+1}u_f = 0 \qquad (1.16)$$

The system can now be described by the two (algebraic) stoichiometric relations along with any four of the differential equations (1.7) through (1.12). The dimension of the system then becomes four instead of six, something which offers a great simplification for the analysis. In the analysis which follows equations (1.7), (1.8), (1.10), (1.11), (1.15) and (1.16) have been used in order to describe the system.

POSSIBLE STEADY STATES

The system described above has the following steady states:

SS1: $x_i=0$, $y_i=0$ $i=1, 2$ $u_1=\dfrac{R(1+\eta\gamma)+1}{[R(\gamma+1)+1]}u_f$, $u_2=\dfrac{1+\eta\gamma}{\gamma+1}u_f$

Both populations wash out from the system.

SS2: $x_i>0$, $y_i=0$ $i=1, 2$

Population A establishes itself in the system and excludes its competitor, population B.

SS3: $x_i=0$, $y_i>0$ $i=1, 2$

Population B establishes itself in the system and excludes its competitor, population A. Case symmetric to the previous one.

SS4: $x_i>0$, $y_i>0$ $i=1, 2$

The two competing populations coexist in a steady state.

Observe that due to the interconnection of the two reactors if a population survives it has to do so in both vessels.

II ANALYSIS OF THE NON-SPLITTING SYSTEM

MODEL EQUATIONS

In this section the analysis of the non-splitting system is presented. The configuration of the system is shown in Fig.2 and its difference from the general system (shown in Fig.1) is the fact that the externally fed medium goes in one of the two vessels only. Mathematically, this implies that the parameters η and γ (introduced previously) are both equal to zero.

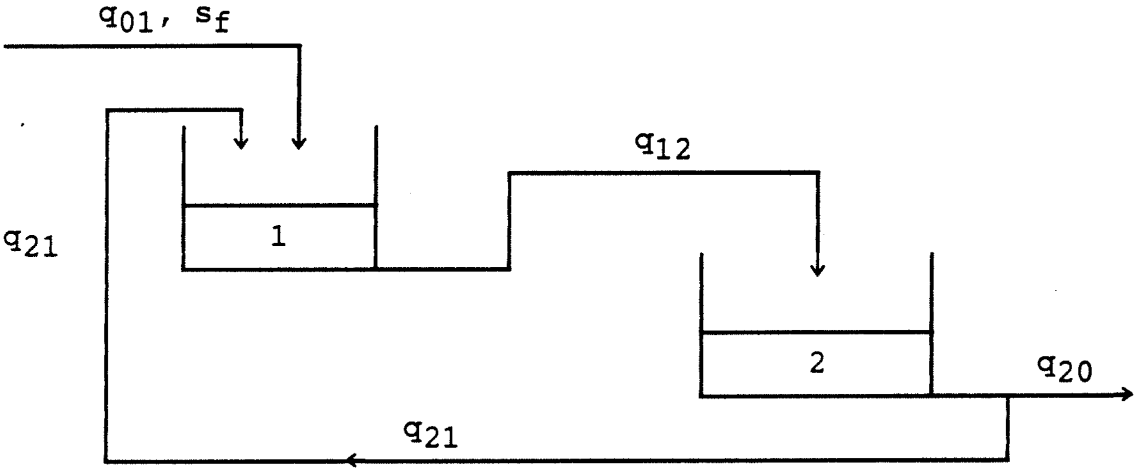


Figure 2: The Non-Splitting System

In this case, eqns.(1.7) through (1.12) become:

$$\frac{dx_1}{d\vartheta} = R\alpha x_2 - (R+1)\alpha x_1 + f(u_1)x_1 \tag{2.1}$$

$$\frac{dy_1}{d\vartheta} = R\alpha y_2 - (R+1)\alpha y_1 + g(u_1)y_1 \tag{2.2}$$

$$\frac{du_1}{d\vartheta} = \alpha u_f + R\alpha u_2 - (R+1)\alpha u_1 - f(u_1)x_1 - g(u_1)y_1 \tag{2.3}$$

$$\frac{dx_2}{d\vartheta} = \beta(R+1)\alpha x_1 - \beta(R+1)\alpha x_2 + f(u_2)x_2 \tag{2.4}$$

$$\frac{dy_2}{d\vartheta} = \beta(R+1)\alpha y_1 - \beta(R+1)\alpha y_2 + g(u_2)y_2 \tag{2.5}$$

$$\frac{du_2}{d\vartheta} = \beta(R+1)\alpha u_1 - \beta(R+1)\alpha u_2 - f(u_2)x_2 - g(u_2)y_2 \tag{2.6}$$

where,

$$f(u_i)=\frac{u_i}{1+u_i}, \qquad g(u_i)=\frac{\varphi u_i}{\omega+u_i} \qquad i = 1,\ 2$$

As argued in the previous section two differential equations can be substituted by two algebraic equations (stoichiometric relations). The stoichiometric relations given by equations (1.15) and (1.16) become in this case:

$$u_f = x_1 + y_1 + u_1 \tag{2.7}$$

$$u_f = x_2 + y_2 + u_2 \tag{2.8}$$

In the analysis which follows eqns.(2.1), (2.2), (2.7), (2.4), (2.5) and (2.8) are used to describe the system. This is the simplest case possible for the problem studied in the present thesis. The main question here is if this simplest possible case can lead to coexistence of the two competitors and if so under what conditions. Furthermore, this case can be viewed as a first-crude-approximation of a tubular reactor with recycle.

The possible steady states for the system are those presented in the previous section. The local stability of each one of the possible steady states is studied by examining the character of the eigenvalues of the Jacobian matrix of the system which is the following:

$$\underline{\underline{S}} = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix}$$

where,

$a_{11} = f_1 - (R+1)\alpha - x_1F_1$

$a_{12} = -x_1F_1$

$a_{13} = R\alpha$

$a_{21} = -y_1G_1$

$a_{22} = g_1 - (R+1)\alpha - y_1G_1$

$a_{24} = R\alpha$

$a_{31} = (R+1)\beta\alpha$

$a_{33} = f_2 - (R+1)\beta\alpha - x_2F_2$

$a_{34} = -x_2F_2$

$a_{42} = (R+1)\beta\alpha$

$a_{43} = -y_2G_2$

$$a_{44} = g_2 - (R+1)\beta\alpha - y_2 G_2$$

$$a_{14} = a_{23} = a_{32} = a_{41} = 0$$

with,

$$f_i = f(u_i) \qquad g_i = g(u_i) \qquad i = 1, 2$$

$$F_i = F(u_i) = \frac{df_i}{du_i} = \frac{1}{(1+u_i)^2} \qquad i = 1, 2$$

$$G_i = G(u_i) = \frac{dg_i}{du_i} = \frac{\varphi\omega}{(\omega+u_i)^2} \qquad i = 1, 2$$

ANALYSIS OF SS1 (WASHOUT STEADY STATE)

This steady state implies that $x_i=y_i=0$ and $u_i=u_f$, i=1, 2 and it is always meaningful.

For this steady state the Jacobian matrix $\underset{\sim}{S}$ becomes a little simpler since some of its elements become zero. Furthermore, all off-diagonal elements of the matrix are non-negative and thus the (local)stability criteria for SS1 can be deduced by using Sevastyanov's lemma [29], and they are the following:

$$f(u_f) - (R+1)\alpha < 0 \tag{2.9}$$

$$g(u_f) - (R+1)\alpha < 0 \tag{2.10}$$

$$[f(u_f)-(R+1)\alpha][f(u_f)-(R+1)\beta\alpha] - R(R+1)\beta\alpha^2 > 0 \tag{2.11}$$

$$[g(u_f)-(R+1)\alpha][g(u_f)-(R+1)\beta\alpha] - R(R+1)\beta\alpha^2 > 0 \tag{2.12}$$

After some algebraic manipulations, the conditions (2.9) through (2.12) can be lumped into a single condition for the stability of SS1, namely:

$$\alpha > \max\{ Kf(u_f), Kg(u_f) \} \tag{2.13}$$

where,

$$K = \frac{(R+1)(\beta+1) + \{(R+1)[R(\beta+1)^2+(\beta-1)^2]\}^{\frac{1}{2}}}{2\beta(R+1)} \tag{2.13a}$$

One can easily see that K is a positive number always larger than unity. Furthermore, K increases as R increases or as β decreases. These observations, coupled with the condition (2.13) suggest both design (small β) and operating (α small and R large) criteria in order to avoid washout which is totally undesirable.

ANALYSIS OF SS2

This steady state arises when $x_i>0$ and $y_i=0$, i=1,2. It implies that one population establishes itself in both vessels by winning the competition and excluding its competitor. The values of x_i and u_i, i=1, 2 in this case are given as solution(s) of the following equations:

$$f(u_1)x_1 + R\alpha x_2 - (R+1)\alpha x_1 = 0 \tag{2.14}$$

$$f(u_2)x_2 + \beta(R+1)\alpha x_1 - \beta(R+1)\alpha x_2 = 0 \tag{2.15}$$

$$u_1 = u_f - x_1 \tag{2.16}$$

$$u_2 = u_f - x_2 \tag{2.17}$$

This steady state is meaningful if and only if $x_i>0$ and $0<u_i<u_f$, i=1, 2. It is obvious from (2.15) that for a meaningful SS2 it must be $x_1<x_2$ which coupled with (2.16) and (2.17) implies that it must also be $u_1>u_2$.

Solving eqns.(2.14) and (2.15) for x_2 and equating the two resulting expressions one gets:

$$\frac{f(u_1) - (R+1)\alpha}{R\alpha} = \frac{\beta(R+1)\alpha}{f(u_2) - \beta(R+1)\alpha}$$

or $[f_1-(R+1)\alpha][f_2-(R+1)\beta\alpha] = R(R+1)\beta\alpha^2$ (2.18)

Upon further manipulation eqn.(2.18) yields

$$u_2 = \frac{Au_1 + B}{Cu_1 + D} \qquad (2.19)$$

where,

$A = \beta(R+1)(\alpha-\alpha^2)$

$B = - \beta(R+1)\alpha^2$

$C = (R+1)[\beta\alpha^2-(\beta+1)\alpha] + 1$

$D = (R+1)(\beta\alpha^2-\alpha)$

Using eqns.(2.14), (2.16), (2.17) and (2.19) one gets the following equation in u_1:

$$M_3u_1^3 + M_2u_1^2 + M_1u_1 + M_0 = 0 \qquad (2.20)$$

where,

$M_3 = [-(R+1)\alpha+1]C$

$M_2 = [u_fC+RA-(R+1)(C+D)]\alpha+(D-u_fC)$

$M_1 = [R(A+B)+u_f(C+D)-(R+1)D]\alpha - u_fD$

$M_0 = (RB+u_fD)\alpha$

For any given set of operating and system parameters (α,u_f,R,β) one can solve eqn.(2.20) to find u_1 and then expressions (2.19), (2.16) and (2.17) yield the values for u_2, x_1 and x_2, respectively. In general, the system can have up to three different SS2.

The (local) stability of SS2 is determined by the eigenvalues of the Jacobian matrix, which in this case are given as roots of the following quadratics:

$$P_1(\lambda) = \lambda^2 + [R\alpha\frac{x_2}{x_1}+(R+1)\beta\alpha\frac{x_1}{x_2}+x_1F_1+x_2F_2]\lambda$$

$$+ R\alpha\frac{x_2}{x_1}x_2F_2+(R+1)\beta\alpha\frac{x_1}{x_2}x_1F_1+x_1x_2F_1F_2 = 0 \quad (2.21)$$

and,

$$P_2(\lambda) = \lambda^2 - [g_1-(R+1)\alpha+g_2-(R+1)\beta\alpha]\lambda$$

$$+ [g_1-(R+1)\alpha][g_2-(R+1)\beta\alpha] - R(R+1)\beta\alpha^2 = 0 \quad (2.22)$$

It is easy to show that the quadratic $P_1(\lambda)=0$ has always real and negative roots thus the stability of SS2 is determined by the roots of $P_2(\lambda)=0$ only.

If λ_1 and λ_2 are the roots of $P_2(\lambda)=0$, then from eqn.(2.22) one can easily see that λ_1 and λ_2 are always real and hence for a stable SS2 the following two inequalities have to be satisfied:

$$\lambda_1+\lambda_2 = [g_1-(R+1)\alpha] + [g_2-(R+1)\beta\alpha] < 0 \quad (2.23)$$

and,

$$\lambda_1\lambda_2 = [g_1-(R+1)\alpha][g_2-(R+1)\beta\alpha]-R(R+1)\beta\alpha^2 > 0 \quad (2.24)$$

Actually, upon further manipulation one can show that conditions (2.23) and (2.24) can be substituted by the following single criterion:

$$\alpha > \frac{(R+1)(\beta g_1+g_2) + \{(R+1)[(R+1)(\beta g_1+g_2)^2-4\beta g_1g_2]\}^{\frac{1}{2}}}{2\beta(R+1)} \quad (2.25)$$

One can get some further insight for SS2 by taking into consideration the mutual disposition of the f(u) and g(u) curves (which are the specific growth rate curves of the two populations in dimensionless form). There are four possible dispositions as shown in Fig.4

Case a:

This case arises when the following conditions are met:

$$\omega > \varphi, \; \varphi < 1$$

and it implies that $f(u)>g(u)$ for any u. Hence, the following inequalities are true in this case:

$$f_1-(R+1)\alpha > g_1-(R+1)\alpha \tag{2.26}$$

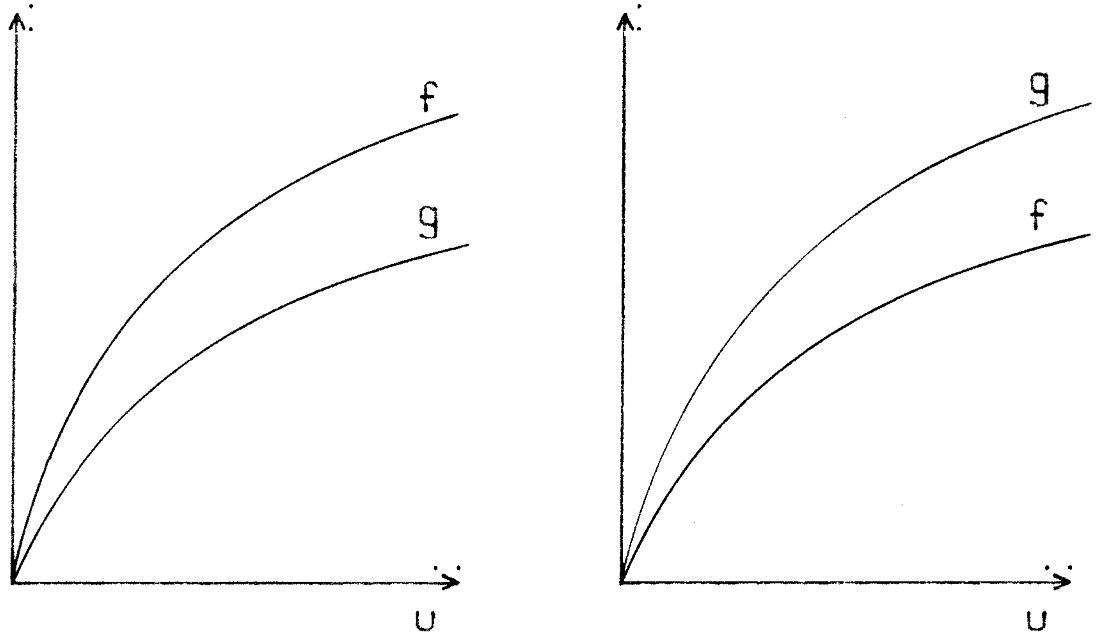
$$f_2-(R+1)\beta\alpha > g_2-(R+1)\beta\alpha \tag{2.27}$$

It is easy to see from (2.14) and (2.15) that

$$f_1-(R+1)\alpha < 0 \quad \text{and} \quad f_2-(R+1)\beta\alpha < 0$$

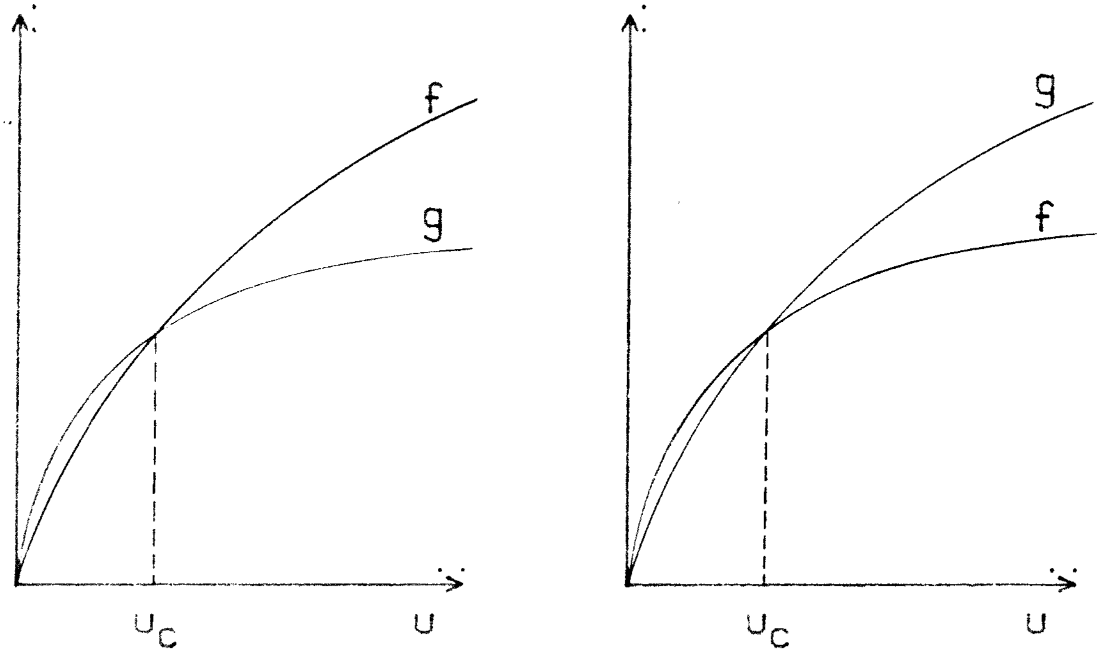
Now if the inequalities (2.26) and (2.27) are added they yield (2.23) while when they are multiplied and equation (2.18) is used they yield (2.24).

The conclusion then is that if $\omega>\varphi$ and $\varphi<1$, SS2 is stable whenever it is meaningful. This result is physically expected since the mutual disposition of the f(u) and g(u) curves considered here implies that the population which can survive in SS2 has always the competitive advantage (it grows faster than its competitor) and thus if survival is possible (i.e. SS2 is meaningful) it will be unconditionally stable.



(a) $\omega > \varphi$, $\varphi < 1$

(b) $\omega < \varphi$, $\varphi > 1$



(c) $\omega < \varphi < 1$

(d) $\omega > \varphi > 1$

Figure 4: The possible mutual dispositions of the specific growth rate curves

Case b:

This case arises when the following conditions are met:

$\omega < \varphi, \ \varphi > 1$

This case is opposite to case a considered above, and one can show following a procedure analogous to the one used in case a that SS2 is unstable whenever it is meaningful. This again is the result of the fact that the population which is predicted to survive in SS2 never has the competitive advantage and hence SS2 is unattainable.

Case c:

This case arises when $\omega < \varphi < 1$ and the two curves cross each other at a value u_c of u with

$$u_c = \frac{\omega - \varphi}{\varphi - 1} \tag{2.28}$$

If $u_1 > u_2 > u_c$, then it is like having case a and SS2 is stable provided that it is meaningful.

If $u_2 < u_1 < u_c$, then it is like having case b and SS2 is always unstable.

If $u_1 > u_c > u_2$, then SS2 if meaningful it is also stable if and only if the condition (2.25) is satisfied.

Case d:

This case arises when $\omega > \varphi > 1$ and the two curves cross each other at $u = u_c$ where u_c is again given by the relation (2.28).

If $u_1>u_2>u_c$, then it is like having case b and SS2 is always unstable.

If $u_2<u_1<u_c$, then it is like having case a and SS2 is stable whenever it is meaningful.

If $u_1>u_c>u_2$, then the condition (2.25) must be satisfied in order for a meaningful SS2 to be stable.

This concludes the analysis of SS2. The only thing which has remained unresolved is whether more than one SS2 are really possible. As it has been shown previously, due to the fact that the value of u_1 is given as the solution to the cubic equation (2.20), theoretically up to three SS2 are possible. Extensive numerical studies with the system have never yielded more than one meaningful SS2. It can be claimed then, with enough confidence, that SS2 is unique, it does not exhibit any multiplicity.

ANALYSIS OF SS3

This steady state arises when $x_i=0$ and $y_i>0$, $i=1, 2$. The case is symmetric to SS2 hence the analysis will not be repeated. If x_i is interchanged with y_i and f_i is interchanged with g_i ($i=1, 2$) in the results of SS2, the results of SS3 are obtained. There are only two equations which have to be slightly modified, namely:

$$u_2 = \frac{A'u_1 + B'}{C'u_1 + D'}$$

where,

$$A' = \beta\omega(R+1)(\varphi\alpha-\alpha^2)$$

$$B' = -\beta\omega^2(R+1)\alpha^2$$

$$C' = (R+1)[\beta\alpha^2-(\beta+1)\varphi\alpha] + \varphi^2$$

$$D' = \omega(R+1)(\beta\alpha^2-\varphi\alpha)$$

and,

$$M_3'u_1^3 + M_2'u_1^2 + M_1'u_1 + M_0' = 0$$

where,

$$M_3' = [-(R+1)\alpha+\varphi]C'$$

$$M_2' = [u_fC'+RA'-(R+1)(C'\omega+D')]\alpha+\varphi(D'-u_fC')$$

$$M_1' = [R(A'\omega+B')+u_f(C'\omega+D')-(R+1)\omega D']\alpha - \varphi u_fD'$$

$$M_0' = (RB'+u_fD')\omega\alpha$$

Again, theoretically there are up to three possible SS3 but extensive numerical studies (as in the case of SS2) have never yielded more than one meaningful SS3 hence with enough confidence it can be claimed that SS3 (as its analogue SS2) does not exhibit multiplicity, it is unique.

It is interesting to note that all eigenvalues of SS2 and SS3 are always real. Hence no oscillatory phenomena are expected during transients, something which has been confirmed via computer simulations.

ANALYSIS OF THE COEXISTENCE STEADY STATE (SS4)

This is the most interesting steady state as far as this study is concerned. For a meaningful SS4 it must be:

$$x_i > 0, \quad y_i > 0, \quad 0 < u_i < u_f \qquad i=1,\ 2$$

In order to find the values of the six variables one has to solve the following system of algebraic equations:

$$R\alpha x_2 - (R+1)\alpha x_1 + f(u_1)x_1 = 0 \tag{2.29}$$

$$R\alpha y_2 - (R+1)\alpha y_1 + g(u_1)y_1 = 0 \tag{2.30}$$

$$\beta(R+1)\alpha x_1 - \beta(R+1)\alpha x_2 + f(u_2)x_2 = 0 \tag{2.31}$$

$$\beta(R+1)\alpha y_1 - \beta(R+1)\alpha y_2 + g(u_2)y_2 = 0 \tag{2.32}$$

$$u_f = x_1 + y_1 + u_1 \tag{2.33}$$

$$u_f = x_2 + y_2 + u_2 \tag{2.34}$$

From eqns.(2.29) through (2.32) one can get the following relations:

$$f_1 - (R+1)\alpha = -R\alpha\frac{x_2}{x_1} \tag{2.35}$$

$$g_1 - (R+1)\alpha = -R\alpha\frac{y_2}{y_1} \tag{2.36}$$

$$f_2 - (R+1)\beta\alpha = -(R+1)\beta\alpha\frac{x_1}{x_2} \tag{2.37}$$

$$g_2 - (R+1)\beta\alpha = -(R+1)\beta\alpha\frac{y_1}{y_2} \tag{2.38}$$

By multiplying the expressions (2.35) and (2.37) one gets:

$$[f_1-(R+1)\alpha][f_2-(R+1)\beta\alpha] = R(R+1)\beta\alpha^2 \tag{2.39}$$

Similarly, by multiplying the expressions (2.36) and (2.38) one gets:

$$[g_1-(R+1)\alpha][g_2-(R+1)\beta\alpha] = R(R+1)\beta\alpha^2 \tag{2.40}$$

Observe that for a meaningful SS4 all the left hand side parts of eqns.(2.35) through (2.38) have to be negative. Also observe that for a meaningful SS4, eqn.(2.31) requires that $x_1<x_2$ while eqn.(2.32) requires that $y_1<y_2$. These two inequalities along with eqns.(2.33) and (2.34) imply that it must be $u_1>u_2$. The consideration of the mutual disposition of the specific growth rate curves f(u) and g(u) (shown in Fig.4) can again reveal some important information.

In case a, i.e. when $f(u)>g(u)$ for any u one can get:

$$g_1-(R+1)\alpha < f_1-(R+1)\alpha < 0 \tag{2.41}$$

$$g_2-(R+1)\beta\alpha < f_2-(R+1)\beta\alpha < 0 \tag{2.42}$$

By multiplying the inequalities (2.41) and (2.42) and using equality (2.39) one gets

$$[g_1-(R+1)\alpha][g_2-(R+1)\beta\alpha] > R(R+1)\beta\alpha^2$$

The above inequality implies that the relation (2.40) can not be satisfied in case a, in other words coexistence is impossible in this case.

Following a procedure similar to the above one can now easily show that coexistence is not possible in the case b (Fig.4) either.

At this point one can conclude that the crossing of the specific growth rate curves is a necessary condition for coexistence.

For the cases c and d (Fig.4) one can show easily that if $u_1>u_2>u_c$ or $u_c>u_1>u_2$ coexistence is impossible. Hence the system may have a meaningful coexistence steady state only if $u_2<u_c<u_1$ which implies that:

$g_2 > f_2$ and $g_1 < f_1$ (case c)

or

$g_2 < f_2$ and $g_1 > f_1$ (case d)

One can conclude then that in order for the system to have a meaningful steady state of coexistence not only the specific growth rate curves of the two competitors must cross each other but also the conditions must be such that one population has the competitive advantage (grows faster) in one vessel while its competitor has the advantage in the other vessel. This finding is in accordance with that of Stephanopoulos and Fredrickson [14].

The value of u_1 is a solution to the quadratic

$$N(u_1) = N_2u_1^2 + N_1u_1 + N_0 = 0 \qquad (2.43)$$

where,

$$N_2=(R+1)\beta\alpha^3-(R+1)[\alpha_c+\beta(1+\varphi)]\alpha^2+[(R+1)\beta\varphi+R\varphi+(\varphi+1)\alpha_c]\alpha-\varphi\alpha_c$$

$$N_1=(R+1)\beta(\omega+1)\alpha^3-(R+1)[\beta(\omega+\varphi)+(\omega+1)\alpha_c]\alpha^2+(\omega+\varphi)\alpha_c\alpha$$

$$N_0=\omega(R+1)\alpha^2(\beta\alpha-\alpha_c)$$

with,

$$\alpha_c = \frac{\omega - \varphi}{\omega - 1}$$

With u_1 known the rest of the variables can be found through the following expressions:

$$u_2 = \frac{(R+1)\beta\alpha[u_1(1-\alpha)-\alpha]}{[(R+1)\alpha(\beta\alpha-\beta-1)+1]u_1+(R+1)\alpha(\beta\alpha-1)} \tag{2.44}$$

$$x_1 = \frac{(u_f-u_1)(\alpha-g_1)-(u_1-u_2)R\alpha}{f_1 - g_1} \tag{2.45}$$

$$y_1 = \frac{(u_1-u_2)R\alpha-(\alpha-f_1)x_1}{\alpha - g_1} \tag{2.46}$$

$$x_2 = \frac{[(R+1)\alpha-f_1]x_1}{R\alpha} \tag{2.47}$$

$$y_2 = \frac{[(R+1)\alpha-g_1]y_1}{R\alpha} \tag{2.48}$$

The quadratic (2.43) will yield real values for u_1 if and only if its discriminant Δ, is positive. After some algebraic manipulations one can show that

$$\Delta = \beta^2\alpha^2(R+1)^2(\omega-1)^2(\alpha-K_1\alpha_c)(\alpha-K\alpha_c)(\alpha-\Theta)(\alpha-H) \tag{2.49}$$

where K is given by (2.13a) while,

$$K_1 = \frac{(R+1)(\beta+1) - \{(R+1)[R(\beta+1)^2+(\beta-1)^2]\}^{\frac{1}{2}}}{2(R+1)\beta} \tag{2.50}$$

$$\Theta = \frac{(R+1)(\beta+1)\alpha_c - \Delta_1^{\frac{1}{2}}}{2(R+1)\beta} \tag{2.51}$$

$$H = \frac{(R+1)(\beta+1)\alpha_c + \Delta_1^{\frac{1}{2}}}{2(R+1)\beta} \tag{2.52}$$

with,

$$\Delta_1 = (R+1)[R(\beta+1)^2+(\beta-1)^2]\alpha_c^2 + \frac{16\omega\varphi R(R+1)\beta}{(\omega-1)^2} \tag{2.53}$$

One can easily show that

$$\theta < K_1\alpha_c < K\alpha_c < H \tag{2.54}$$

Hence a possibly meaningful coexistence steady state requires that α must be chosen such that:

$$\alpha < \theta \quad \text{or} \quad K_1\alpha_c < \alpha < K\alpha_c \quad \text{or} \quad \alpha > H \tag{2.55}$$

since each of the inequalities above guarantees that $\Delta > 0$ (i.e. u_1 real).

In fact, the selection of α for coexistence is more restricted than what inequalities (2.55) suggest as it can be shown from the following considerations:

Using eqn.(2.35) and taking into account the fact that it must be $x_2>x_1$ one can conclude that it must be

$$f_1-(R+1)\alpha < -R\alpha \quad \text{or} \quad f_1 < \alpha \tag{2.56}$$

As it has been shown previously, it must be $u_c<u_1$ which combined with (2.56) leads to the following condition:

$$\alpha > \alpha_c = \frac{\omega - \varphi}{\omega - 1} \tag{2.57}$$

If eqn.(2.36) along with the fact that it must be $y_2>y_1$ is used, it leads again to the condition (2.57). Hence α_c is the lower bound for the values of α that may lead to coexistence.

Using eqn.(2.39) and taking into consideration that it must be $u_2<u_1$ (which implies that $f_2<f_1$) one concludes that it must be:

$$(R+1)\beta\alpha^2 - (R+1)(\beta+1)f_1\alpha + f_1^2 < 0$$

or equivalently

$$K_1f_1 < \alpha < Kf_1 \tag{2.58}$$

where K_1 and K are given by (2.50) and (2.13a), respectively.

Similarly, using equation (2.40) one can conclude that it must be

$$K_1g_1 < \alpha < Kg_1 \tag{2.59}$$

From eqn.(2.35) one can get that

$$x_2 - x_1 = \frac{(\alpha-f_1)x_1}{R\alpha} \tag{2.60}$$

while from eqn.(2.36) one can get that

$$y_2 - y_1 = \frac{(\alpha-g_1)y_1}{R\alpha} \tag{2.61}$$

Since it must be $x_2>x_1$ and $y_2>y_1$, eqns.(2.60) and (2.61) imply that it must be

$$\alpha > \max\{f_1, g_1\} \tag{2.62}$$

Because of the fact that $K_1<1$, one can combine the inequalities (2.58), (2.59) and (2.62) into the following single condition

$$\max\{f_1, g_1\} < \alpha < \min\{Kf_1, Kg_1\} \tag{2.63}$$

It is interesting to observe that

$$\max\{f_1, g_1\} > \alpha_c \tag{2.64}$$

and $$\min\{Kf_1, Kg_1\} < \min\{Kf(u_f), Kg(u_f)\} \tag{2.65}$$

Now, because of (2.63) and (2.64), the inequalities (2.55) have to be restricted only to the following:

$$\alpha_c < \alpha < K\alpha_c \quad \text{or} \quad \alpha > H \tag{2.66}$$

From eqns.(2.43) and (2.44) one can make two very interesting observations. The first is that the values of u_1 and u_2 are independent of the value of u_f. This implies that for a given system of populations (i.e. φ and ω) and for given α, R and β when u_f varies the values of u_1 and u_2 remain unchanged while the biomass concentrations (x_i, y_i, $i=1,2$) do change. This has been repeatedly observed in the numerical studies. The second observation is that for the special case of $\beta=1$ the values of u_1 and u_2 are the two roots of the quadratic (2.43) something which implies that the coexistence steady state is unique when $\beta=1$. It is not really possible to prove analytically whether SS4 is unique or not in the case where $\beta\neq1$. Nevertheless extensive numerical studies have shown that SS4 is unique and furthermore, that coexistence is impossible when $\alpha>H$. Thus one can conclude that SS4 is unique and that the lower and upper bounds of values of α yielding coexistence are α_c and $K\alpha_c$, respectively.

As it can be observed from all operating diagrams presented (Figures 5-11) and discussed in the following section of this part, the point $(u_{fc},K\alpha_c)=[(\omega-\varphi)/(\varphi-1), K(\omega-\varphi)/(\omega-1)]$ is always a point of the boundary of the domain of coexistence. In fact, it can be proved that this must be so. For $\alpha=K\alpha_c$, eqn.(2.43) gives $u_1=(\omega-\varphi)/(\varphi-1)$

while eqn.(2.44) gives $u_2=u_1$ and then eqns.(2.45) through (2.48) yield $x_1=x_2=y_1=y_2=0$, when $u_f=(\omega-\varphi)/(\varphi-1)$. One can say that the point $(u_{fc},K\alpha_c)$ results in a degenerate solution of coexistence and as it can be seen from all operating diagrams $(u_{fc},K\alpha_c)$ is a common point for the boundaries of coexistence and washout, as expected. Now, since it must be $u_1>u_c$ and also $u_1<u_f$ one can conclude that for coexistence it is necessary to have

$$u_f > u_c = \frac{\omega - \varphi}{\varphi - 1} \tag{2.67}$$

The inequality (2.67) indicates how u_f, the substrate concentration in the feed stream, has to be selected in order for coexistence to be possible. The conditions (2.63), (2.66) and (2.67) are necessary but not sufficient for coexistence. That is, the aforementioned conditions do not guarantee that $0<u_1<u_f$, $0<u_2<u_f$, $x_i>0$, $y_i>0$, $i=1,2$. Due to the complexity of the expressions one cannot find analytically the exact boundaries of the domain(s) in which SS4 is indeed meaningful. One has to rely upon numerical solutions but the analysis presented here provides very good guidance as to where one should numerically search for coexistence.

As far as the (local) stability of SS4 is concerned, one has to determine the character of the four eigenvalues of the Jacobian matrix which in this case are given as the roots of the following polynomial:

$$\lambda^4 + C_3\lambda^3 + C_2\lambda^2 + C_1\lambda + C_0 = 0 \qquad (2.68)$$

where,

$$C_3 = R\alpha\left(\frac{x_2}{x_1} + \frac{y_2}{y_1}\right) + (R+1)\beta\alpha\left(\frac{x_1}{x_2} + \frac{y_1}{y_2}\right)$$
$$+ x_1F_1 + y_1G_1 + x_2F_2 + y_2G_2$$

$$C_2 = R\alpha\left[(x_1F_1+x_2F_2+y_2G_2)\frac{y_2}{y_1} + (y_1G_1+x_2F_2+y_2G_2)\frac{x_2}{x_1}\right]$$
$$+(R+1)\beta\alpha\left[(x_1F_1+x_2F_2+y_1G_1)\frac{y_1}{y_2}+(x_1F_1+y_1G_1+y_2G_2)\frac{x_1}{x_2}\right]$$
$$+ R^2\alpha^2\frac{x_2y_2}{x_1y_1} + R(R+1)\beta\alpha^2\left(\frac{x_1y_2}{x_2y_1} + \frac{x_2y_1}{x_1y_2}\right)$$
$$+ (R+1)^2\beta^2\alpha^2\frac{x_1y_1}{x_2y_2} + x_1x_2F_1F_2 + x_1y_2F_1G_2$$
$$+ x_2y_1F_2G_1 + y_1y_2G_1G_2$$

$$C_1 = R\alpha(x_2F_2+y_2G_2)\left(x_1F_1\frac{y_2}{y_1} + y_1G_1\frac{x_2}{x_1}\right)$$
$$+ (R+1)\beta\alpha(x_1F_1+y_1G_1)\left(x_2F_2\frac{y_1}{y_2} + y_2G_2\frac{x_1}{x_2}\right)$$
$$+ R(R+1)\beta\alpha^2\left[(x_1F_1+y_2G_2)\frac{x_1y_2}{x_2y_1} + (x_2F_2+y_1G_1)\frac{x_2y_1}{x_1y_2}\right]$$
$$+ R^2\alpha^2(x_2F_2+y_2G_2)\frac{x_2y_2}{x_1y_1}+(R+1)^2\beta^2\alpha^2(x_1F_1+y_1G_1)\frac{x_1y_1}{x_2y_2}$$

$$C_0 = R(R+1)^2\beta^2\alpha^4\frac{F_1G_2}{x_2y_1f_1g_2}\left(1+\frac{x_2y_1f_2g_1}{x_1y_2f_1g_2}\right)(x_1y_2-x_2y_1)^2$$

Observe that C_0, C_1, C_2, C_3 are positive when SS4 is meaningful. When the Ruth-Hurwitz [30] criteria are checked for eqn.(2.68) it turns out that they are always satisfied provided that SS4 is meaningful. The algebra is fairly extensive and for this reason the proof is not presented here. One concludes then that SS4 is stable whenever meaningful. The Ruth-Hurwitz criteria do not provide information as to whether the eigenvalues are real or complex. Nevertheless, extensive computer simulations have never shown any damped oscillatory behavior hence it seems that all eigenvalues are real (and negative).

Before concluding the analysis of the steady states for the non-splitting system there are two things that have to be mentioned:

1. The stability analysis of each steady state is based on the eigenvalues of the Jacobian matrix hence theoretically the results hold locally only, computer simulations though have indicated that the same results hold globally as well.

2. It cannot be shown analytically if for a given set of parameters more than one of SS1 through SS4 is meaningful and stable. Numerical studies have indicated that this is not possible, i.e. the steady states are mutually exclusive.

OPERATING DIAGRAMS AND THE EFFECT OF THE PARAMETERS

The analysis which has been presented in the previous sections of this thesis has yielded a number of conditions which when satisfied imply that the system will be at one of the possible steady states (SS1 through SS4). The conditions in most of the cases and especially in the case of the coexistence steady state, are very complicated and thus one cannot by simply inspecting them provide an answer to the following questions:

Can one really find values in the parameter space for which the conditions are satisfied?

If there are values of the parameters which satisfy the conditions, are these values discrete or do they form a subspace (range) in the parameters space? In the former case, due to the ever existing fluctuations in some parameters (e.g. flow rate) the steady state predicted is practically unattainable while in the latter case the system can indeed be operated at the predicted steady state.

What changes does the system undergo when some parameters are adjusted to different values, i.e. what is the effect of the various parameters on the behavior of the system?

In order to answer the foregoing questions one has to perform numerical studies.

The model has six parameters, namely α, u_f, R, β, φ, and ω. The parameters φ and ω can be called system parameters in the sense that given the type of organisms and the identity of the rate-limiting substrate, their values are fixed (provided that the temperature is constant and that the substrate transferred from one chemostat to the other is qualitatively similar to the fresh one, assumptions that are made throughout this study). In the results presented here, φ and ω have been fixed at 0.4 and 0.125, respectively and the reason for not presenting results for other values of φ and ω is that they are qualitatively the same as those obtained for the adopted values. The parameter β can be classified as a design parameter in the sense that its value depends on the selection of the volume of the two tanks. Keeping the values of all other parameters constant and varying β one gets a comparison among design alternatives. The parameters α, R and u_f are the operating parameters in the sense that they can be freely and easily adjusted in a given system in order to get one behavior or the other. It is interesting to present the results in the form of operating diagrams, an idea first introduced by Jost et al [31]. In this case the operating diagrams should be 3-dimensional (α, R, u_f) or even 4-dimensional if one wants to study simultaneously the effect of the parameter β. Although 3-dimensional diagrams can be constructed it is not easy to read them due to their complexity, and for this reason the operating diagrams presented here are projections in the α-u_f plane.

Operating diagrams for the non-splitting system are presented in Figures 5 through 11. In all figures the values for φ and ω are 0.4 and 0.125, respectively as stated also previously. In Figures 5 through 8, R is fixed at 0.1 while the values for β are 0.2, 0.25, 0.6 and 1.0, respectively. Figure 9 is for the case where β=0.2 and R=3 while Figures 10 and 11 are for the cases where β=1.5 and R is 0.01 and 1.0, respectively.

The first thing to observe from the diagrams is that the coexistence steady state (SS4) arises for ranges of values in the operating parameters space hence such a result is practically attainable and not only a mathematical possibility. One can also observe that the crossing point of the curves $Kf(u_f)$ and $Kg(u_f)$ (i.e. the point $(u_{fc}, K\alpha_c)$) is always a point of a boundary of SS4 and furthermore, that coexistence does not occur for values of u_f less than u_{fc}. These two things have been predicted from the analysis and they have been discussed in the previous section.

In Figure 5 there are in fact two separate regions of coexistence but the upper one is so narrow that it can be considered as a curve rather than a region. Practically one cannot operate the system there and obtain coexistence.

This "curve" can be viewed as a locus of switching points between SS2 and SS3. If one operates in the (lower and actual) region of coexistence there is a range of values of u_f (up to 2.84) where a substantial change in α, either an increase (known as shift-up experiment) or decrease (known as shift-down experiment) leads to the exclusion of the same species (i.e. there is a transition from SS4 to SS3). For values of u_f larger than 2.84 and starting from the domain of coexistence, shift-up and shift-down experiments will lead to the exclusion of either one or the other species.

In all diagrams other than the one shown in Figure 5, there is a single region of coexistence the complexity of which varies, for example it becomes less complex as one goes from Figure 6 to Figure 8.

The diagrams shown in Figures 6 and 9 have the following common features: starting from the domain of coexistence there is a range of values of u_f for which either a shift-up or a shift-down in the value of α will lead to SS3, a range of values of u_f for which either a shift-up or a shift-down in the value of α will lead to SS2 and finally there is a range of values of u_f for which a shift-up in the value of α will lead to the exclusion of the species that will survive in a shift-down experiment.

In the diagrams shown in Figures 8, 10 and 11 the boundaries of the region of coexistence always separate different steady states and the same is true except for a very narrow range of values of u_f slightly higher than 1, for the diagram shown in Figure 7. In the diagram shown in Figure 10, the domain of coexistence is so narrow that one can say that in this case coexistence is practically impossible.

The sequence of diagrams shown in Figures 5 through 8 shows the typical behavior of the system when the value of the recycle ratio R is fixed and the value of the volume ratio β increases. One can say that at fixed R, large values of β lead to a decrease in the range of values of α which yield coexistence. In fact, for any value of R, values of β larger than 1 yield unsatisfactory results as it can be seen from the diagrams shown in Figures 10 and 11. From the same diagrams it can be seen that when β is fixed at a value larger than 1, very small values of R make coexistence practically impossible (Figure 10). However for any value of R larger than 1 (but not too high) the picture does not improve from what is shown in Figure 11.

Keeping β fixed at a value less than 1 and varying the value of R one gets the behavior shown in Figures 5 and 9. When the value of R is further increased the shape of the coexistence region remains the same as that shown in Figure

9 with the only difference being that the S-shaped parts of the curves move to the right (i.e. to higher u_f values).

In the case where the value of R is very large, regardless of the values for the other parameters one expects that coexistence is impossible (except for discrete values of α) since a very large R practically implies a homogeneous environment (like in a single reactor). Numerical studies at very large values of R have indicated that in fact there is a region in the parameter space where coexistence occurs but this region arises for extremely large values of u_f. Hence the existence of the coexistence region is a mathematical rather than a physical result since at very large values of u_f one cannot really talk about rate limitation by the substrate fed at a concentration u_f and in that case either there is no competition or the case is of no interest in the sense that the values of u_f are not physically possible. In fact for reasonable values of u_f the model does predict the impossibility of coexistence at very large values of R.

Numerical studies for other values of ω and φ, always satisfying the condition $\omega<\varphi<1$, have indicated that the results are the same with those presented here. Numerical studies for the case where $\omega>\varphi>1$ have not been performed but the results will be the same since by naming population A as population B and vice-versa one falls again in the case where $\omega<\varphi<1$.

In conclusion there are two things that need to be emphasized:

Coexistence is indeed possible in the case of the non-splitting system, and

For a wider range of coexistence it is better to select values of β being less than 1, that is the smaller vessel must be the one in which the growth medium is fed.

Table 1: Parameter Values used for the Operating Diagrams shown in Figures 5-11

Fig. No.	φ	ω	β	R
5	0.4	0.125	0.2	0.1
6	"	"	0.25	"
7	"	"	0.6	"
8	"	"	1.0	"
9	"	"	0.2	3.0
10	"	"	1.5	0.01
11	"	"	"	1.0

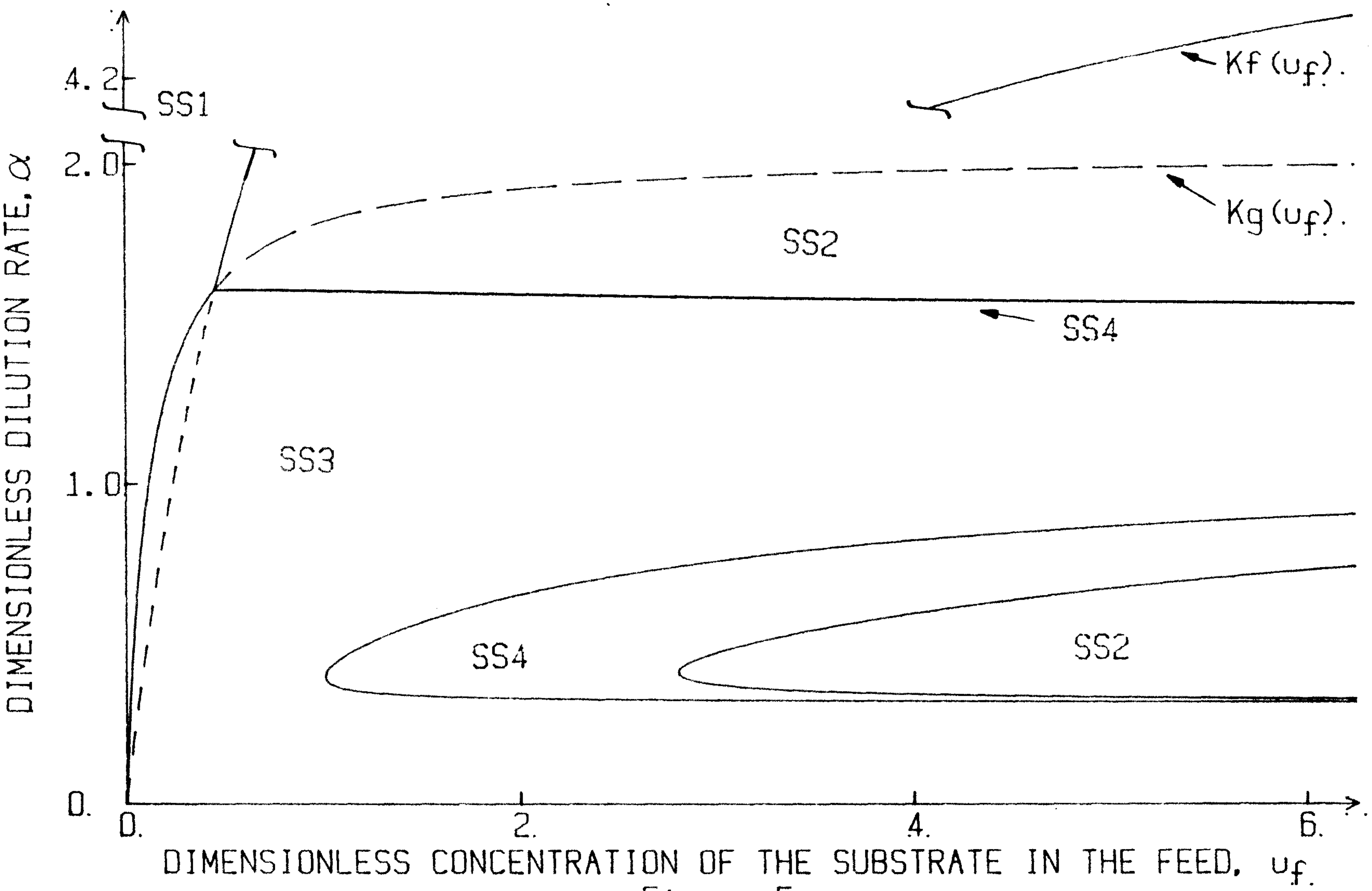

4.2
2.0
1.0
0.
SS1
SS2
SS3
SS4
SS4
SS2
Kf (u_f).
Kg (u_f).
SS4
DIMENSIONLESS DILUTION RATE, α
0.
2.
4.
6.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 5.

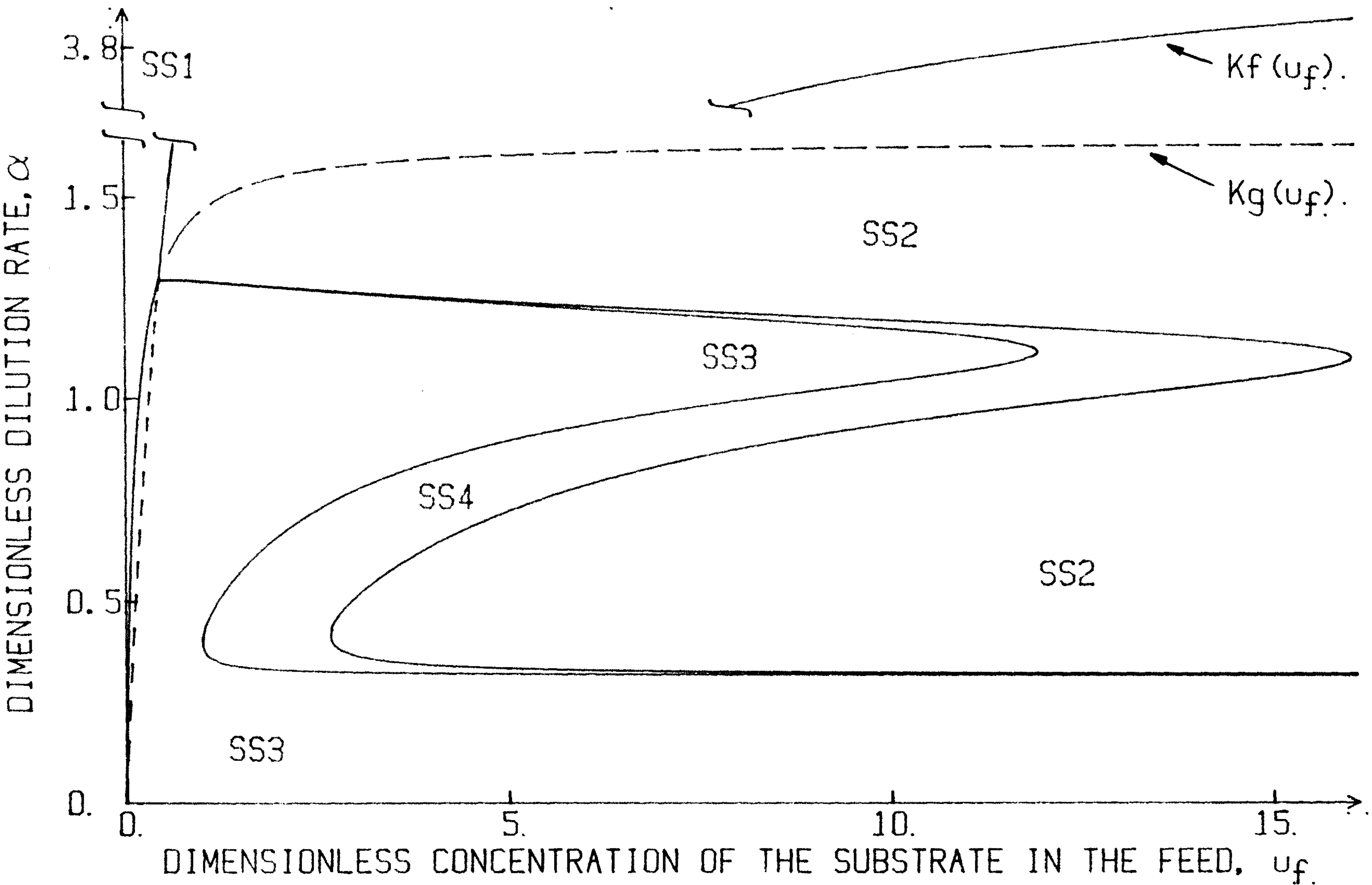

3.8
1.5
1.0
0.5
0.
0.
5.
10.
15.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
SS1
$K_f(u_f)$.
$K_g(u_f)$.
SS2
SS3
SS4
SS2
SS3

Figure 6.

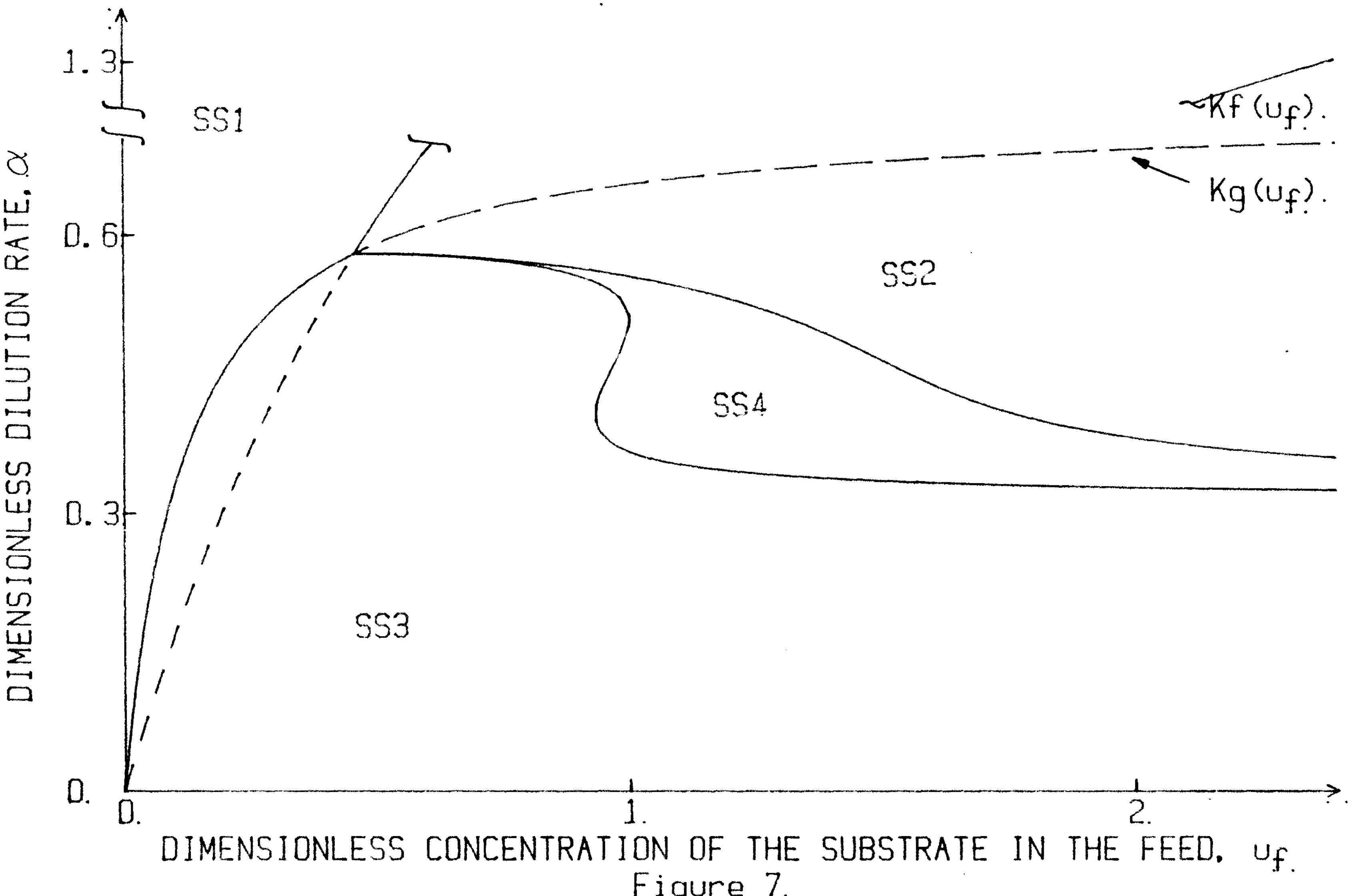

1.3
0.6
0.3
0.
0.
1.
2.
SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 7.

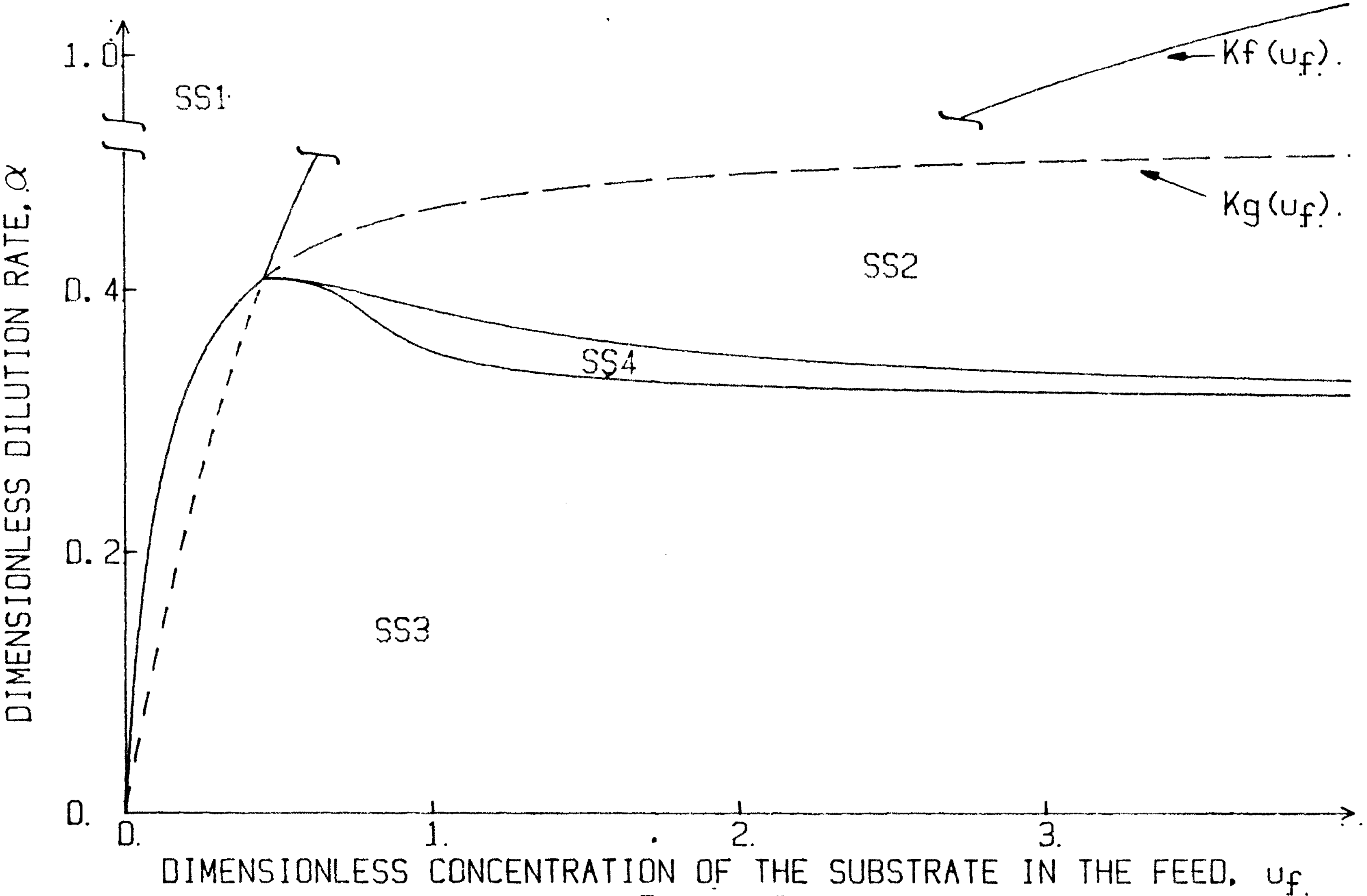

1.0
0.4
0.2
0.
0.
1.
2.
3.
SS1
SS2
SS3
SS4
Kf(uf).
Kg(uf).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 8.

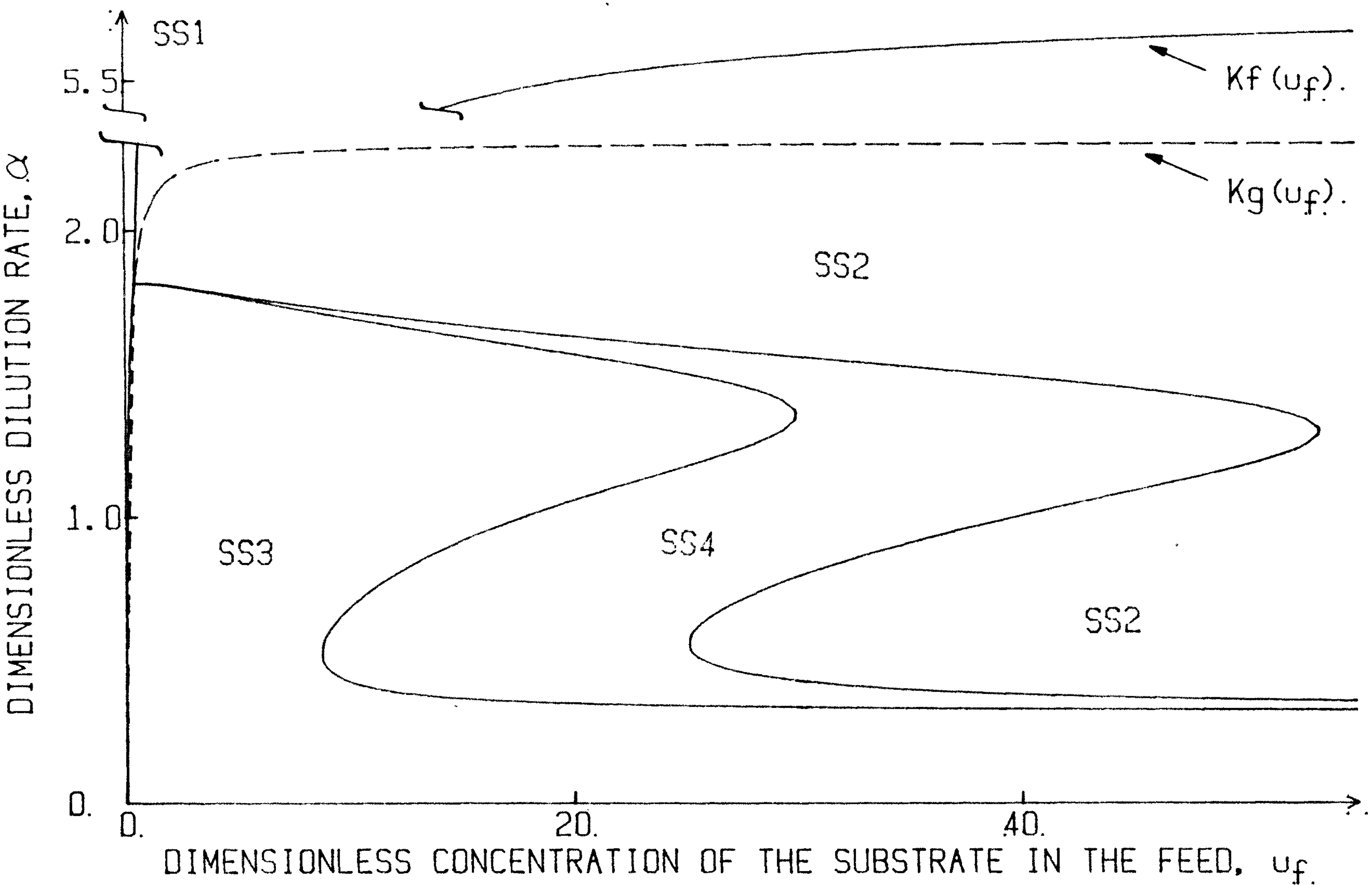

SS1
5.5
2.0
1.0
0.
Kf (uf).
Kg (uf).
SS2
SS3
SS4
SS2
0.
20.
40.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 9.

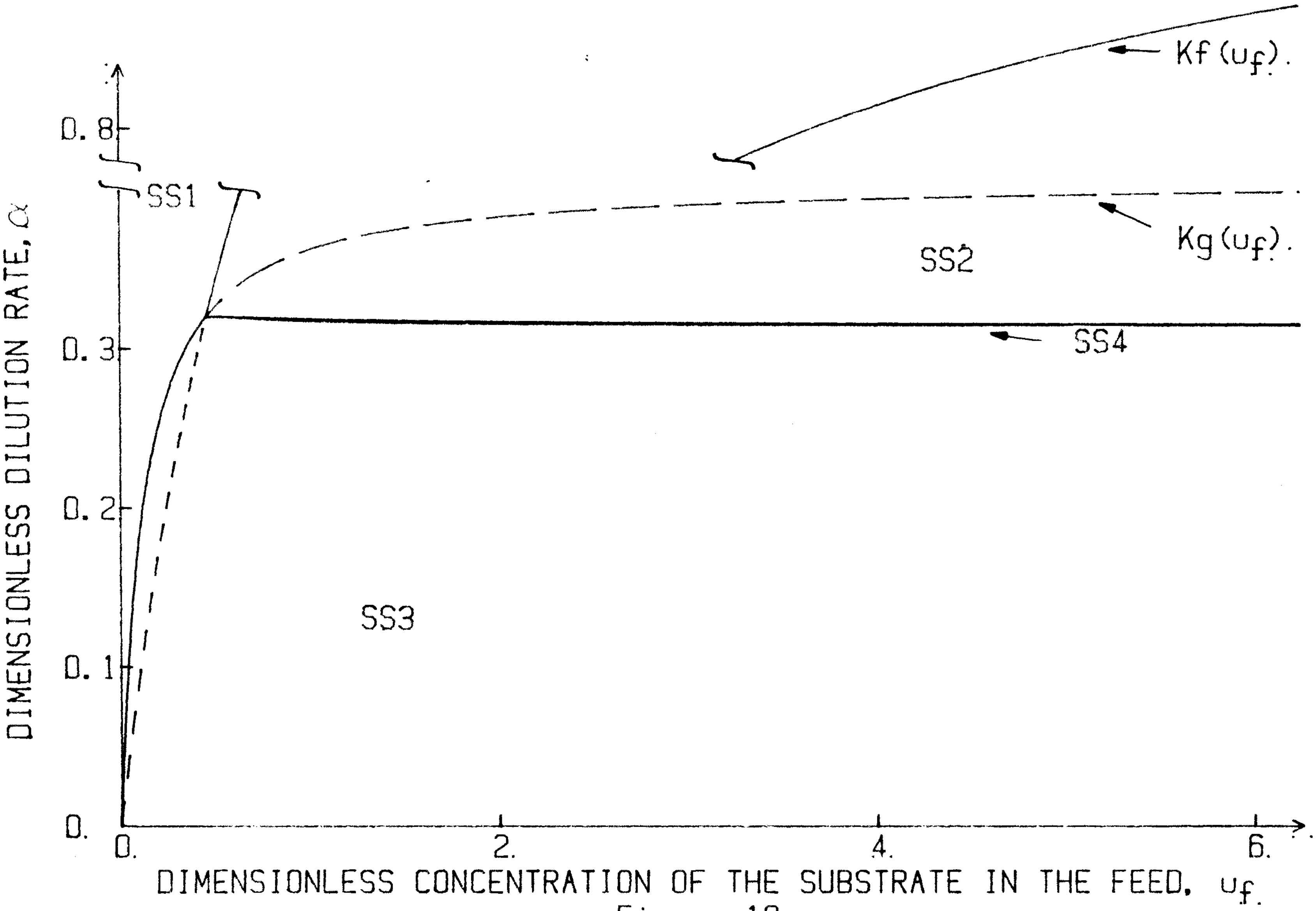

DIMENSIONLESS DILUTION RATE, α
0.8
0.3
0.2
0.1
0.
0.
2.
4.
6.
SS1
SS2
SS3
SS4
$Kf(u_f)$.
$Kg(u_f)$.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 10.

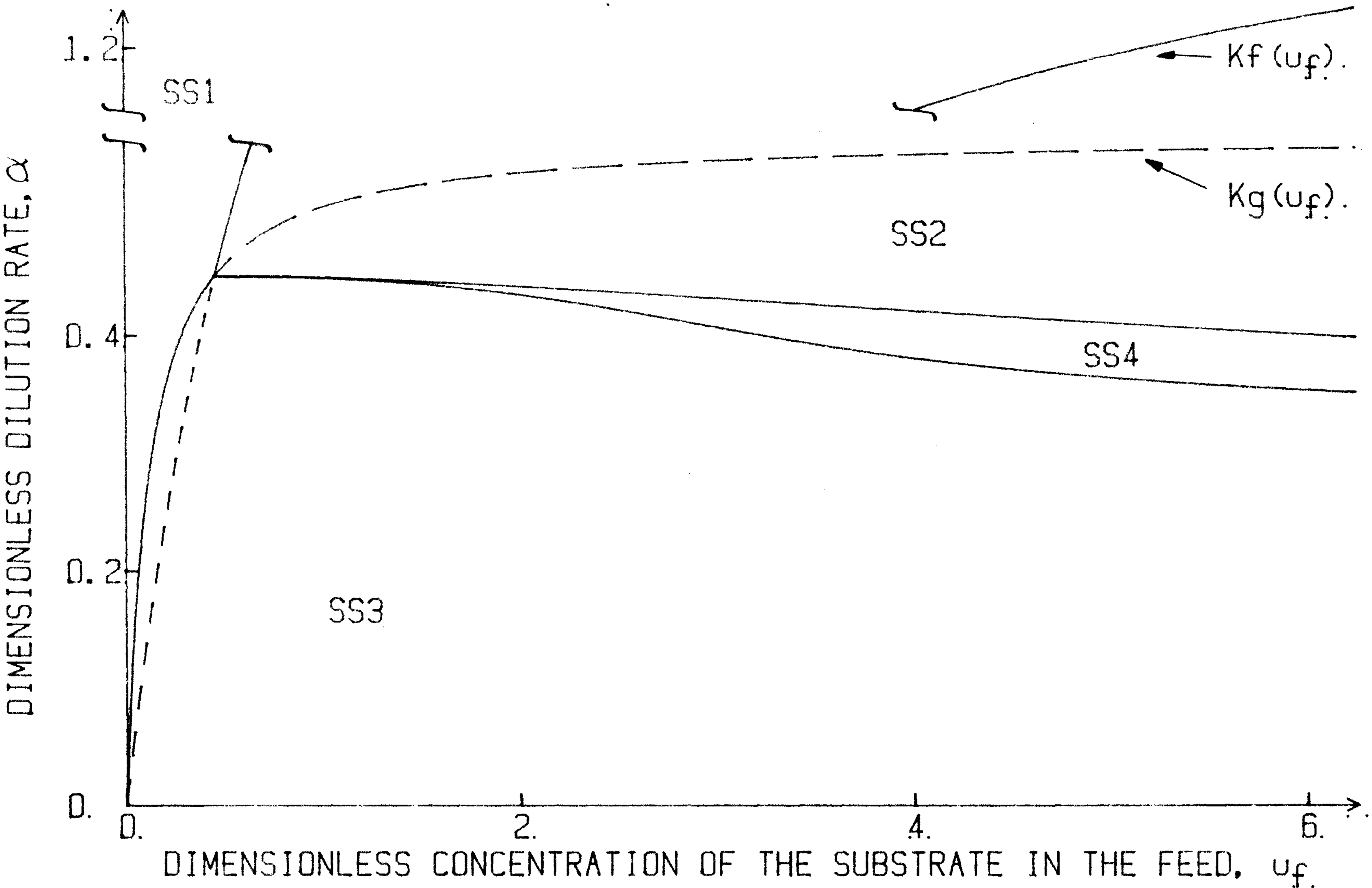

1.2
D.4
D.2
D.
D.
2.
4.
6.
SS1
SS2
SS3
SS4
Kf (u_f).
Kg (u_f).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 11.

III ANALYSIS OF THE SPLITTING SYSTEM

MODEL EQUATIONS

In this section the case where both reactors (chemostats) are fed with fresh medium is studied. It is assumed that the fresh medium going in either reactor has the same composition hence it can be thought as splitting a single external feed stream between the two vessels, and this is why the term "Splitting System" has been adopted.

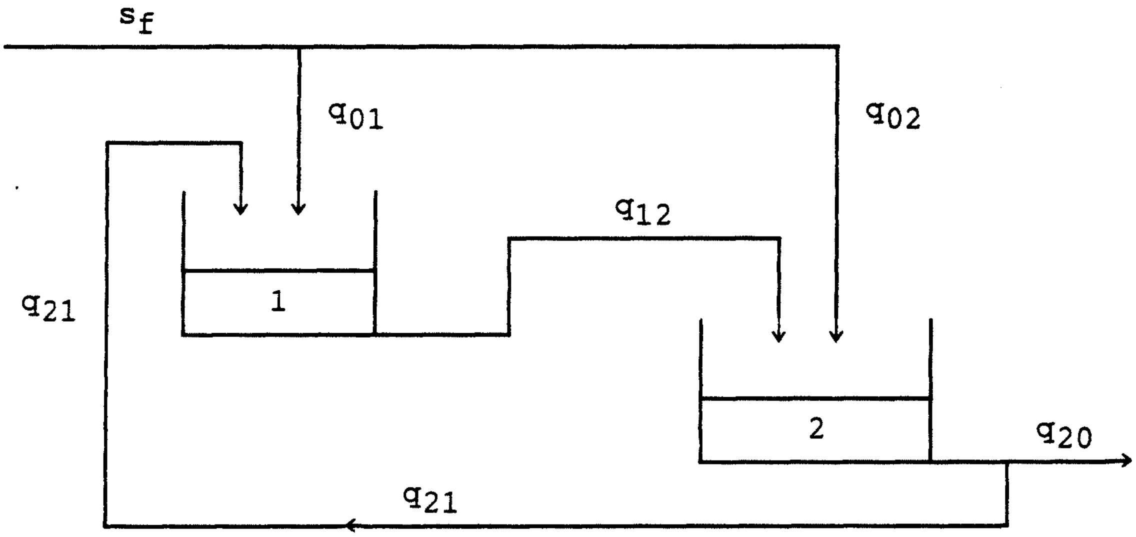


Figure 3: The Splitting System

The configuration of the system is shown in Figure 3. It must be noted that Stephanopoulos and Fredrickson [14] in a short communication, have showed that this system can lead to coexistence and they have given some conditions under which coexistence arises. The reasons for studying the same system here are to provide a detailed analysis of the possible steady states, to construct operating diagrams and to compare this system with the non-splitting case analyzed in the previous part of this thesis (a case which had not been studied previously).

The equations describing the system are equations (1.7) through (1.12) when the parameter η is set as equal to unity. The equations then take the following form:

$$\frac{dx_1}{d\vartheta} = R(\gamma+1)\alpha x_2 - [R(\gamma+1)+1]\alpha x_1 + f(u_1)x_1 \tag{3.1}$$

$$\frac{dy_1}{d\vartheta} = R(\gamma+1)\alpha y_2 - [R(\gamma+1)+1]\alpha y_1 + g(u_1)y_1 \tag{3.2}$$

$$\frac{du_1}{d\vartheta} = \alpha u_f + R(\gamma+1)\alpha u_2 - [R(\gamma+1)+1]\alpha u_1 - f(u_1)x_1 - g(u_1)y_1 \tag{3.3}$$

$$\frac{dx_2}{d\vartheta} = \beta[R(\gamma+1)+1]\alpha x_1 - \beta(R+1)(\gamma+1)\alpha x_2 + f(u_2)x_2 \tag{3.4}$$

$$\frac{dy_2}{d\vartheta} = \beta[R(\gamma+1)+1]\alpha y_1 - \beta(R+1)(\gamma+1)\alpha y_2 + g(u_2)y_2 \tag{3.5}$$

$$\frac{du_2}{d\vartheta} = \alpha\beta\gamma u_f + \beta[R(\gamma+1)+1]\alpha u_1 - \beta(R+1)(\gamma+1)\alpha u_2 - f(u_2)x_2 - g(u_2)y_2 \tag{3.6}$$

Two of the differential equations above can be replaced by the two stoichiometric equations described by eqns.(1.15) and (1.16) which now become

$$u_f = x_1 + y_1 + u_1 \tag{3.7}$$

$$u_f = x_2 + y_2 + u_2 \tag{3.8}$$

It is interesting to notice here that the stoichiometric relations for the splitting and the non-splitting system are identical.

In the analysis which follows eqns.(3.1), (3.2), (3.7), (3.4), (3.5) and (3.8) are used to describe the system. The possible steady states for the system are those presented in the section I of the thesis. The local stability of each possible steady state is studied by examining the character of the eigenvalues of the Jacobian matrix of the system which is the following:

$$\underline{\underline{S}} = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & a_{23} & a_{24} \\ a_{31} & a_{32} & a_{33} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{bmatrix}$$

where,

$$a_{11} = f_1 - [R(\gamma+1)+1]\alpha - x_1F_1$$

$$a_{12} = -x_1F_1$$

$$a_{13} = R(\gamma+1)\alpha$$

$$a_{21} = -y_1G_1$$

$$a_{22} = g_1 - [R(\gamma+1)+1]\alpha - y_1G_1$$

$$a_{24} = R(\gamma+1)\alpha$$

$$a_{31} = [R(\gamma+1)+1]\beta\alpha$$

$$a_{33} = f_2 - (R+1)(\gamma+1)\beta\alpha - x_2F_2$$

$$a_{34} = -x_2F_2$$

$$a_{42} = [R(\gamma+1)+1]\beta\alpha$$

$$a_{43} = -y_2G_2$$

$$a_{44} = g_2 - (R+1)(\gamma+1)\beta\alpha - y_2G_2$$

$$a_{14} = a_{23} = a_{32} = a_{41} = 0$$

with,

$$f_i = f(u_i), \qquad g_i = g(u_i) \qquad i = 1, 2$$

$$F_i = F(u_i) = \frac{df_i}{du_i} = \frac{1}{(1+u_i)^2} \qquad i = 1, 2$$

$$G_i = G(u_i) = \frac{dg_i}{du_i} = \frac{\varphi\omega}{(\omega+u_i)^2} \qquad i = 1, 2$$

ANALYSIS OF SS1 (WASHOUT STEADY STATE)

This steady state implies that $x_i=y_i=0$ and $u_i=u_f$, i=1, 2 and it is always meaningful.

All off-diagonal elements of the Jacobian matrix evaluated at SS1 are non-negative and hence, using Sevastyanov's lemma [29] (as on p.32) one obtains the following conditions for the (local) stability of SS1

$$f(u_f) - [R(\gamma+1)+1]\alpha < 0 \qquad (3.9)$$

$$g(u_f) - [R(\gamma+1)+1]\alpha < 0 \qquad (3.10)$$

$$\{f(u_f)-[R(\gamma+1)+1]\alpha\}[f(u_f)-(R+1)(\gamma+1)\beta\alpha] - R(\gamma+1)[R(\gamma+1)+1]\beta\alpha^2 > 0 \qquad (3.11)$$

$$\{g(u_f)-[R(\gamma+1)+1]\alpha\}[g(u_f)-(R+1)(\gamma+1)\beta\alpha] - R(\gamma+1)[R(\gamma+1)+1]\beta\alpha^2 > 0 \qquad (3.12)$$

It must be stated here that conditions (3.11) and (3.12) are exactly opposite to those published in the literature [14], something which most probably has to be attributed to a printing error.

After some algebraic manipulations the four conditions above can be substituted by a single condition, namely

$$\alpha > \max\{ Kf(u_f), Kg(u_f) \} \qquad (3.13)$$

where,

$$K = \frac{[\beta(R+1)(\gamma+1)+R(\gamma+1)+1] + \Delta^{\frac{1}{2}}}{2\beta[(R(\gamma+1)+1](\gamma+1)} \qquad (3.13a)$$

with,

$$\Delta = \{\beta(\gamma+1)-[R(\gamma+1)+1]\}^2+[\beta R(\gamma+1)]^2 + 2\beta R(\gamma+1)[\beta(\gamma+1)+R(\gamma+1)+1]$$

It can be easily seen that K decreases as γ increases. This observation coupled with condition (3.13), suggests that when all parameters except α and γ are kept constant, an increase in the splitting ratio results in a wider range of values of α under which washout occurs, something surely undesirable.

One can also observe that the relation of the value of K to unity, strongly depends on the product of the values of β and γ. Namely,

If $\beta\gamma > 1$, then $K < 1$

If $\beta\gamma = 1$, then $K = 1$

If $\beta\gamma < 1$, then $K > 1$

The relation of the value of K to unity influences significantly the behavior of the system, something which is discussed later in this section.

ANALYSIS OF SS2

This steady state arises when $x_i > 0$ and $y_i = 0$, $i=1, 2$. It implies that one population establishes itself in both vessels by winning the competition and excluding its competitor. The values of x_i and u_i, $i=1, 2$ in this case are given as solution(s) of the following equations:

$$f(u_1)x_1 + R(\gamma+1)\alpha x_2 - [R(\gamma+1)+1]\alpha x_1 = 0 \tag{3.14}$$

$$f(u_2)x_2 + \beta[R(\gamma+1)+1]\alpha x_1 - \beta(R+1)(\gamma+1)\alpha x_2 = 0 \tag{3.15}$$

$$u_1 = u_f - x_1 \tag{3.16}$$

$$u_2 = u_f - x_2 \tag{3.17}$$

In the case of the non-splitting system it has been shown that for a meaningful SS2 it must be $u_1 > u_2$ and $x_1 > x_2$. These conditions do not have necessarily to hold in order to get a meaningful SS2 in the case of the splitting system. This can be seen both mathematically and physically as following:

Mathematically, from eqn.(3.15) one can write:

$$x_2 - x_1 = \frac{f_2 - \alpha\beta\gamma}{\beta\alpha[R(\gamma+1)+1]} x_2$$

In the case of the non-splitting system (i.e. $\gamma=0$), the right-hand side of the equality above has to be positive for a meaningful SS2 hence it must be $x_2>x_1$ which, via the stoichiometric relations, implies that $u_1>u_2$. If γ is not zero (i.e. for the splitting system) there is nothing to necessarily force the right-hand side of the equality above to be positive hence one may have either $x_2>x_1$ or $x_1>x_2$ and correspondingly (via the stoichiometric relations again) either $u_2<u_1$ or $u_1<u_2$.

Physically, when the splitting ratio is high one expects that the amount of fresh rate-limiting substrate going in the second vessel may (because it will also depend on the volumes of vessels) be higher than that going in the first vessel and this would most probably result in $u_2>u_1$ and $x_2<x_1$ which is opposite of what happens in the non-splitting system.

Based on the results of extensive numerical studies, the following have been observed (for a meaningful SS2):

when $\beta\gamma>1$ then $u_2 > u_1$ and $x_2 < x_1$ (3.18)

when $\beta\gamma<1$ then $u_2 < u_1$ and $x_2 > x_1$ (3.19)

In the special case where $\beta\gamma=1$ it will be proved in the following that $u_1=u_2$ and $x_1=x_2$.

Rearranging steady state eqns.(3.14) & (3.15) one gets:

$$\frac{f_1-[R(\gamma+1)+1]\alpha}{R(\gamma+1)\alpha} = \frac{\beta[R(\gamma+1)+1]\alpha}{f_2-\beta(R+1)(\gamma+1)\alpha}$$

or $\{f_1-[R(\gamma+1)+1]\alpha\}\{f_2-\beta(R+1)(\gamma+1)\alpha\}=\beta R(\gamma+1)[R(\gamma+1)+1]\alpha^2$ (3.20)

Upon further manipulation eqn.(3.20) yields

$$u_2 = \frac{A_1u_1 + B_1}{C_1u_1 + D_1} \tag{3.21}$$

where,

$A_1 = \beta(\gamma+1)\{(R+1)\alpha-[R(\gamma+1)+1]\alpha^2\}$

$B_1 = -\beta(\gamma+1)[R(\gamma+1)+1]\alpha^2$

$C_1 = \beta(\gamma+1)[R(\gamma+1)+1]\alpha^2-\{\beta(\gamma+1)(R+1)+[R(\gamma+1)+1]\}\alpha+1$

$D_1 = [R(\gamma+1)+1][\beta(\gamma+1)\alpha^2-\alpha]$

Using eqns.(3.14), (3.16), (3.17) and (3.21) one gets the following equation in u_1:

$$J_3u_1^3 + J_2u_1^2 + J_1u_1 + J_0 = 0 \tag{3.22}$$

where,

$J_3 = \{-[R(\gamma+1)+1]\alpha+1\}C_1$

$J_2 = [u_fC_1+R(\gamma+1)A_1-[R(\gamma+1)+1](C_1+D_1)]\alpha + D_1 - u_fC_1$

$J_1 = \{R(\gamma+1)(A_1+B_1)+u_f(C_1+D_1)-[R(\gamma+1)+1]D_1\}\alpha - u_fD_1$

$J_0 = [R(\gamma+1)B_1+u_fD_1]\alpha$

After u_1 is calculated from equation (3.22) for a given set of parameter values $(\alpha,u_f,\beta,\gamma,R)$ its value(s) can be used to calculate u_2, x_1, and x_2 via equations (3.21), (3.16) and (3.17), respectively. Due to the cubic nature of equation (3.22), theoretically up to three different SS2 are possible. Numerical studies though, have indicated that if a meaningful SS2 is possible it is unique.

In the special case where $\beta\gamma=1$ (which leads to $K=1$) the situation becomes much simpler as it is shown in the following:

Using equations (3.14) and (3.15) and after some algebraic manipulations one obtains

$$\{[R(\gamma+1)+1](\beta+1)\alpha-f_2+\frac{x_1}{(1+u_1)(1+u_2)}\}(u_2-u_1) = 0 \quad (3.23)$$

Furthermore, form eqn.(3.15) it can be seen that for a meaningful SS2 it must be:

$$\beta(R+1)(\gamma+1)\alpha > f_2 \quad \text{or} \quad (R+1)(\beta+1)\alpha > f_2 \quad (3.23a)$$

One can also easily see that

$$[R(\gamma+1)+1](\beta+1) > (R+1)(\beta+1) \quad (3.23b)$$

Combining the inequalities (3.23a) and (3.23b) one concludes that it must be:

$$[R(\gamma+1)+1](\beta+1)\alpha > f_2$$

The last inequality implies that the quantity in the braces in equation (3.23) is positive for any meaningful SS2. Hence, equation (3.23) cannot be satisfied unless $u_1=u_2$. This implies, through equations (3.16) and (3.17) that it must also be $x_1=x_2$. These two equalities imply that when $\beta\gamma=1$ and the system is at SS2, the environment is identical in both vessels, i.e. the environment is not spatially heterogeneous. In this case the steady state equations (3.14) through (3.17) reduce into a system of two equations, namely

$$\alpha - f(u) = 0, \quad \text{from which one gets} \quad u = \frac{\alpha}{1-\alpha}$$

and, $x = u_f - u$

where, $x = x_1 = x_2$ and $u = u_1 = u_2$

It should be noted here that the value for u is independent of u_f, something which is not true if $\beta\gamma \neq 1$.

The (local) stability of SS2 is determined by the eigenvalues of the Jacobian matrix, which in this case are given as roots of the following quadratics:

$$Q_1(\lambda) = \lambda^2 + \{R(\gamma+1)\alpha\frac{x_2}{x_1} + [R(\gamma+1)+1]\beta\alpha\frac{x_1}{x_2} + x_1F_1 + x_2F_2\}\lambda$$

$$+R(\gamma+1)\alpha\frac{x_2}{x_1}x_2F_2 + [R(\gamma+1)+1]\beta\alpha\frac{x_1}{x_2}x_1F_1 + x_1x_2F_1F_2 = 0 \quad (3.24)$$

and,

$$Q_2(\lambda) = \lambda^2 - \{g_1 - [R(\gamma+1)+1]\alpha + g_2 - \beta(R+1)(\gamma+1)\alpha\}\lambda$$

$$+\{g_1 - [R(\gamma+1)+1]\alpha\}[g_2 - \beta(R+1)(\gamma+1)\alpha] - \beta R(\gamma+1)[R(\gamma+1)+1]\alpha^2 = 0$$

(3.25)

It is easy to show that the quadratic $Q_1(\lambda)=0$ has always real and negative roots thus the stability of SS2 is determined by the roots of $Q_2(\lambda)=0$ only.

If λ_1 and λ_2 are the roots of $Q_2(\lambda)=0$, then from eqn. (3.25) one can see that λ_1 and λ_2 are always real and hence for a stable SS2 the following two inequalities have to be satisfied:

$$\lambda_1+\lambda_2 = g_1 - [R(\gamma+1)+1]\alpha + g_2 - \beta(R+1)(\gamma+1)\alpha < 0 \qquad (3.26)$$

and,

$$\lambda_1\lambda_2 = \{g_1-[R(\gamma+1)+1]\alpha\}[g_2-\beta(R+1)(\gamma+1)\alpha] - \beta R(\gamma+1)[R(\gamma+1)+1]\alpha^2 > 0 \qquad (3.27)$$

Actually, upon further manipulation one can show that conditions (3.26) and (3.27) can be substituted by the following single criterion:

$$\alpha > \frac{\beta(R+1)(\gamma+1)g_1+[R(\gamma+1)+1]g_2 \quad + \Delta^{\frac{1}{2}}}{2\beta(\gamma+1)[R(\gamma+1)+1]} \qquad (3.28)$$

with,

$$\Delta = \{\beta(\gamma+1)g_1-[R(\gamma+1)+1]g_2\}^2+\beta^2R(R+2)(\gamma+1)^2g_1^2 + 2\beta R(\gamma+1)[R(\gamma+1)+1]g_1g_2 > 0$$

One can get some further insight for SS2 by taking into consideration the mutual disposition of the f(u) and g(u) curves. There are four possible dispositions as shown in Fig.4. Following the same procedure as in the case of the non-splitting system one can easily see the following:

When the specific growth rate curves do not cross, in the case where $\omega>\varphi$ and $\varphi<1$ (Fig.4a), SS2 is always stable if meaningful. While in the case where $\omega<\varphi$ and $\varphi>1$ (Fig. 4b), it is always unstable.

When the specific growth rate curves cross each other, something which occurs at the value u_c of u given by

$$u_c = \frac{\omega - \varphi}{\varphi - 1} \tag{3.29}$$

then,

if $1>\varphi>\omega$ (Fig.4c), SS2 is stable if meaningful and if both u_1 and u_2 are larger than u_c; SS2 is unstable if both u_1 and u_2 are less than u_c while if either $u_1>u_c>u_2$ or $u_2>u_c>u_1$ and SS2 is meaningful its stability cannot be determined right away and the criterion given by (3.28) has to be checked.

if $1<\varphi<\omega$ (Fig.4d), SS2 is stable if meaningful and if both u_1 and u_2 are less than u_c. SS2 is unstable if both u_1 and u_2 are larger than u_c, while for any other relationship among u_1, u_2 and u_c the stability of a meaningful SS2 will again be determined via the condition (3.28).

ANALYSIS OF SS3

This steady state arises when $x_i=0$ and $y_i>0$, $i=1,2$. The case is symmetric to SS2 hence the analysis will not be repeated. If x_i is interchanged with y_i and f_i is interchanged with g_i $(i=1, 2)$ in the results of SS2, the results of SS3 are obtained. There are only two equations which have to be slightly modified, namely:

$$u_2 = \frac{A_1'u_1 + B_1'}{C_1'u_1 + D_1'} \tag{3.29a}$$

where,

$$A_1' = \beta\omega(\gamma+1)\{(R+1)\varphi\alpha-[R(\gamma+1)+1]\alpha^2\}$$

$$B_1' = -\beta\omega^2(\gamma+1)[R(\gamma+1)+1]\alpha^2$$

$$C_1' = \beta(\gamma+1)[R(\gamma+1)+1]\alpha^2-\{\beta(\gamma+1)(R+1)+[R(\gamma+1)+1]\}\varphi\alpha+\varphi^2$$

$$D_1' = \omega[R(\gamma+1)+1][\beta(\gamma+1)\alpha^2-\alpha\varphi]$$

and,

$$J_3'u_1^3 + J_2'u_1^2 + J_1'u_1 + J_0' = 0$$

where,

$$J_3' = \{-[R(\gamma+1)+1]\alpha + \varphi\}C_1'$$

$$J_2' = \{u_fC_1'+R(\gamma+1)A_1' - [R(\gamma+1)+1](C_1'\omega+D_1')\}\alpha + \varphi(D_1'-u_fC_1')$$

$$J_1' = \{R(\gamma+1)(A_1'\omega+B_1')+u_f(C_1'\omega+D_1')-[R(\gamma+1)+1]\omega D_1'\}\alpha - \varphi u_fD_1'$$

$$J_0' = \omega[R(\gamma+1)B_1'+u_fD_1']\alpha$$

Again as in the case of SS2, numerical studies have shown that whenever a meaningful SS3 arises, it is unique despite the fact that mathematically the equations do not exclude the possibility for multiple SS3.

In the special case where $\beta\gamma=1$ the values for the variables are given by the expressions:

$$u_1 = u_2 = \frac{\omega\alpha}{\varphi - \alpha} = u$$

and, $$y_1 = y_2 = u_f - u = y$$

As in the case of SS2, when $\beta\gamma=1$ the environment is homogeneous if the system is at SS3.

One should note that all eigenvalues of SS2 and SS3 always real. Hence no oscillatory phenomena are expected during transients, something which has been confirmed by computer simulations. The same behavior is exhibited by the non-splitting system as it has been discussed in part II of the thesis.

ANALYSIS OF THE COEXISTENCE STEADY STATE (SS4)

For a meaningful SS4 it must be:

$$x_i > 0, \quad y_i > 0, \quad 0 < u_i < u_f \qquad i=1,\ 2$$

In order to find the values of the six variables one has to solve the following system of algebraic equations:

$$R(\gamma+1)\alpha x_2 - [R(\gamma+1)+1]\alpha x_1 + f(u_1)x_1 = 0 \tag{3.30}$$

$$R(\gamma+1)\alpha y_2 - [R(\gamma+1)+1]\alpha y_1 + g(u_1)y_1 = 0 \tag{3.31}$$

$$\beta[R(\gamma+1)+1]\alpha x_1 - \beta(R+1)(\gamma+1)\alpha x_2 + f(u_2)x_2 = 0 \tag{3.32}$$

$$\beta[R(\gamma+1)+1]\alpha y_1 - \beta(R+1)(\gamma+1)\alpha y_2 + g(u_2)y_2 = 0 \tag{3.33}$$

$$u_f = x_1 + y_1 + u_1 \tag{3.34}$$

$$u_f = x_2 + y_2 + u_2 \tag{3.35}$$

From eqns.(3.30) through (3.33) one can get the following relations:

$$f_1 - [R(\gamma+1)+1]\alpha = -R(\gamma+1)\alpha\frac{x_2}{x_1} \tag{3.36}$$

$$g_1 - [R(\gamma+1)+1]\alpha = -R(\gamma+1)\alpha\frac{y_2}{y_1} \tag{3.37}$$

$$f_2 - \beta(R+1)(\gamma+1)\alpha = -\beta[R(\gamma+1)+1]\alpha\frac{x_1}{x_2} \tag{3.38}$$

$$g_2 - \beta(R+1)(\gamma+1)\alpha = -\beta[R(\gamma+1)+1]\alpha\frac{y_1}{y_2} \qquad (3.39)$$

By multiplying the expressions (3.36) and (3.38) one gets:

$$\{f_1-[R(\gamma+1)+1]\alpha\}[f_2-\beta(R+1)(\gamma+1)\alpha] = \beta R[R(\gamma+1)+1](\gamma+1)\alpha^2 \qquad (3.40)$$

Similarly, by multiplying the expressions (3.37) and (3.39) one gets:

$$\{g_1-[R(\gamma+1)+1]\alpha\}[g_2-\beta(R+1)(\gamma+1)\alpha] = \beta R[R(\gamma+1)+1](\gamma+1)\alpha^2 \qquad (3.41)$$

Observe that for a meaningful SS4 all the left hand side parts of eqns.(3.36) through (3.39) have to be negative.

Using a procedure similar to that followed for the case of the non-splitting system (see part II) one concludes that the two competitors cannot coexist unless their specific growth rate curves cross each other (Fig.4c & 4d). If the specific growth rate curves cross each other, coexistence cannot be excluded only in the case where either $u_1>u_c>u_2$ or $u_2>u_c>u_1$. These two conditions imply physically that in each one of the two vessels a different microbial species has the competitive advantage. This result (which is in accordance with what has been published in [14]), is identical with the result found in part II. The only difference between the splitting and the non-splitting systems is that the condition $u_2>u_c>u_1$ cannot lead to a meaningful coexistence steady state for the non-splitting case.

The value of u_1 is a solution to the quadratic

$$I(u_1) = I_2u_1^2 + I_1u_1 + I_0 = 0 \tag{3.42}$$

where,

$$I_2=\beta(\gamma+1)[R(\gamma+1)+1]^2\alpha^3 - [R(\gamma+1)+1]\alpha^2\{\beta(\gamma+1)(R+1)(\varphi+1) +[R(\gamma+1)+1]\alpha_c\}+\{\beta(\gamma+1)(R+1)^2\varphi+[R(\gamma+1)+1][R\varphi+(1+\varphi)\alpha_c]\}\alpha - (R+1)\varphi\alpha_c$$

$$I_1=[R(\gamma+1)+1]\{\beta(\gamma+1)[R(\gamma+1)+1](\omega+1)\alpha^3 - [\beta(\gamma+1)(R+1)(\omega+\varphi) + [R(\gamma+1)+1](\omega+1)\alpha_c]\alpha^2 + (\omega+\varphi)\alpha_c\alpha\}$$

$$I_0=\omega[R(\gamma+1)+1]^2\alpha^2[\beta(\gamma+1)\alpha-\alpha_c]$$

with,

$$\alpha_c = \frac{\omega - \varphi}{\omega - 1} \tag{3.43}$$

With u_1 known the rest of the variables can be found through the following expressions:

$$u_2 = \frac{W_1}{W_2} \tag{3.44}$$

where,

$$W_1 = \beta(\gamma+1)\alpha\{[(R+1)-[R(\gamma+1)+1]\alpha]u_1-[R(\gamma+1)+1]\alpha\}$$

$$W_2 = \{\beta(\gamma+1)[R(\gamma+1)+1]\alpha^2-[\beta(\gamma+1)(R+1)+[R(\gamma+1)+1]]\alpha+1\}u_1 + [R(\gamma+1)+1][\beta(\gamma+1)\alpha^2-\alpha]$$

$$x_1 = \frac{(u_f-u_1)(\alpha-g_1)-(u_1-u_2)R(\gamma+1)\alpha}{f_1 - g_1} \tag{3.45}$$

$$y_1 = \frac{(u_1-u_2)R(\gamma+1)\alpha-(\alpha-f_1)x_1}{\alpha - g_1} \tag{3.46}$$

$$x_2 = \frac{[R(\gamma+1)+1]\alpha - f_1}{R(\gamma+1)\alpha} x_1 \tag{3.47}$$

$$y_2 = \frac{[R(\gamma+1)+1]\alpha - g_1}{R(\gamma+1)\alpha} y_1 \tag{3.48}$$

In the special case where $\beta\gamma=1$ and if $\alpha=\alpha_c$, where α_c is given by (3.43), equation (3.42) yields as solution $u_1=u_c$, where u_c is given by (3.29). When $\alpha=\alpha_c$ and $u_1=u_c$, equation (3.44) yields that u_2 is also equal to u_c. Hence it is $u_1=u_2=u_c$. In this case equations (3.30) and (3.31) or equations (3.32) and (3.33) imply that it is $x_1=x_2$ and $y_1=y_2$. Obviously in this case the environment is homogeneous. It must be noted that in this case x and y cannot be exactly specified since they have to satisfy a single equation only, namely:

$$x + y = u_f - u_c$$

Mathematically, the system has one degree of freedom in this case.

Extensive numerical studies for the case where $\beta\gamma=1$ have indicated that except for $\alpha=\alpha_c$ there is no other value of α resulting in a meaningful coexistence steady state.

Since coexistence occurs for a discrete value of α only, it is practically unattainable as in the case where pure and simple competition takes place in a single vessel.

At this point one can conclude that $\beta\gamma=1$ implies a spatially uniform environment regardless of the steady state the system is at. In the present study the use of two vessels was exactly in order to make the environment heterogeneous and hence make the coexistence of the two competitors possible. It is then a very important finding that β and γ must be always selected in a way such that $\beta\gamma \neq 1$ if one is interested in the coexistence steady state. This is a new finding, it is not mentioned in [14].

The quadratic (3.42) will yield real values for u_1 if and only if its discriminant Δ, is positive. After some algebraic manipulations one can show that

$$\Delta = \beta^2\alpha^2(\gamma+1)^2[R(\gamma+1)+1]^4(\omega-1)^2(\alpha-\theta')(\alpha-K_1\alpha_c)(\alpha-K\alpha_c)(\alpha-H') \tag{3.49}$$

where K is given by (3.13a) while,

$$K_1 = \frac{[\beta(R+1)(\gamma+1)+R(\gamma+1)+1] - \Delta_1^{\frac{1}{2}}}{2\beta[(R(\gamma+1)+1](\gamma+1)} \tag{3.50}$$

$$\theta' = \frac{[\beta(R+1)(\gamma+1)+[R(\gamma+1)+1]]\alpha_c - \Delta_2^{\frac{1}{2}}}{2\beta(\gamma+1)[R(\gamma+1)+1]} \tag{3.51}$$

$$H' = \frac{[\beta(R+1)(\gamma+1)+[R(\gamma+1)+1]]\alpha_c + \Delta_2^{\frac{1}{2}}}{2\beta(\gamma+1)[R(\gamma+1)+1]} \tag{3.52}$$

with,

$$\begin{aligned}\Delta_1 &= \{\beta(\gamma+1)-[R(\gamma+1)+1]\}^2+[\beta R(\gamma+1)]^2 \\ &\quad + 2\beta R(\gamma+1)[\beta(\gamma+1)+R(\gamma+1)+1] \\ \Delta_2 &= \{(R^2+2R)\beta^2(\gamma+1)^2+2R\beta(\gamma+1)[R(\gamma+1)+1]+[\beta(\gamma+1) \\ &\quad -[R(\gamma+1)+1]]^2\}(\omega-1)^4\alpha_c^2 + 16\beta(\gamma+1)[R(\gamma+1)+1] \\ &\quad (\omega-1)^2R\phi\omega\end{aligned} \tag{3.53}$$

One can easily show that

$$\Theta' < K_1\alpha_c < K\alpha_c < H' \qquad (3.54)$$

Hence a possibly meaningful coexistence steady state requires that α must be chosen such that:

$$\alpha < \Theta' \quad \text{or} \quad K_1\alpha_c < \alpha < K\alpha_c \quad \text{or} \quad \alpha > H' \qquad (3.55)$$

since each of the inequalities above guarantees that $\Delta > 0$ (i.e. u_1 real).

In fact from the numerical studies performed for this system, it turns out that the selection of α for coexistence is much more restricted than what the inequalities (3.55) suggest. Namely,

$$\text{if} \quad \beta\gamma > 1 \quad \text{it must be} \quad \frac{\alpha_c}{\beta\gamma} < \alpha < K\alpha_c$$

while,

$$\text{If} \quad \beta\gamma < 1 \quad \text{it must be} \quad \alpha_c < \alpha < K\alpha_c$$

The numerical studies have also indicated that whenever SS4 arises it does not exhibit any multiplicity. Furthermore, when $\beta\gamma>1$ it turns out that $u_2>u_c>u_1$ while when $\beta\gamma<1$ it is $u_2<u_c<u_1$.

The aforementioned observations from the numerical studies cannot, unfortunately, be proved analytically due to the complexity of the system equations.

From eqns.(3.42) and (3.44) one can observe that the values of u_1 and u_2 are independent of the value of u_f.

This implies that for a given system of populations (i.e. φ and ω) and for given α, R, β, and γ, when u_f varies the values of u_1 and u_2 remain unchanged while the biomass concentrations (x_i, y_i, i=1,2) do change. This has been always observed in the numerical studies and the same thing happens in the non-splitting system as well.

As in the case of the non-splitting system, one can observe from all operating diagrams (which are discussed in detail in the next section) for the system studied here that the point

$$(u_c,\ K\alpha_c) = \left(\frac{\omega - \varphi}{\varphi - 1},\ K\frac{\omega - \varphi}{\omega - 1}\right)$$

is always a point of the boundary of the domain of coexistence. One can in fact show that this has to be so. Assume that $u_1=u_c$ is a solution to the steady state equations. If $u_1=u_c$ then it must be $f_1=g_1=\alpha_c$. Using the last equality and combining (3.30) and (3.32) one gets:

$$f_2 - \beta(R+1)(\gamma+1)\alpha = \frac{\beta R(\gamma+1)[R(\gamma+1)+1]\alpha^2}{\alpha_c - [R(\gamma+1)+1]\alpha} \qquad (3.56)$$

$$g_2 - \beta(R+1)(\gamma+1)\alpha = \frac{\beta R(\gamma+1)[R(\gamma+1)+1]\alpha^2}{\alpha_c - [R(\gamma+1)+1]\alpha} \qquad (3.57)$$

Comparing the equations (3.56) and (3.57) one can easily conclude that it must be $f_2=g_2$, something which is true only if $f_2=g_2=\alpha_c$. The last equality implies that $u_2=u_c$. Substituting $f_2=\alpha_c$ in eqn.(3.56) (or equivalently, $g_2=\alpha_c$ in eqn.(3.57)) one gets a quadratic in α which when solved yields $\alpha=K\alpha_c$. When the equalities $\alpha=K\alpha_c$, $u_1=u_2=u_c$, and $f_1=g_1=\alpha_c$ are substituted in equation (3.3) the following equation is obtained:

$$(K - 1)(u_f - u_c)\alpha_c = 0 \tag{3.58}$$

At this point one has to distinguish between two cases:

<u>Case I.</u> $K = 1$ (which arises only if $\beta\gamma = 1$)

In this case equation (3.58) is always satisfied.

<u>Case II.</u> $K \neq 1$

In this case equation (3.58) is satisfied only if $u_f=u_c$

For the case where $\alpha=K\alpha_c$ and $u_f=u_c$ equations (3.30) through (3.32) yield $x_1=x_2=y_1=y_2=0$.

From the foregoing analysis one can conclude that the point $(u_{fc},K\alpha_c)$ results in a degenerate case of coexistence and that it must be a common point of the boundaries of SS1 and SS4 something which is in fact observed in all operating diagrams. Mathematically speaking the point $(u_{fc},K\alpha_c)$ is a bifurcation point from SS1 to SS4,

Since for a meaningful SS4 it must be true that $u_c<\max\{u_1,u_2\}<u_f$ one can conclude that for coexistence it is necessary to have

$$u_f > u_c = \frac{\omega - \varphi}{\varphi - 1} \tag{3.59}$$

The condition (3.59) provides guidance as to how u_f has to be selected if one hopes to get coexistence of the competitors (in numerical or experimental studies).

As far as the (local) stability of SS4 is concerned, one has to determine the character of the four eigenvalues of the Jacobian matrix which in this case are given as the roots of the following polynomial:

$$\lambda^4 + D_3\lambda^3 + D_2\lambda^2 + D_1\lambda + D_0 = 0 \qquad (3.60)$$

where,

$$D_3 = R(\gamma+1)\alpha\left(\frac{x_2}{x_1} + \frac{y_2}{y_1}\right) + \beta[R(\gamma+1)]\alpha\left(\frac{x_1}{x_2} + \frac{y_1}{y_2}\right)$$
$$+ x_1F_1 + y_1G_1 + x_2F_2 + y_2G_2$$

$$D_2 = R^2(\gamma+1)^2\alpha^2\frac{x_2y_2}{x_1y_1} + \beta^2[R(\gamma+1)+1]^2\alpha^2\frac{x_1y_1}{x_2y_2}$$
$$+ R(\gamma+1)\beta[R(\gamma+1)+1]\alpha^2\left(\frac{x_2y_1}{x_1y_2} + \frac{x_1y_2}{x_2y_1}\right)$$
$$+ R(\gamma+1)\alpha[(x_2F_2+y_1G_1+y_2G_2)\frac{x_2}{x_1}+(x_1F_1+x_2F_2+y_2G_2)\frac{y_2}{y_1}]$$
$$+\beta[R(\gamma+1)+1]\alpha[(x_1F_1+y_1G_1+y_2G_2)\frac{x_1}{x_2} + (x_1F_1+x_2F_2$$
$$+y_1G_1)\frac{y_1}{y_2}]+x_1x_2F_1F_2+x_1y_2F_1G_2+x_2y_1F_2G_1+y_1y_2G_1G_2$$

$$D_1 = R^2(\gamma+1)^2\alpha^2\frac{x_2y_2}{x_1y_1}(x_2F_2+y_2G_2)+ \beta^2[R(\gamma+1)+1]^2\alpha^2\frac{x_1y_1}{x_2y_2}$$
$$(x_1F_1+y_1G_1)+R(\gamma+1)\alpha^2\beta[R(\gamma+1)+1][(x_1F_1+y_2G_2)\frac{x_1y_2}{x_2y_1}$$

$$+ (x_2F_2+y_1G_1)\frac{x_2y_1}{x_1y_2}]+R(\gamma+1)\alpha(x_2F_2+y_2G_2)$$

$$(x_1F_1\frac{y_2}{y_1} + y_1G_1\frac{x_2}{x_1})$$

$$+ \beta[R(\gamma+1)+1]\alpha(x_1F_1+y_1G_1)(x_2F_2\frac{y_1}{y_2} + y_2G_2\frac{x_1}{x_2})$$

$$D_0 = R(\gamma+1)^2\beta^2\alpha^4[R(\gamma+1)+1]^2\frac{\omega}{\varphi}\ \frac{1}{x_1y_2}\ \frac{1}{(u_1u_2)^2}$$

$$(\frac{x_1y_2}{x_2y_1}f_1g_2 + f_2g_1)(x_1y_2-x_2y_1)^2$$

Observe that D_0, D_1, D_2, D_3 are positive when SS4 is meaningful. When the Ruth-Hurwitz [30] criteria are checked for eqn.(3.60) it turns out that they are always satisfied provided that SS4 is meaningful. The algebra is very extensive and for this reason the proof is not presented here. One concludes then that SS4 is stable whenever meaningful. The Ruth-Hurwitz criteria do not provide information as to whether the eigenvalues are real or complex. Nevertheless, extensive computer simulations have never shown any damped oscillatory behavior hence it seems that all eigenvalues are real (and negative).

Before concluding the analysis of the steady states for this part the remarks made for the non-splitting system have to be repeated:

1. The stability analysis of each steady state is based on the eigenvalues of the Jacobian matrix hence theoretically the results hold locally only, computer simulations though have indicated that the same results hold globally as well.

2. It cannot be shown analytically if for a given set of parameters more than one of SS1 through SS4 is meaningful and stable. Numerical studies have indicated that this is not possible, i.e. the steady states are mutually exclusive.

OPERATING DIAGRAMS AND THE EFFECT OF THE PARAMETERS

The analysis of the splitting system has indicated that provided that a number of conditions (sometimes necessary and sufficient, sometimes necessary but not sufficient) are satisfied, each one of the possible steady states of the system can be meaningful and stable (hence practically realizable). The questions raised in the case of the non-splitting system as to whether there is a range (or ranges) of values in the parameters space where all the conditions concerning a steady state are simultaneously satisfied and as to what are the effects on the system when the parameter values are varied arise in the case of the splitting system as well, and more intensely so since the expressions for the conditions are more complicated due the

the extra parameter, γ which is needed in order to describe the splitting system.

In this section the results of numerical studies, performed in order to answer the aforementioned questions, are presented in the form of the operating diagrams shown in Figures 12 to 38.

The values used for the system parameters ω and φ are 0.125 and 0.4, respectively. They are the same as those used in the numerical studies for the non-splitting system something which helps the comparison of the results obtained for the two systems. The reasons for not presenting results for other values of ω and φ are those stated when the non-splitting system was discussed.

The parameter β (the ratio of the volumes of the two chemostats) is the design parameter while α, u_f, R and γ are the operating parameters in the sense that they can be easily adjusted for a given system (i.e. ω and φ) and design (i.e. β). The operating diagrams in this case are in reality 4-dimensional or even 5-dimensional if one wants to simultaneously compare alternate designs (i.e. the effect of β). The diagrams presented here are 2-dimensional projections of the actual operating diagrams in the α-u_f plane, for various values of β, R and γ.

As it has been discussed in the analysis presented in the previous sections of this part, the value of the product of the parameters β and γ relative to unity is very important for this system and for this reason the operating diagrams presented here are grouped in three categories, namely:

1. $\beta\gamma < 1$ Figures 12-23
2. $\beta\gamma > 1$ Figures 24-37
3. $\beta\gamma = 1$ Figure 38

Within each of the two first groups mentioned above, the diagrams form three series in each one of which two of the parameters R, γ and β are held at fixed values while the third one varies from diagram to diagram.

The diagram shown in Figure 38 is for the case where $\beta\gamma=1$. Regardless of the value of the recycle ratio and the specific values of β and γ the diagram remains qualitatively the same. In this case, as it was shown in the analysis, the system in spatially homogeneous and it is like having a single chemostat only. Coexistence occurs for any value of u_f such that $u_f>u_{fc}$ but only for the special (discrete) value of α equal to $K\alpha_c$. In this case coexistence is practically unattainable since the slightest perturbation in the value of α (unavoidable with even a perfect control device) leads to the exclusion of either one or the other of the competitors. The line (parallel to the axis) at which coexistence occurs is nothing more than the boundary between SS2 and SS3. Mathematically, on this line one of the eigenvalues of the coexistence steady state is equal to zero something which implies that it is a steady state bifurcation point. This is a very important finding of this study, indicating that there is a special case for which the environment is not heterogeneous. In reality, due to perturbations in the values of β and (mainly) γ it will be difficult to have $\beta\gamma=1$ but the finding is important in the sense that $\beta\gamma$ should not be chosen close to unity because the coexistence region will be so narrow that it will be practically non-existing.

All the diagrams which are shown in Figures 12 through 37 have some common features (most of which have been either discussed or proved in the analysis presented earlier). They are the following:

1. No matter how big or how small it is, there is always a region in which SS4 is meaningful and stable, hence with the configuration of the system discussed here one can really achieve (in most of the cases where the region is not negligibly small) coexistence of the two competing species in a steady state.

2. The boundary (or one of the boundaries) of the coexistence steady state always starts from the crossing point of the $Kf(u_f)$ and $Kg(u_f)$ curves [i.e. the point $(u_{fc},K\alpha_c)$].

3. Coexistence never occurs for values of u_f such that $u_f<u_{fc}$.

4. The upper bound of the domain of coexistence never exceeds the value $\alpha=K\alpha_c$, which is the crossing point of the $Kf(u_f)$ and $Kg(u_f)$ curves.

5. The lower bound of the domain of coexistence when $\beta\gamma<1$ is $\alpha=\alpha_c$ the value of which in all diagrams presented here is $(\omega-\varphi)/(\omega-1)=0.314$ while when $\beta\gamma>1$ the lower bound of α is $\alpha_c/\beta\gamma$.

There are some more observations that one can make from the diagrams that are the same with observations made earlier for the non-splitting system. In most of the cases there is a single domain of coexistence the shape of which varies in complexity from very simple (Figures 15,19,20,24, 28,32,35,37) to intermediate (Figures 14,18,23,25,29,33,36) to very complex (Figures13,17,22,26,34). The common feature of the diagrams that were called very simple is that starting from any point of the domain of coexistence, shift-up experiments lead eventually to the exclusion of the population which survives in shift-down experiments. Namely, shift-up experiments force the system to eventually go to SS2 while shift-down experiments force the system to eventually go to SS3. The diagrams of intermediate complexity exhibit the feature of the very simple diagrams discussed above but in addition they have a range of values of u_f either narrow (e.g. Figure 25) or extended (e.g. Figure 29) for which both shift-up and shift-down experiments force the system to eventually go to SS3. The very complex diagrams exhibit the features of the diagrams of intermediate complexity but in addition they have a range of u_f values either narrow (e.g. Figure 34) or extended (e.g. Figure 13) for which both shift-up and shift-down experiments will force the system to eventually go to SS2. All the considerations discussed above are valid only when one starts from the domain of coexistence.

There are also diagrams that have two domains of coexistence (Figures 12,16,21,27,30,31). In all of them the upper region is so narrow that it can be viewed as a curve and hence it is of no practical interest as far as coexistence is concerned. This upper domain or curve is always separating SS2 from SS3. It must be emphasized though that this domain or curve is not parallel to the u_f axis as in the case of the diagram shown in Figure 38. The lower (which is also the actual for practical purposes) domain of coexistence, has (with the exception of the diagram of Figure 30) the characteristics of the diagrams of intermediate complexity discussed previously, as far as the response of the system to shift-up and shift-down experiments is concerned.

In the following, the effects of the various parameters on the behavior of the system are discussed in a systematic fashion.

Case I. $\beta\gamma < 1$ (Figures 12-23)

The effect of the parameter γ (the splitting ratio) on the system can be viewed from the diagrams shown in the sequence of Figures 12-15, for which the respective values of γ are 0.1,0.3,1.0 and 3.0 while the values of β and R are fixed at 0.2 and 0.1, respectively. These diagrams can be also compared with the diagram of Figure 5 which is for the case where $\gamma=0$. It can be observed that initially as the value of γ increases the area of the domain of coexistence increases but for large values of γ the area of the domain of coexistence becomes small. This indicates that when all other parameters (β and R) are fixed there is an optimal value of γ which maximizes the domain of coexistence in the α-u_f plane. It can be also seen that for small values of γ (even $\gamma=0$) the domain of coexistence is satisfactorily large while for large (past the optimum) values of γ the width (in α values) of the domain of coexistence becomes very small or even prohibitive for operation. It must be stated though that the comments for the domain of coexistence being satisfactorily large or not depend also on the actual values of β and R. As an example, in the diagram shown in Figure 20 although γ is small the domain of coexistence is extremely narrow.

The diagrams of the Figures 16-19 show the effect of the parameter β which has the value 0.1, 0.25, 0.35 and 1.0, respectively while R is fixed at 0.1 and γ is fixed at 0.2. In general, one can say that as β increases the domain of coexistence decreases and the decrease is dramatic when β reaches unity. At this point it has to be noted that when comparing the diagrams one has to be careful and properly take into account the scale of the axes since they are not the same in all diagrams. In the case where β is larger unity, when one varies the value of γ, good results are never obtained, see for example Figure 20 for which the values of the parameters β, R and γ are 1.5, 1.0 and 0.2 respectively. If one compares the diagrams of Figures 17 and 6 one can conclude that the domain of coexistence is wider when $\gamma=0.2$ than when $\gamma=0$ although in the latter case and for u_f larger than about 7 coexistence can occur for values of α much higher than when $\gamma=0.2$. In fact, the system is too complex for safely generalizing any observations.

The diagrams shown in Figures 21-23 are for R being 0.01,1.0 and 3.0, respectively while both β and γ are fixed at 0.2. One can observe that the domain of coexistence becomes wider as R increases. Nevertheless, as it was discussed also in the case of the non-splitting system, one has to observe that when R increases the domain of coexisttence shifts to high u_f values for which one does not really expect to have rate-limitation (and consequently competition). In fact, one should observe that for low u_f values, coexistence becomes more and more difficult as R increases, something which is indeed expected since as the recycle ratio increases, the environment becomes more and more homogeneous.

Case II. $\beta\gamma > 1$ (Figures 24-37)

In the diagrams of Figures 24-27 the value of γ is 2.0, 5.0 15.0 and 20.0, respectively while β is fixed at 0.6 and R is fixed at 0.1. One can say that as in the case of Figures 12-15, the domain of coexistence initially increases with γ while for large values of γ the domain of coexistence becomes narrower as γ keeps increasing. Hence it seems that there is an optimal value of γ. An implication of increasing γ is that the actual dilution rate for both vessels increases and as a result the possibility of washing out the culture is higher. One should then select a low value of α for survival of one or possibly both species. It is interesting to observe that the change in the shape of the domain of the domain of coexistence as γ increases in the diagrams of Figures 24-27 is exactly opposite (or a mirror image) of the change occurring in Figures 12-15. The diagrams of Figures 28-31 which are for γ values 1.0, 2.0, 20.0 and 35.0, respectively and for which β

is fixed at 1.5 and R is fixed at 0.1 show again the effect of the parameter γ. The difference between the sequences of Figures 24-27 and 28-31 is that in the former β is fixed at a value less than 1 while in the latter β is fixed at a value larger than 1. One can observe that the width of the domain of coexistence in terms of α values is larger when $\beta\gamma>1$ and $\beta<1$ than when $\beta\gamma>1$ and $\beta>1$. Furthermore, one can observe that when $\beta<1$ it is preferable to have $\beta\gamma<1$ rather than $\beta\gamma>1$ while when $\beta>1$ the opposite is true. The latter observations refer mainly to the maximum possible range of α values.

In the diagrams of Figures 32-34, 27 and 30 the value of β is 0.2, 0.35, 0.5, 0.6 and 1.5, respectively while R is fixed at 0.1 and γ is fixed at 20.0. One can observe that the domain of coexistence initially increases with β but then it decreases (drastically in the case of Figure 30). For the values of R and γ used for the diagrams presented here, the optimal value of β was found to be 0.5 for maximizing the domain of coexistence in the α-u_f plane.

For the diagram shown in Figure 35 the values of β, γ and R are 0.2, 8.0 and 0.1, respectively. It was found that for any other value of R the shape of the coexistence region remained the same and always its width is very narrow. One has to observe that β is less than one. When β is larger than 1, as in Figures 30, 36 and 37 where β=1.5,

$\gamma=20.0$ and R is equal to 0.1, 1.0 and 5.0, respectively, one can observe that the domain of coexistence increases with R but it also shifts to higher u_f values and the remarks made earlier for Figures 21-23 are valid here as well.

It has been shown in the analysis that the value of K depends on the value of the product of the parameters β and γ and in fact K decreases as $\beta\gamma$ increases. This implies (and it can be seen from all diagrams) that the smaller $\beta\gamma$ is the lower are the values of α at which total washout occurs for the system. Furthermore, since coexistence never occurs for $\alpha>K\alpha_c$, a large K value (or low $\beta\gamma$) increases the range of α values where the system is expected to exhibit the behavior of interest.

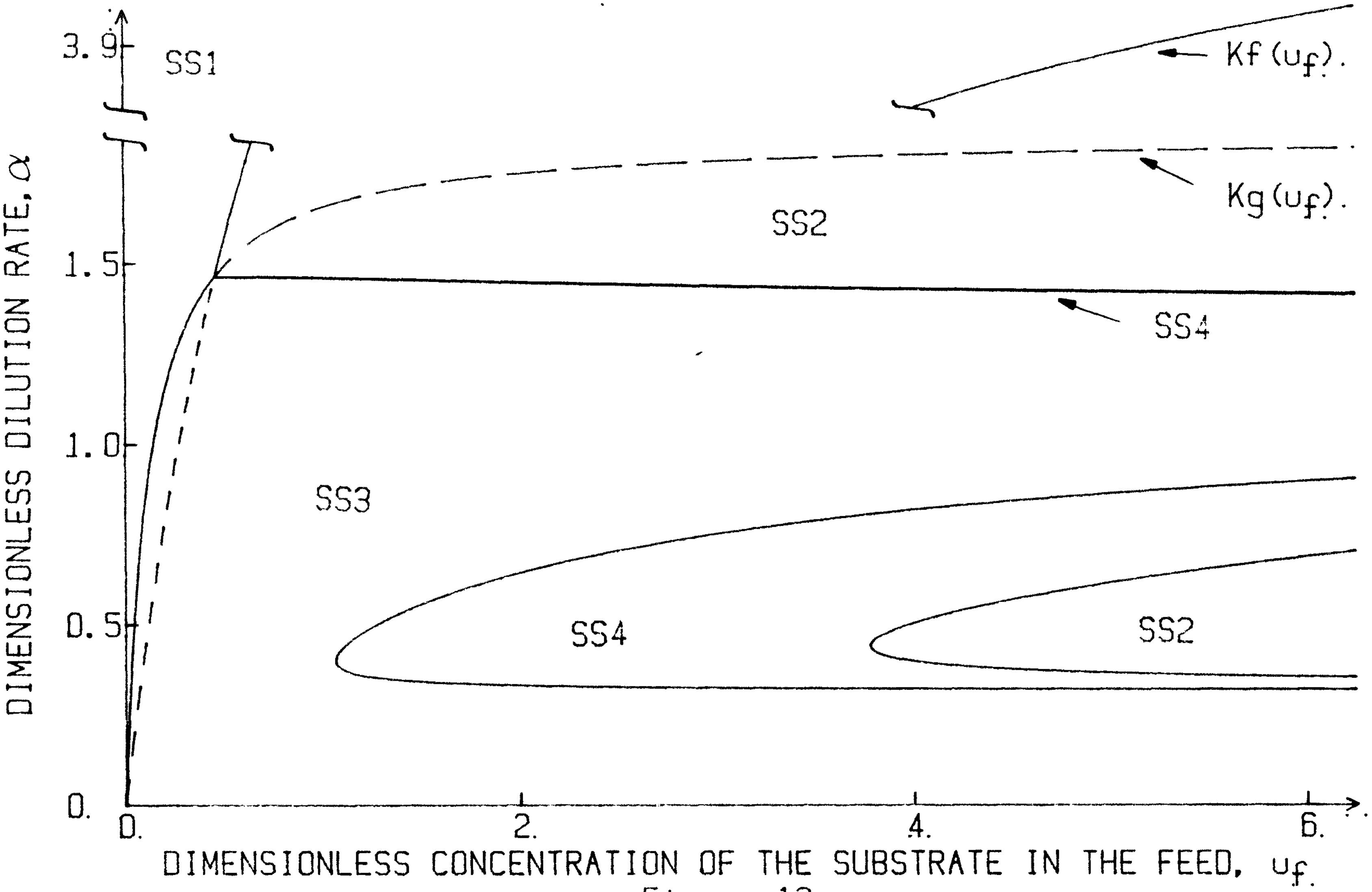
In general one can say that $\beta\gamma<1$ is preferable to $\beta\gamma>1$, but for $\beta\gamma<1$ one cannot say that the smaller $\beta\gamma$ the better, since comparisons made between the non-splitting system where $\beta\gamma=0$ and the splitting system have indicated that in most of the cases the splitting system offers a wider domain of coexistence.

Table 2: Parameter Values used for the Operating Diagrams shown in Figures 12-38

Fig. No.	φ	ω	β	R	γ
12	0.4	0.125	0.2	0.1	0.1
13	"	"	"	"	0.3
14	"	"	"	"	1.0
15	"	"	"	"	3.0
16	"	"	0.1	0.1	0.2
17	"	"	0.25	"	"
18	"	"	0.35	"	"
19	"	"	1.0	"	"
20	"	"	1.5	1.0	0.2
21	"	"	0.2	0.01	0.2
22	"	"	"	1.0	"
23	"	"	"	3.0	"
24	"	"	0.6	2.0	0.1
25	"	"	"	5.0	"
26	"	"	"	15.0	"
27	"	"	"	20.0	"
28	"	"	1.5	1.0	0.1
29	"	"	"	2.0	"
30	"	"	"	20.0	"
31	"	"	"	35.0	"

Table 2 continued

Fig. No.	φ	ω	β	R	γ
32	0.4	0.125	0.2	0.1	20.0
33	"	"	0.35	"	"
34	"	"	0.5	"	"
35	"	"	0.2	0.1	8.0
36	"	"	1.5	1.0	20.0
37	"	"	"	5.0	20.0
38	"	"	$\beta\gamma = 1$		



SS1
SS2
SS3
SS4
SS4
SS2
Kf (u_f).
Kg (u_f).
3.9
1.5
1.0
0.5
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 12.

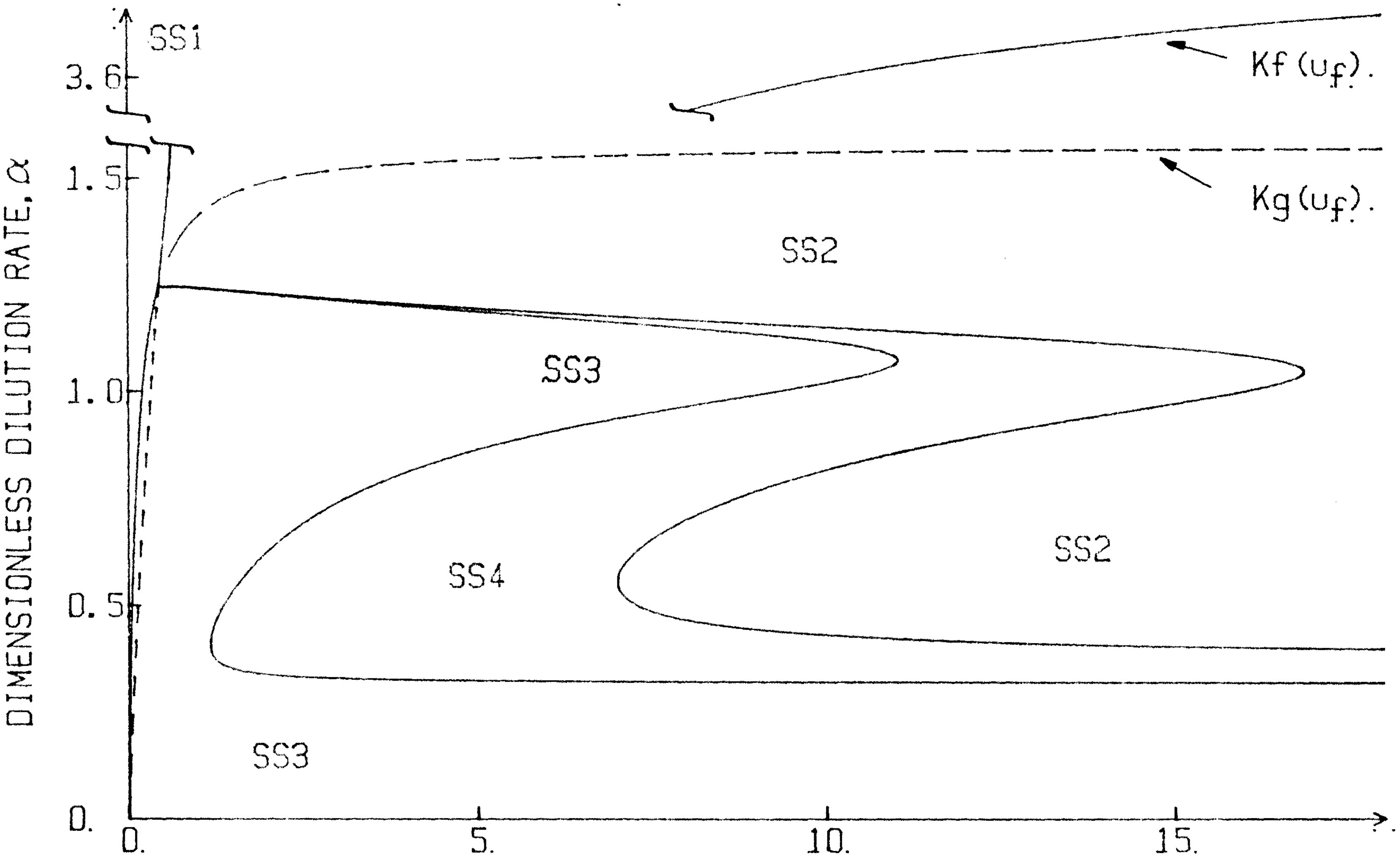

SS1
3.6
1.5
1.0
0.5
0.
Kf (uf).
Kg (uf).
SS2
SS3
SS4
SS2
SS3
0.
5.
10.
15.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 13.

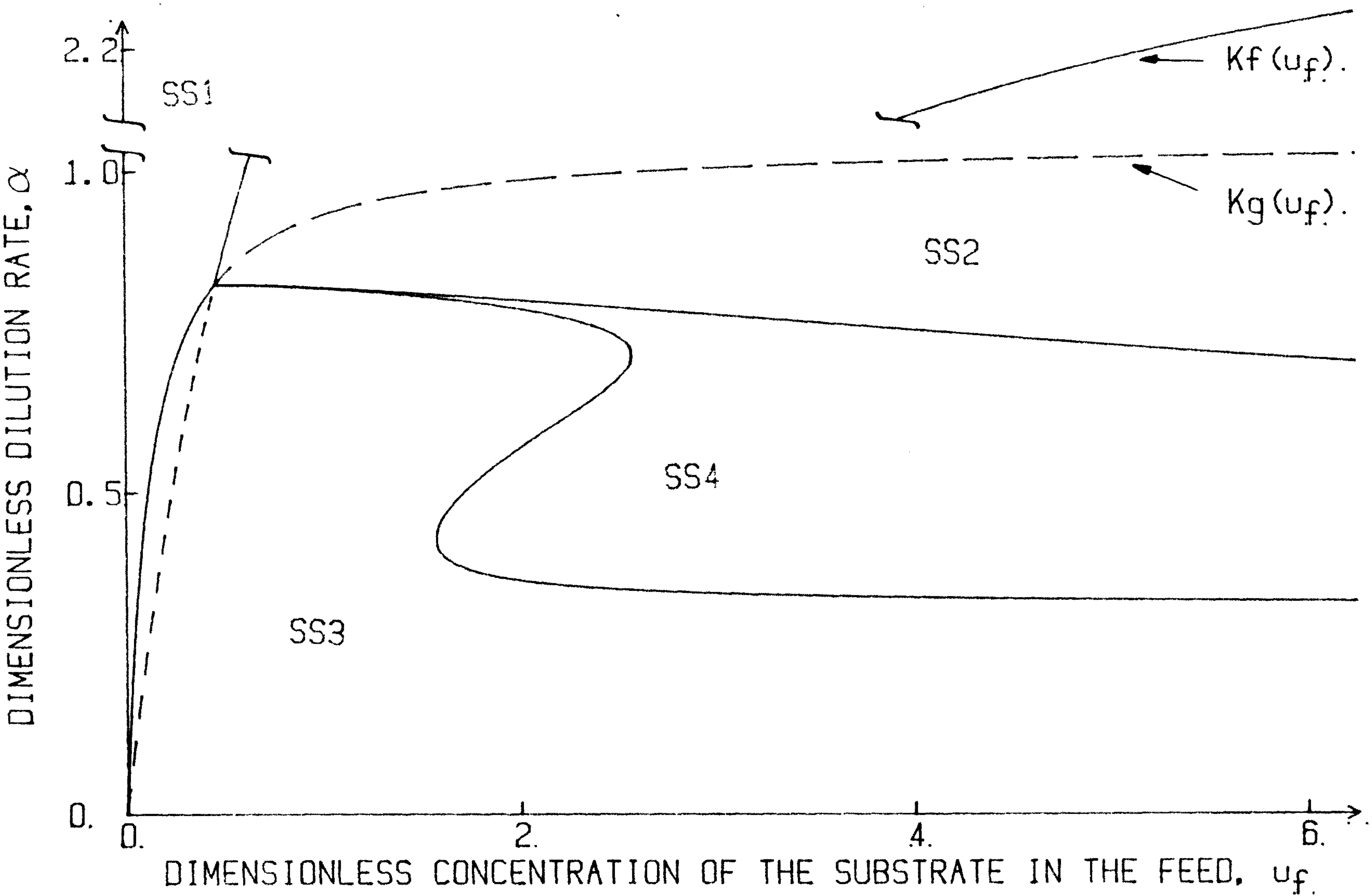

2.2
1.0
0.5
0.
0.
2.
4.
6.
SS1
SS2
SS3
SS4
Kf(u_f).
Kg(u_f).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f

Figure 14.

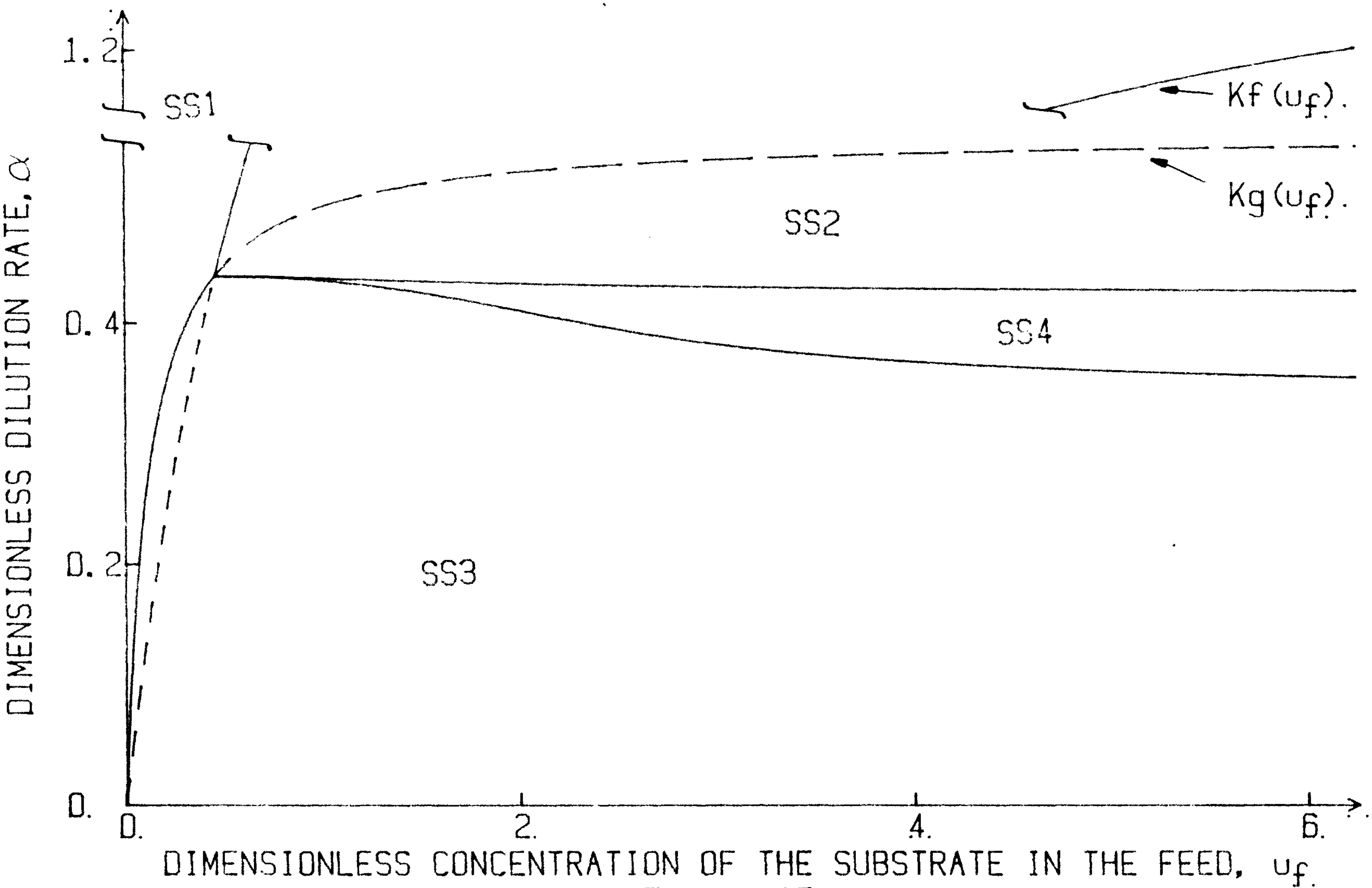
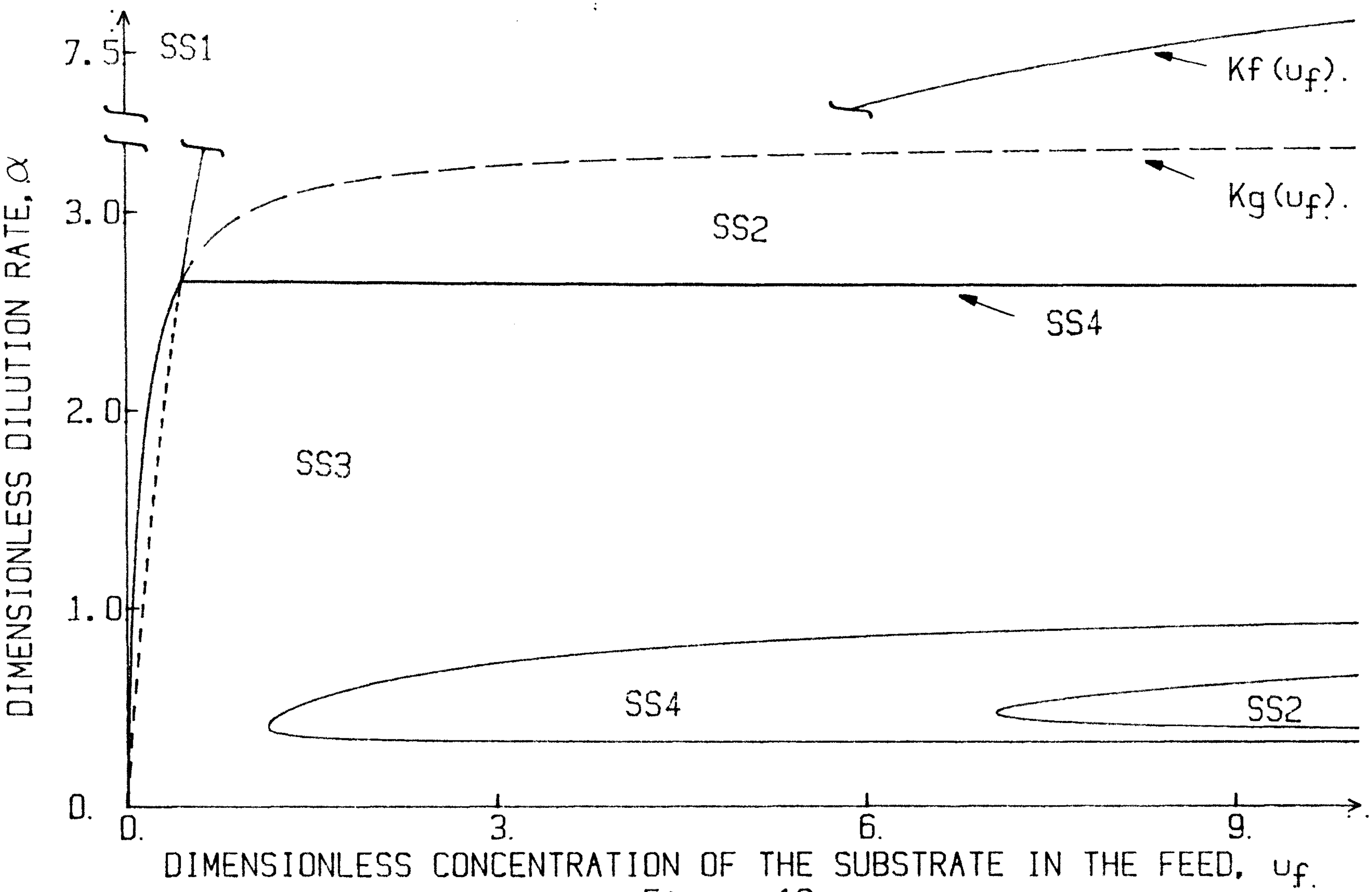
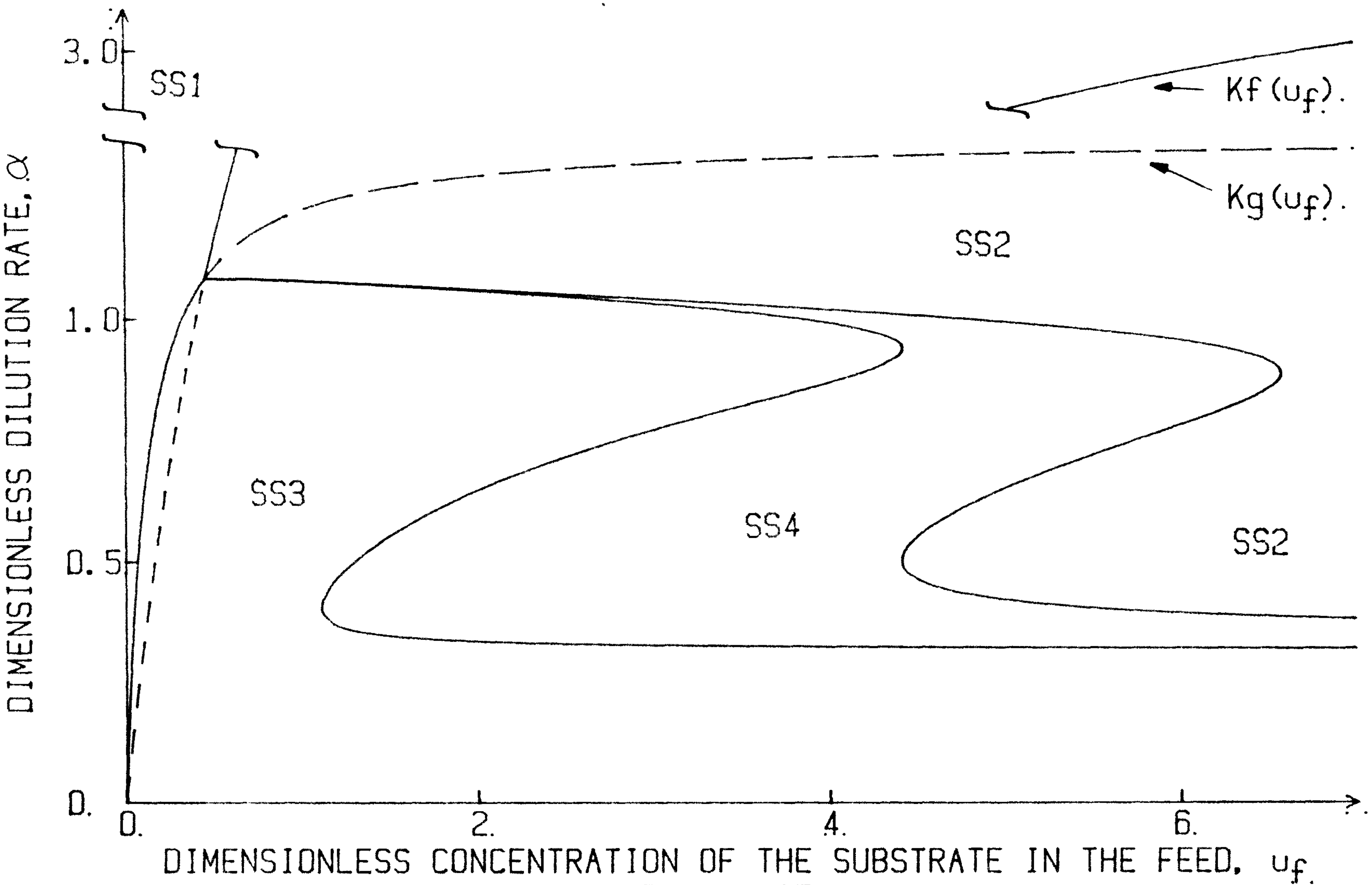

1.2
0.4
0.2
0.
0.
2.
4.
6.
SS1
SS2
SS3
SS4
$Kf(u_f)$.
$Kg(u_f)$.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 15.



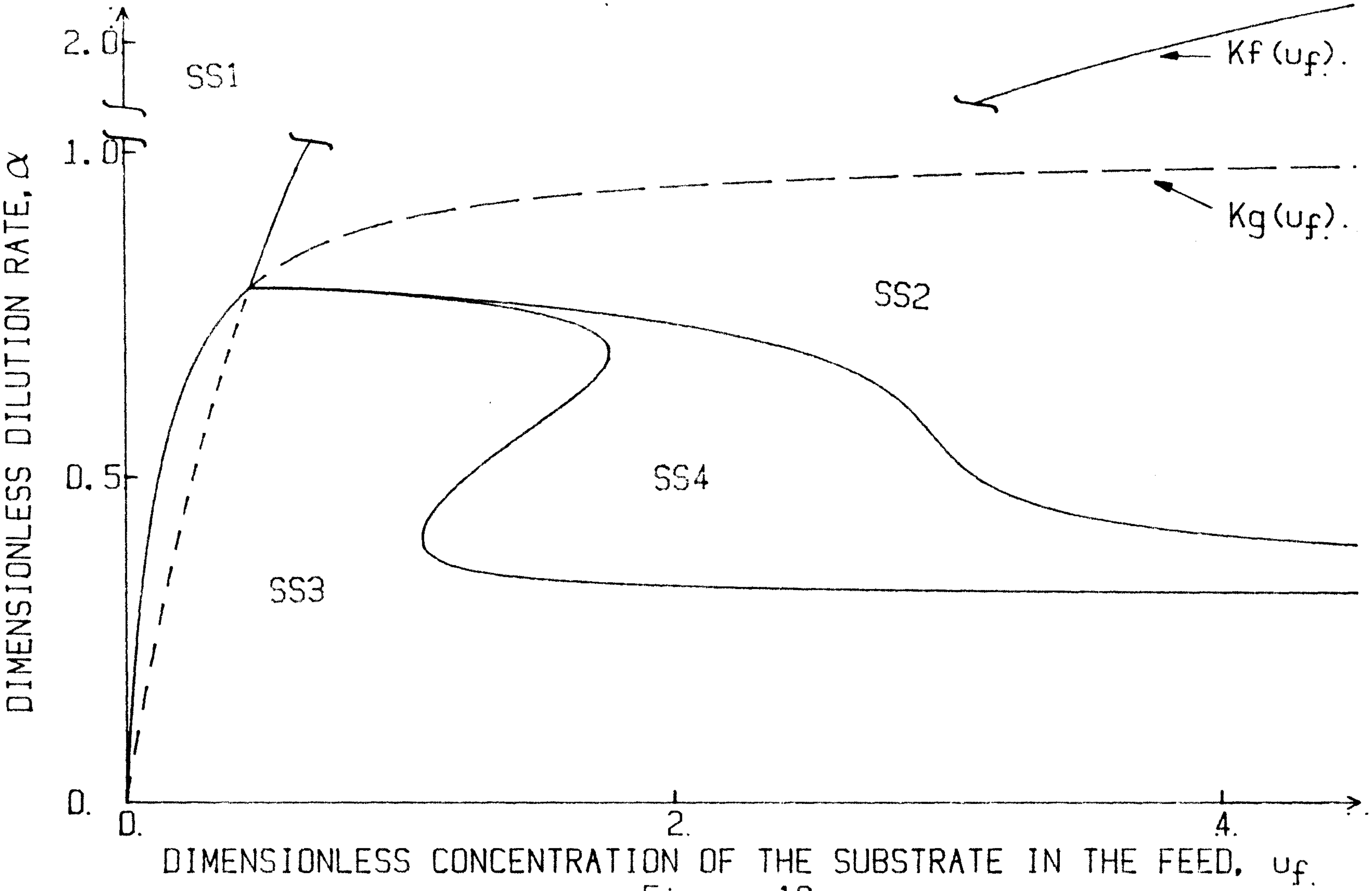
7.5
3.0
2.0
1.0
0.
DIMENSIONLESS DILUTION RATE, α
SS1
SS2
SS3
SS4
SS4
SS2
Kf(u_f).
Kg(u_f).
0.
3.
6.
9.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 16.



3.0
1.0
0.5
0.
0.
2.
4.
6.
SS1
SS2
SS3
SS4
SS2
Kf(uf).
Kg(uf).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 17.



2.0
1.0
0.5
0.
0.
2.
4.
SS1
SS2
SS3
SS4
Kf (u_f).
Kg (u_f).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 18.

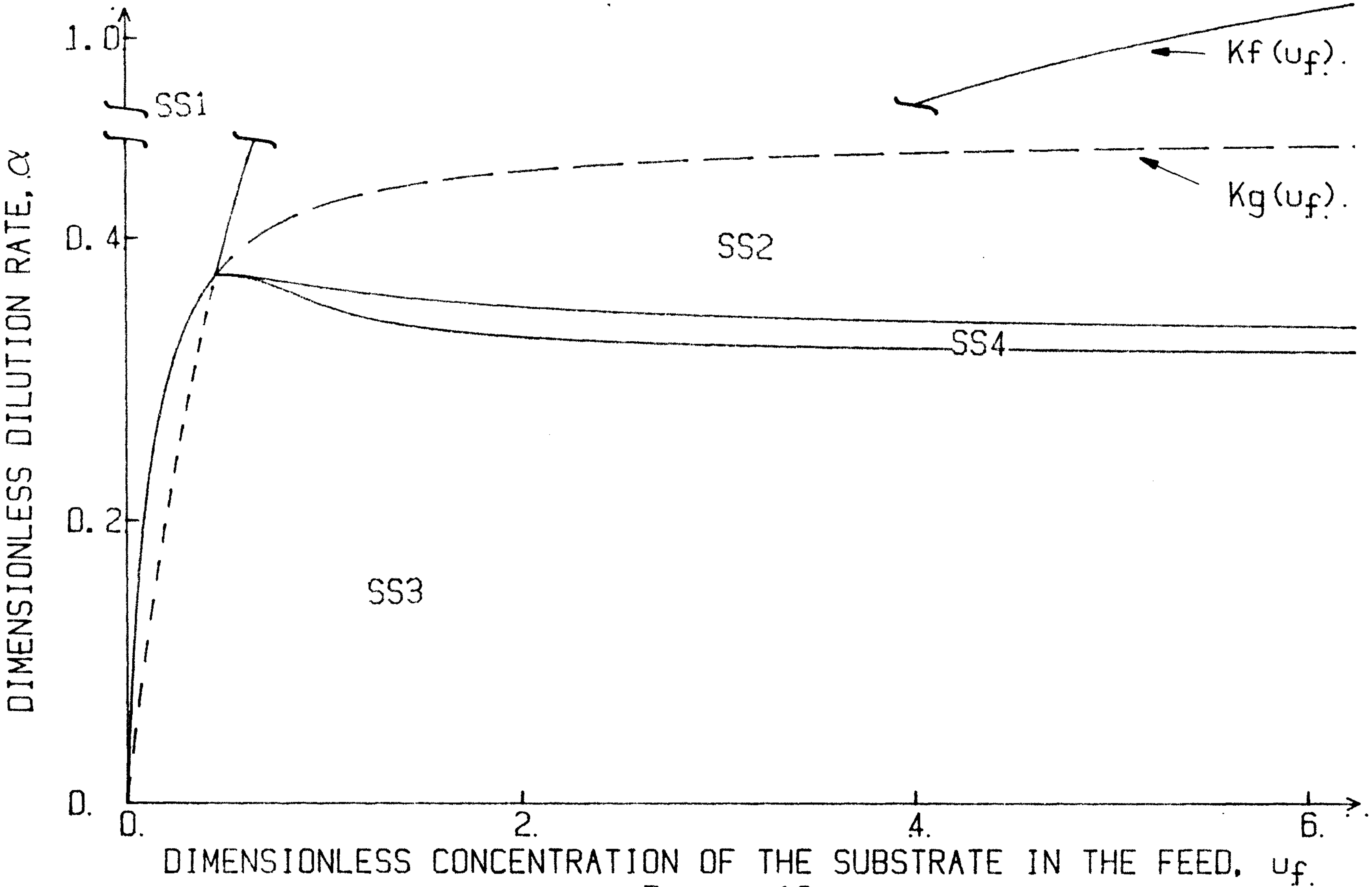
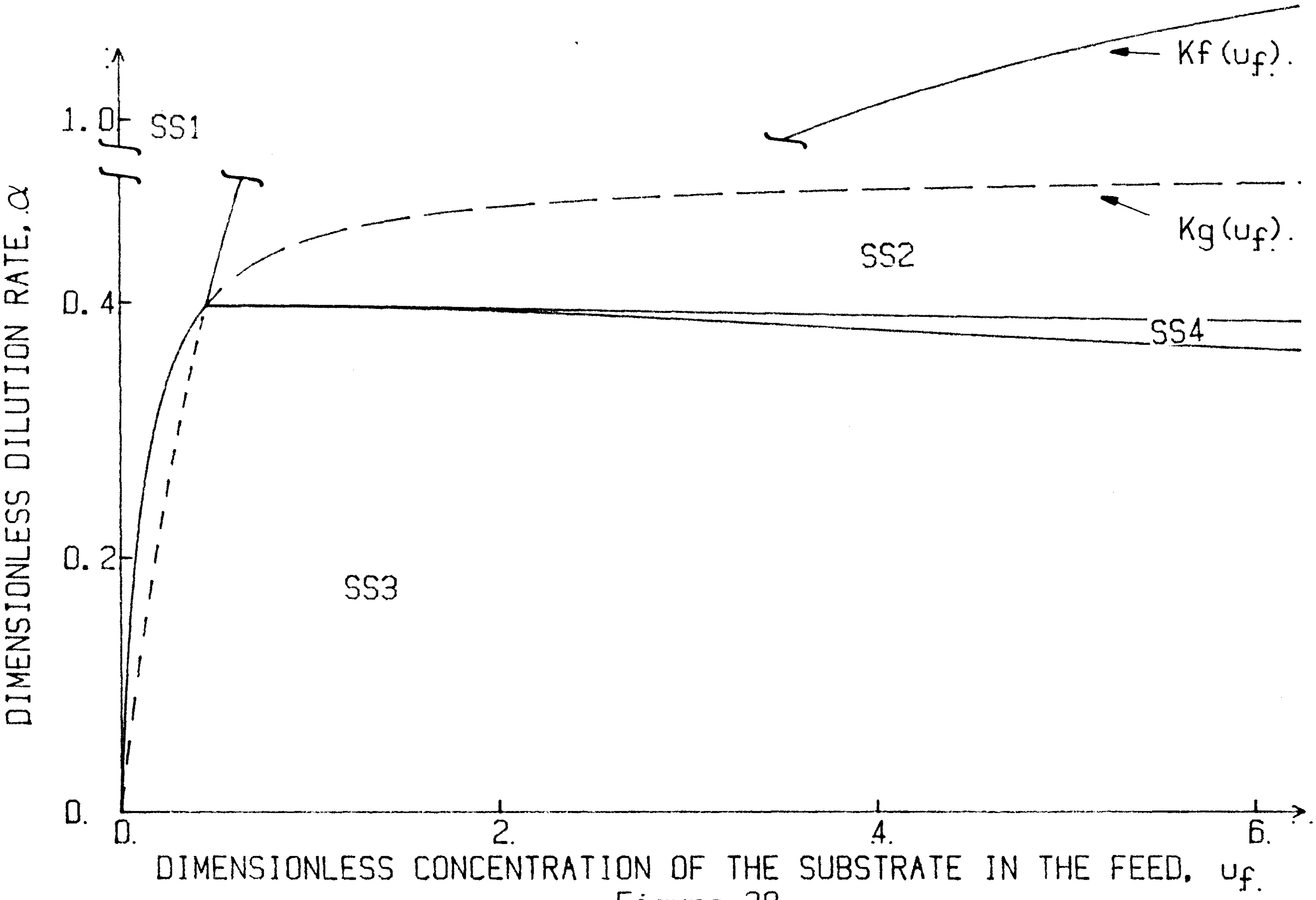

DIMENSIONLESS DILUTION RATE, α
1.0
0.4
0.2
0.
0.
2.
4.
6.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
SS1
SS2
SS3
SS4
$K_f(u_f)$.
$K_g(u_f)$.

Figure 19.



Kf (uf).
Kg (uf).
SS1
SS2
SS3
SS4
1.0
0.4
0.2
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 20.

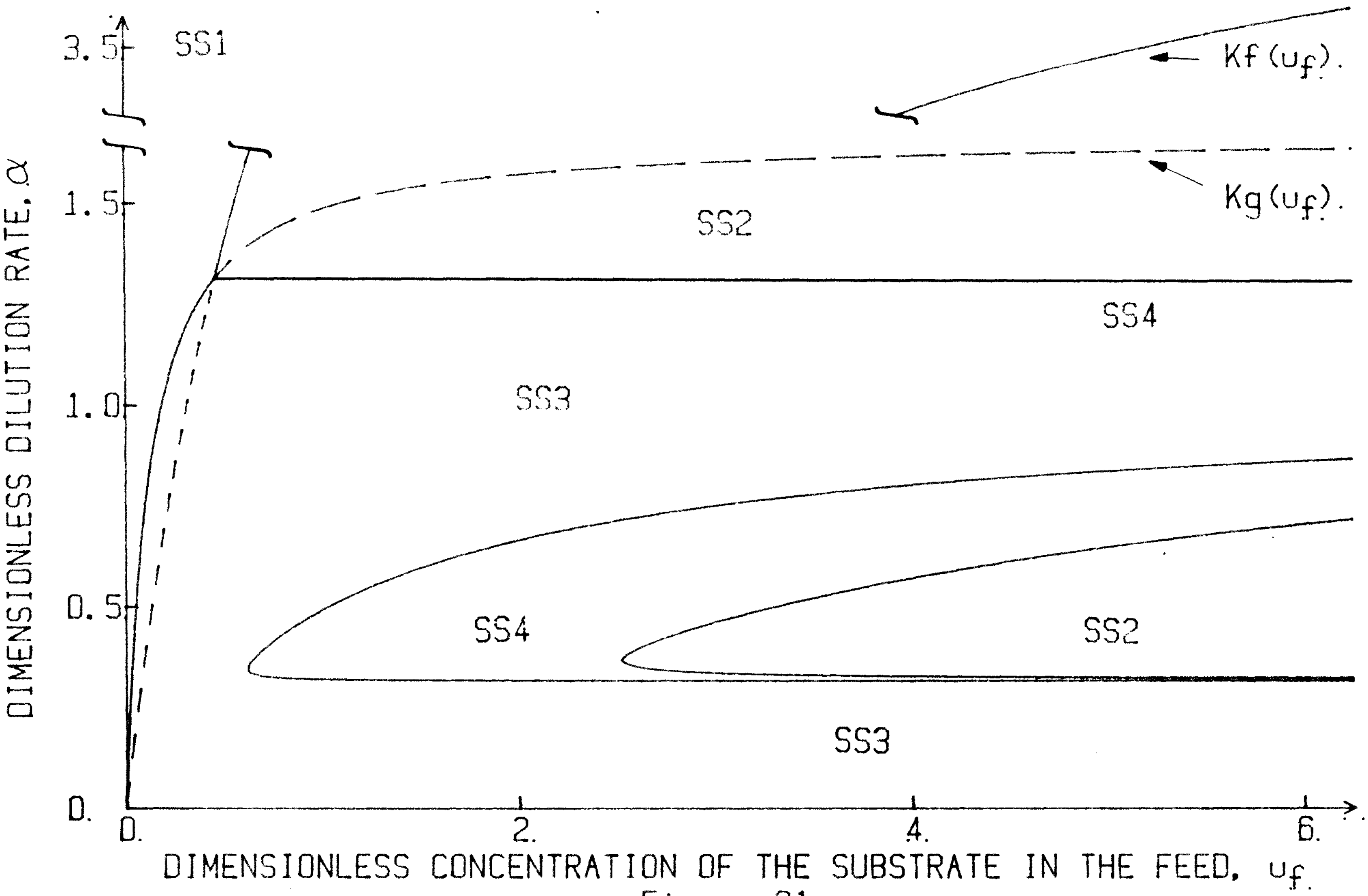

SS1
3.5
Kf (uf).
Kg (uf).
1.5
SS2
SS4
1.0
SS3
0.5
SS4
SS2
SS3
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 21.

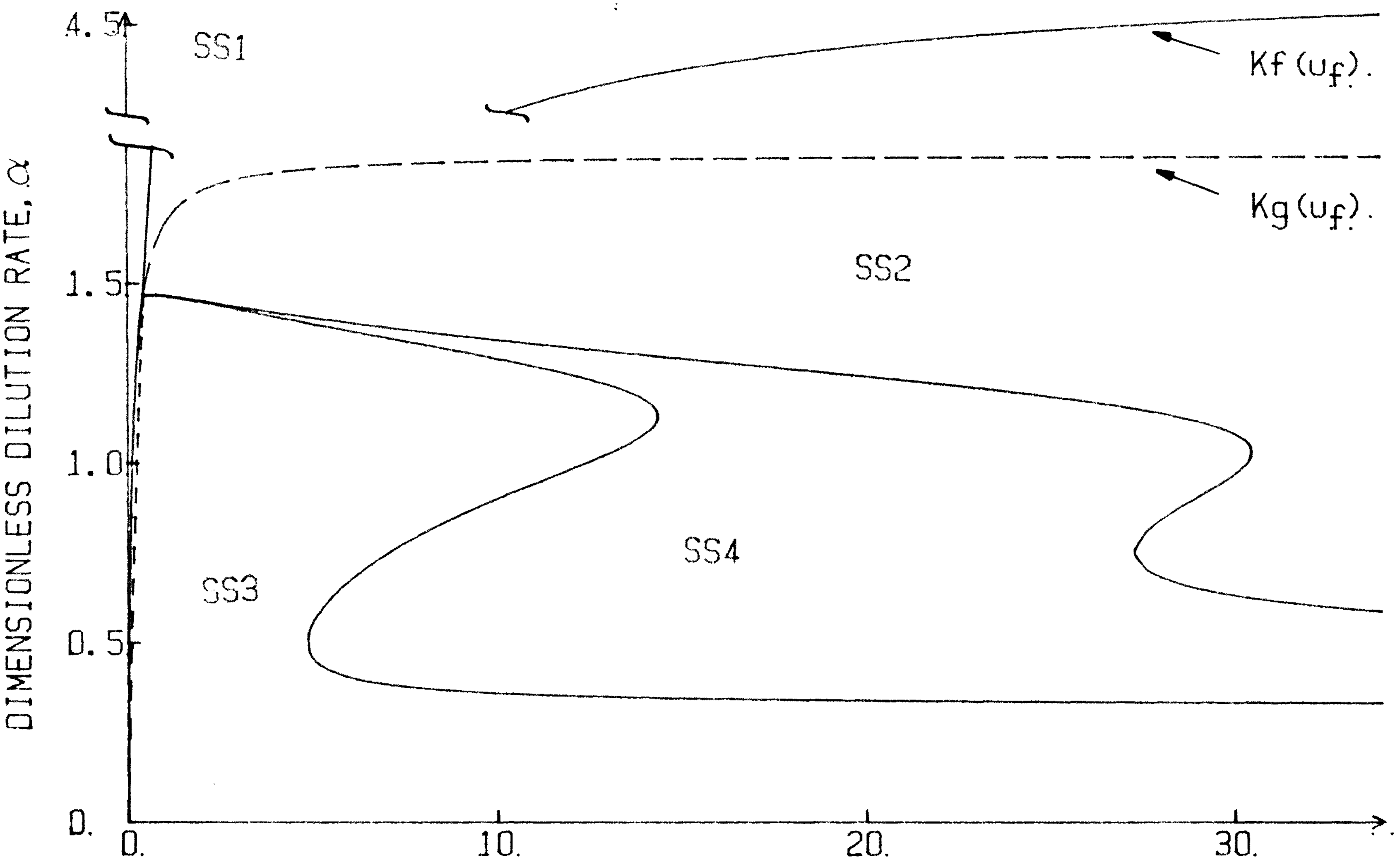

4.5
1.5
1.0
0.5
0.
DIMENSIONLESS DILUTION RATE, α
SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
0.
10.
20.
30.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 22.

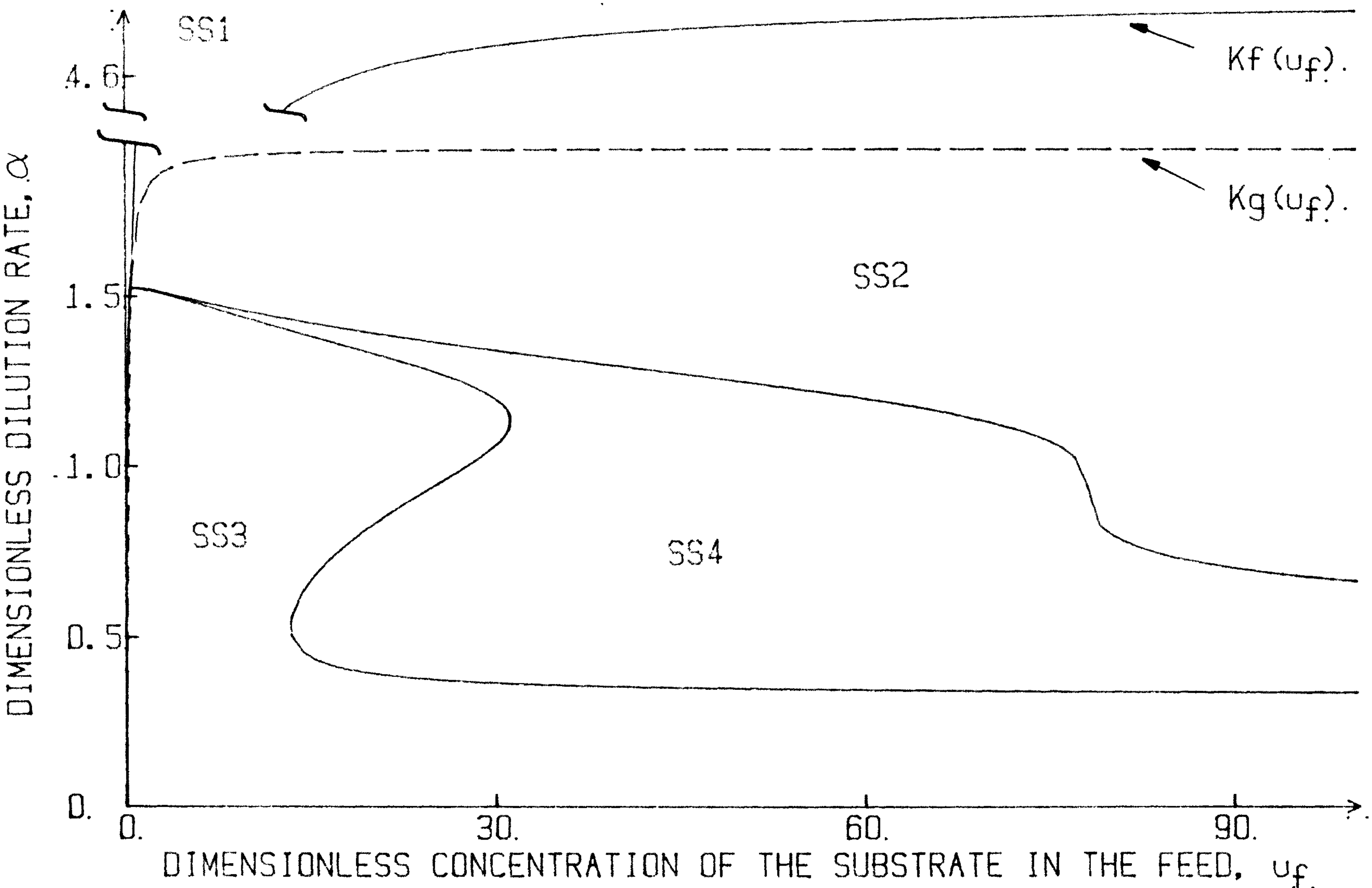
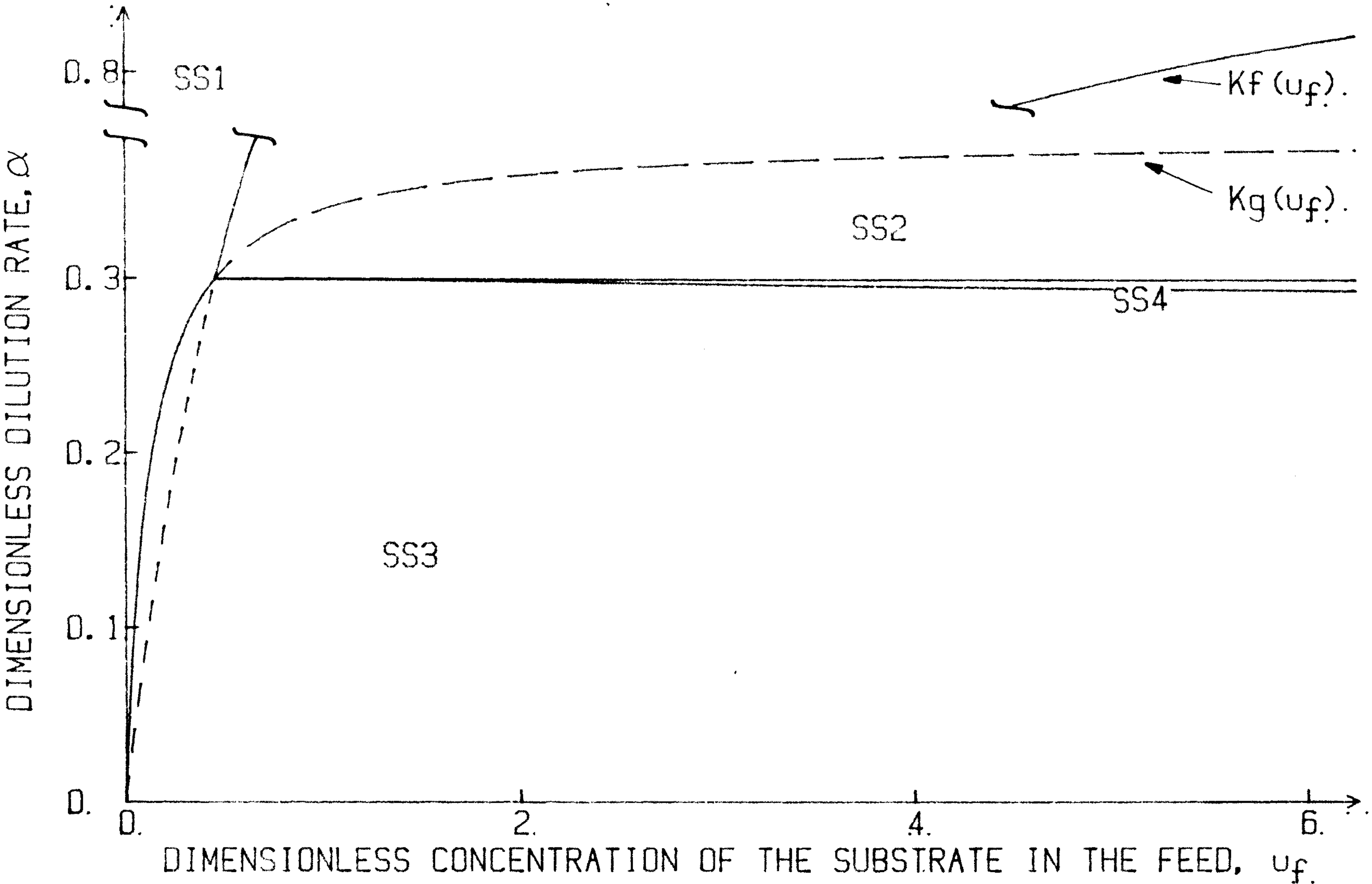

SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
4.6
1.5
1.0
0.5
0.
0.
30.
60.
90.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 23.



SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
0.8
0.3
0.2
0.1
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 24.

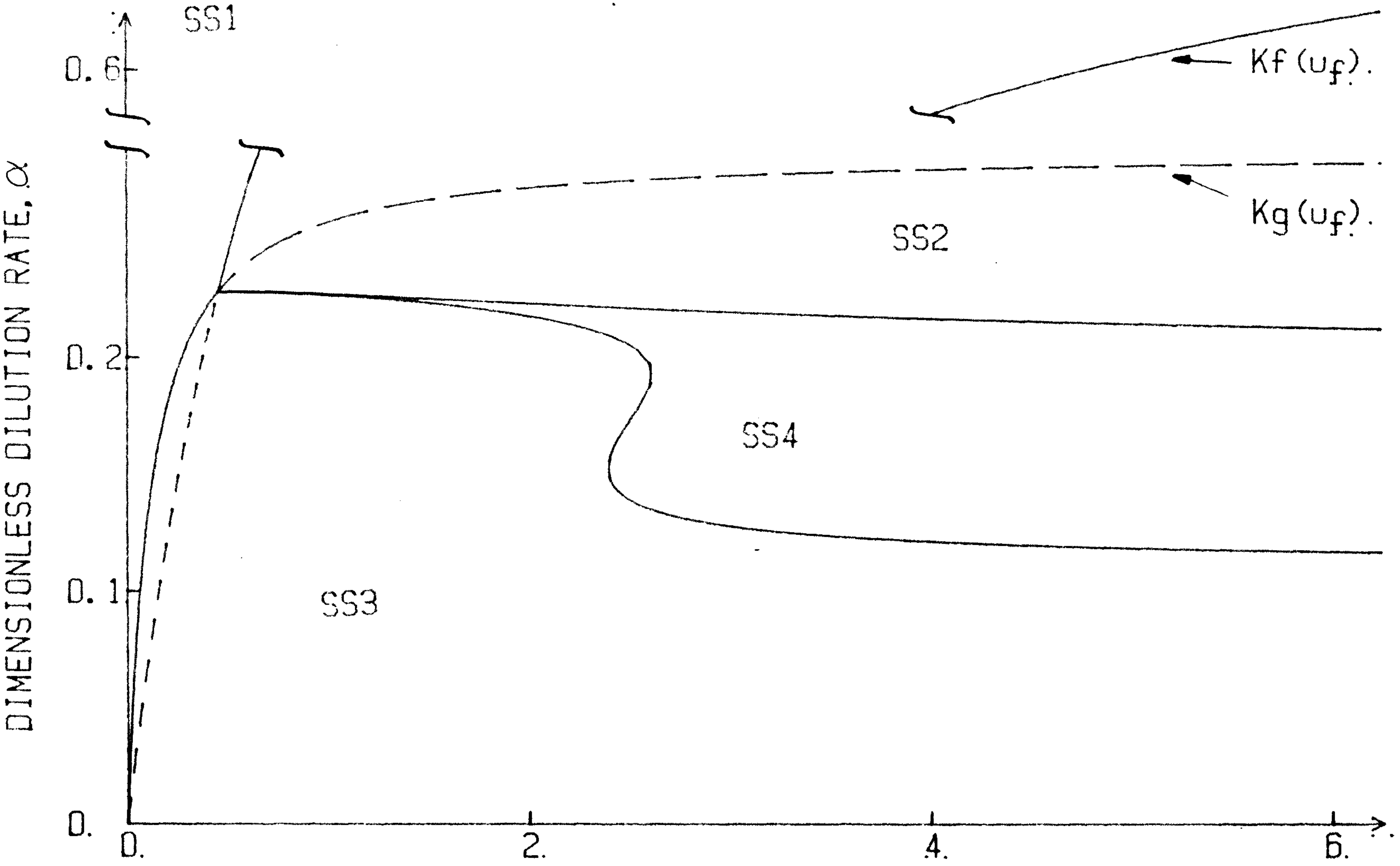

SS1
SS2
SS3
SS4
Kf (u_f).
Kg (u_f).
0.6
0.2
0.1
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 25.

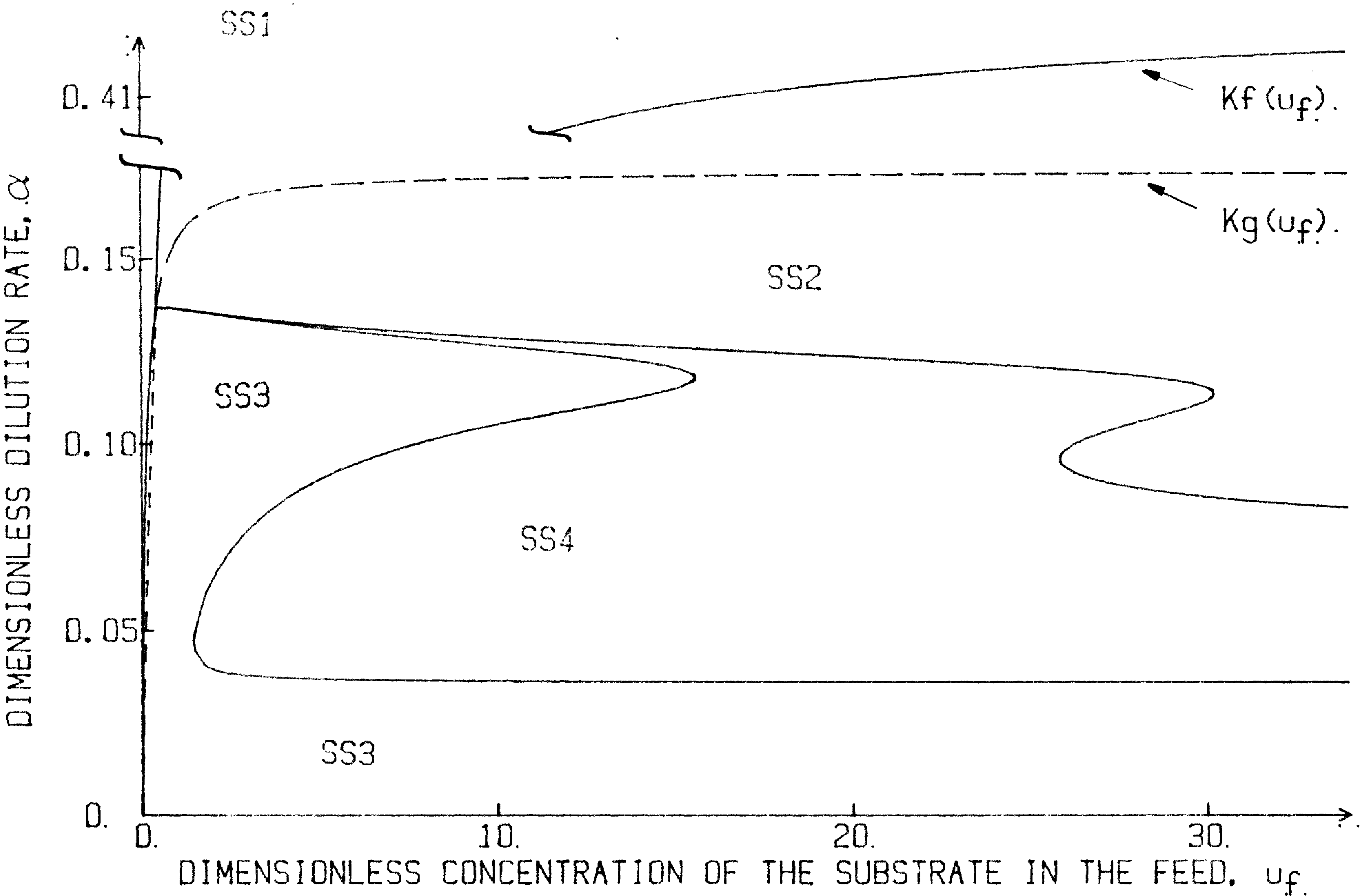

SS1
SS2
SS3
SS4
SS3
Kf (u_f).
Kg (u_f).
0.41
0.15
0.10
0.05
0.
0.
10.
20.
30.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 26.

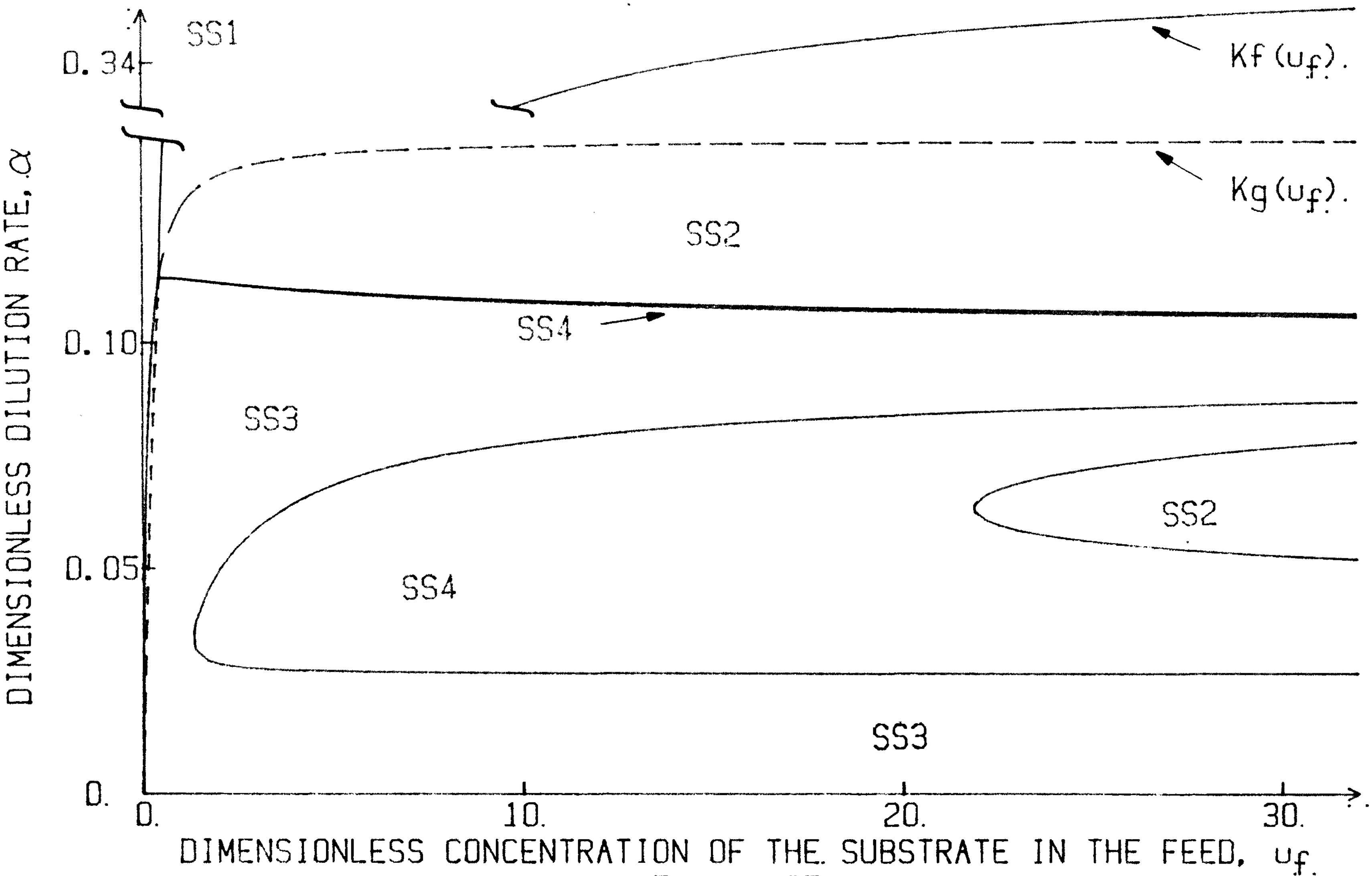

SS1
Kf (u$_f$).
Kg (u$_f$).
SS2
SS4
SS3
SS4
SS2
SS3
D. 34
D. 10
D. 05
D.
D.
10.
20.
30.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u$_f$.

Figure 27.

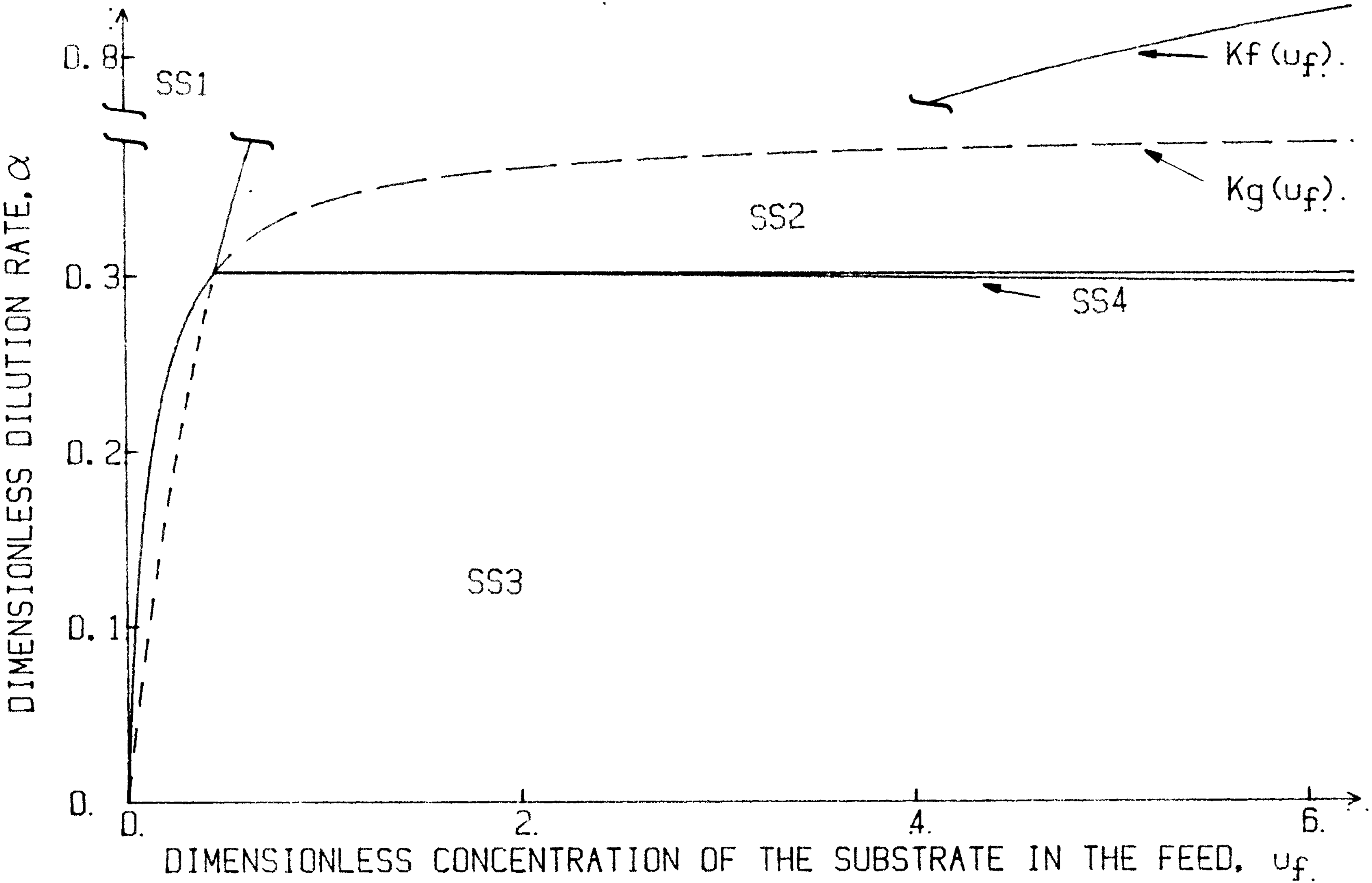
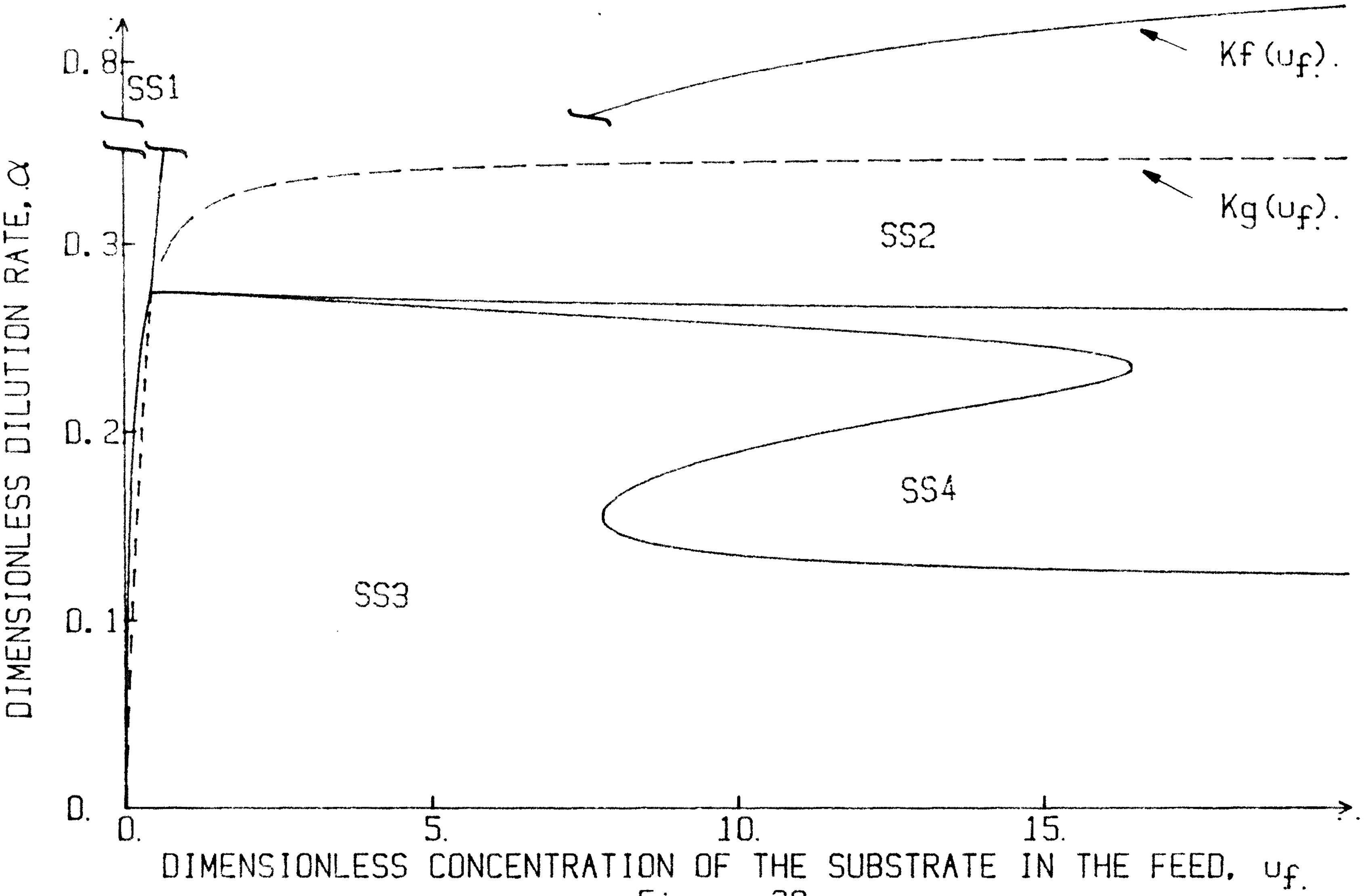

DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
0.
0.1
0.2
0.3
0.8
0.
2.
4.
6.
SS1
SS2
SS3
SS4
Kf (u_f).
Kg (u_f).

Figure 28.



0.8
0.3
0.2
0.1
0.
0.
5.
10.
15.
SS1
SS2
SS3
SS4
Kf(uf).
Kg(uf).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 29.

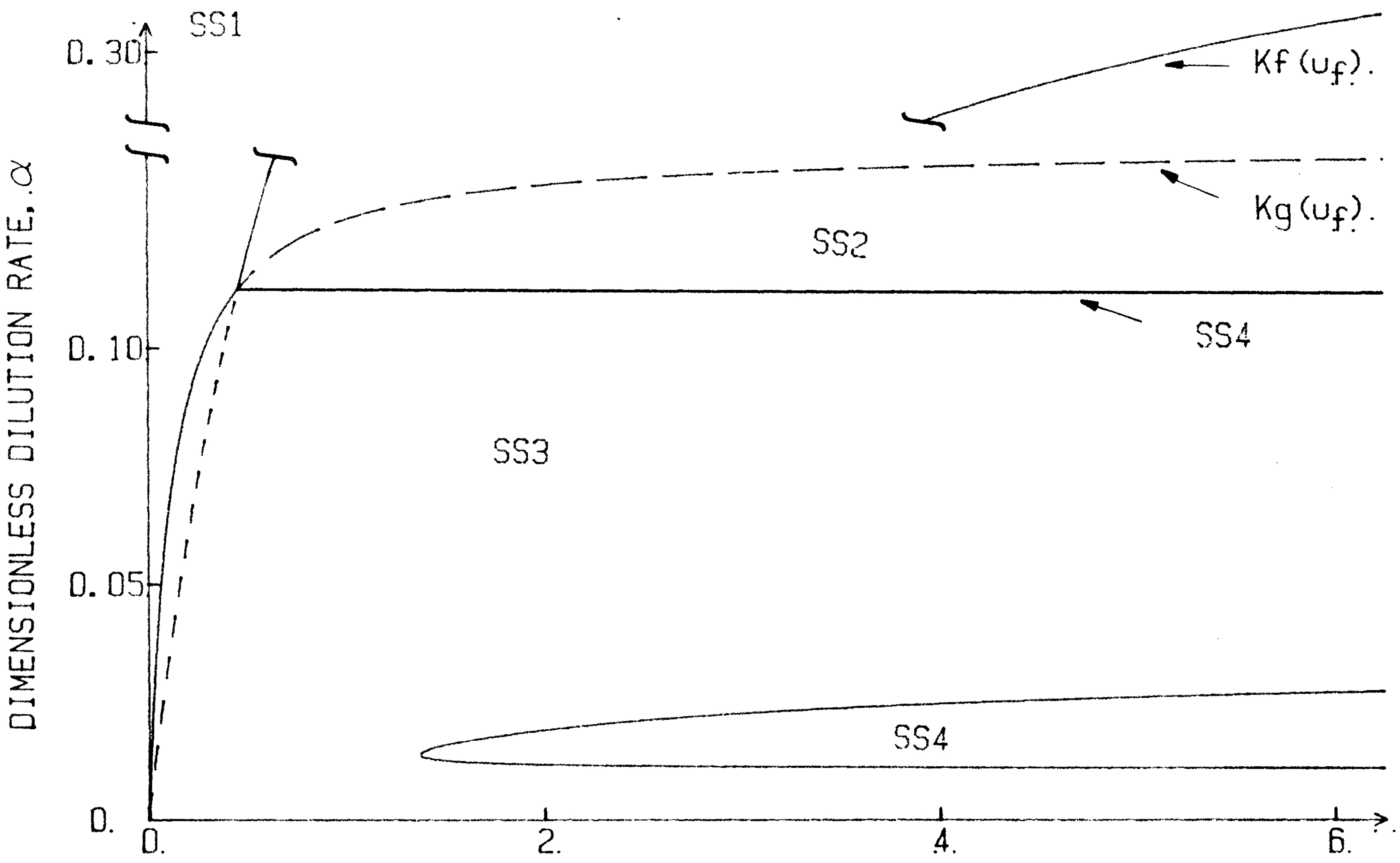

SS1
0.30
0.10
0.05
0.
DIMENSIONLESS DILUTION RATE, α
Kf(u_f).
Kg(u_f).
SS2
SS4
SS3
SS4
0.
2.
4.
6.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 30.

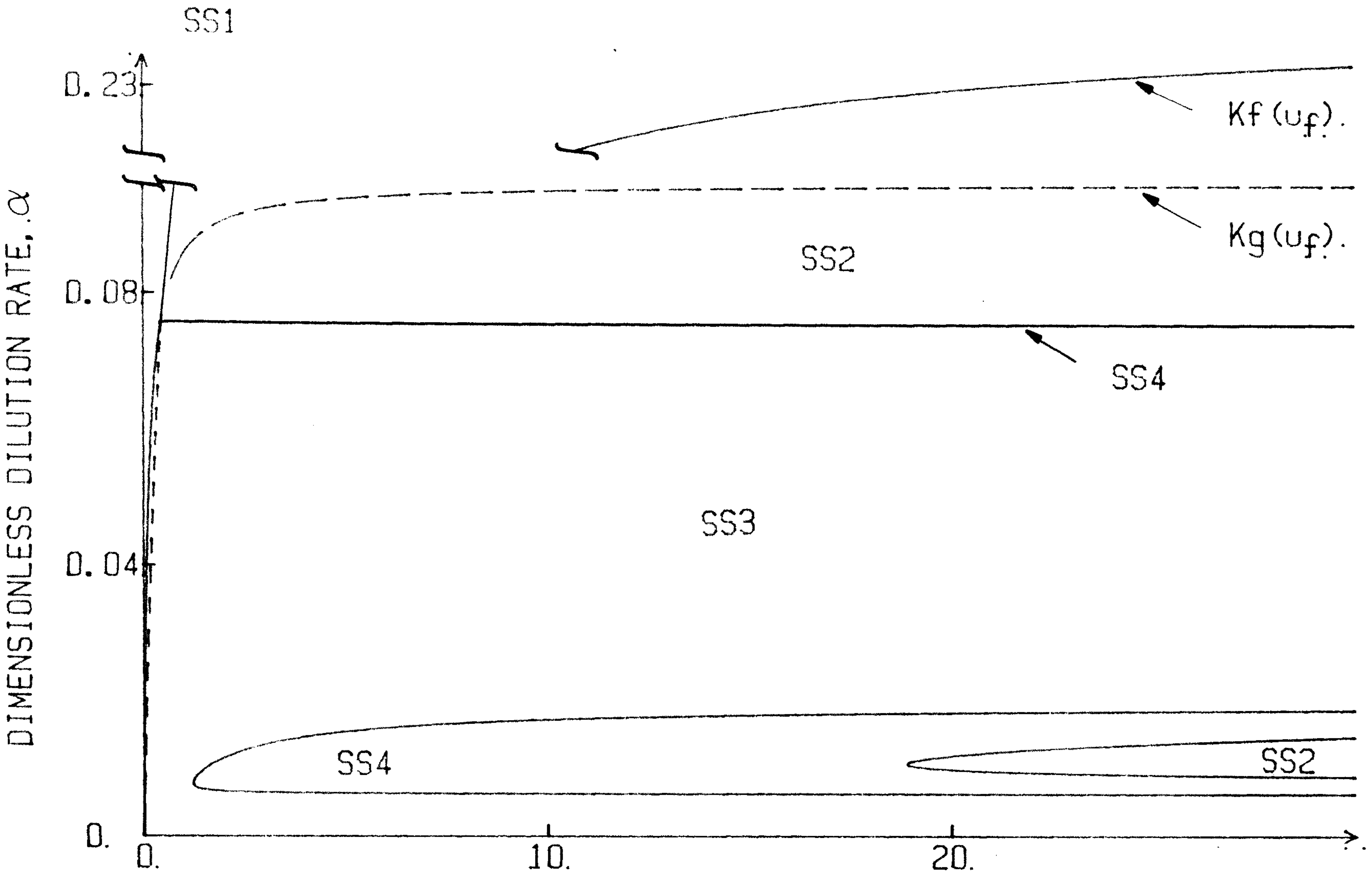
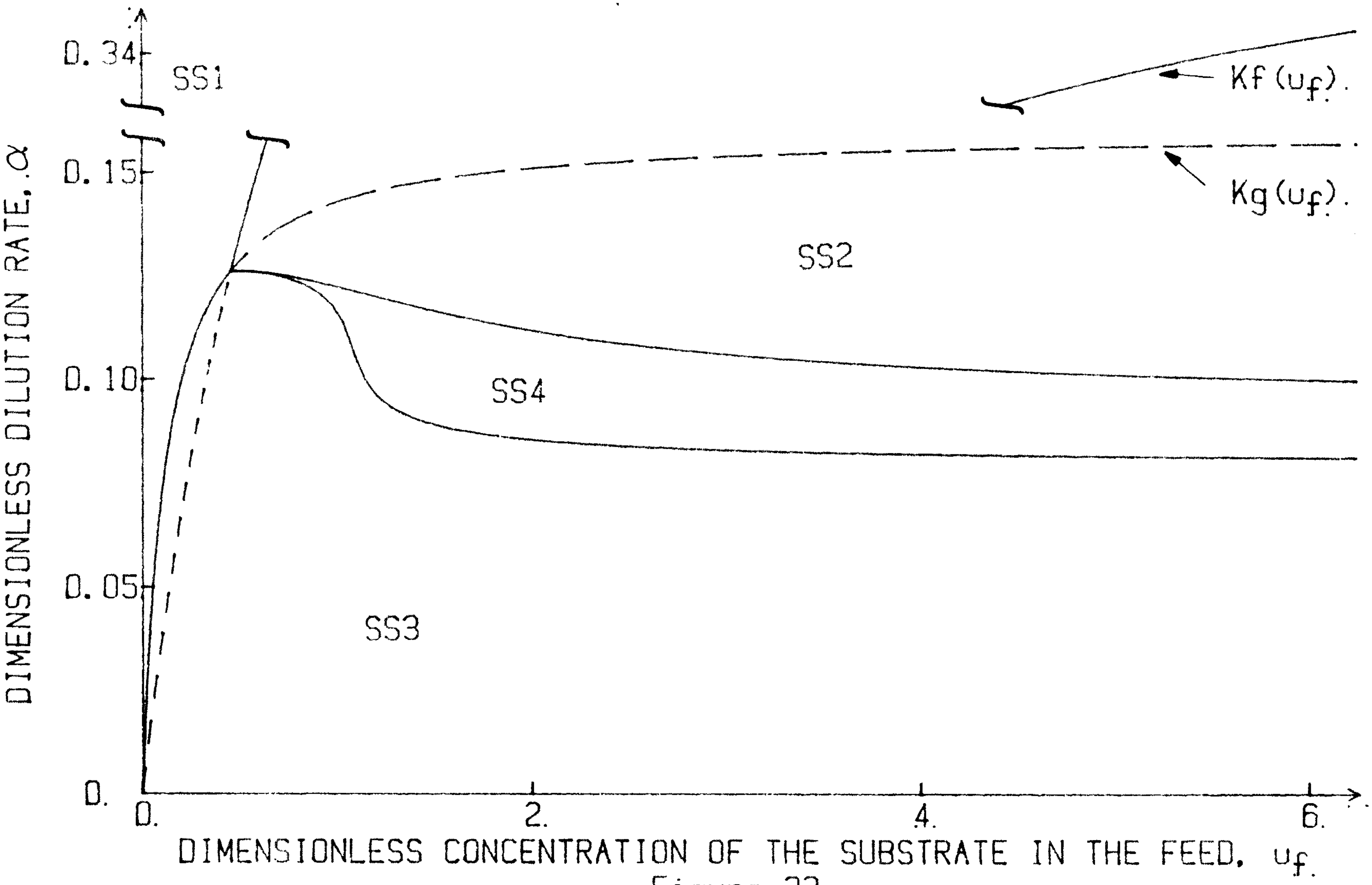

SS1
0.23
0.08
0.04
0.
0.
10.
20.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
Kf (u_f).
Kg (u_f).
SS2
SS4
SS3
SS4
SS2

Figure 31.



D. 34
D. 15
D. 10
D. 05
D.
D.
2.
4.
6.
SS1
SS2
SS3
SS4
$Kf(u_f)$.
$Kg(u_f)$.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 32.

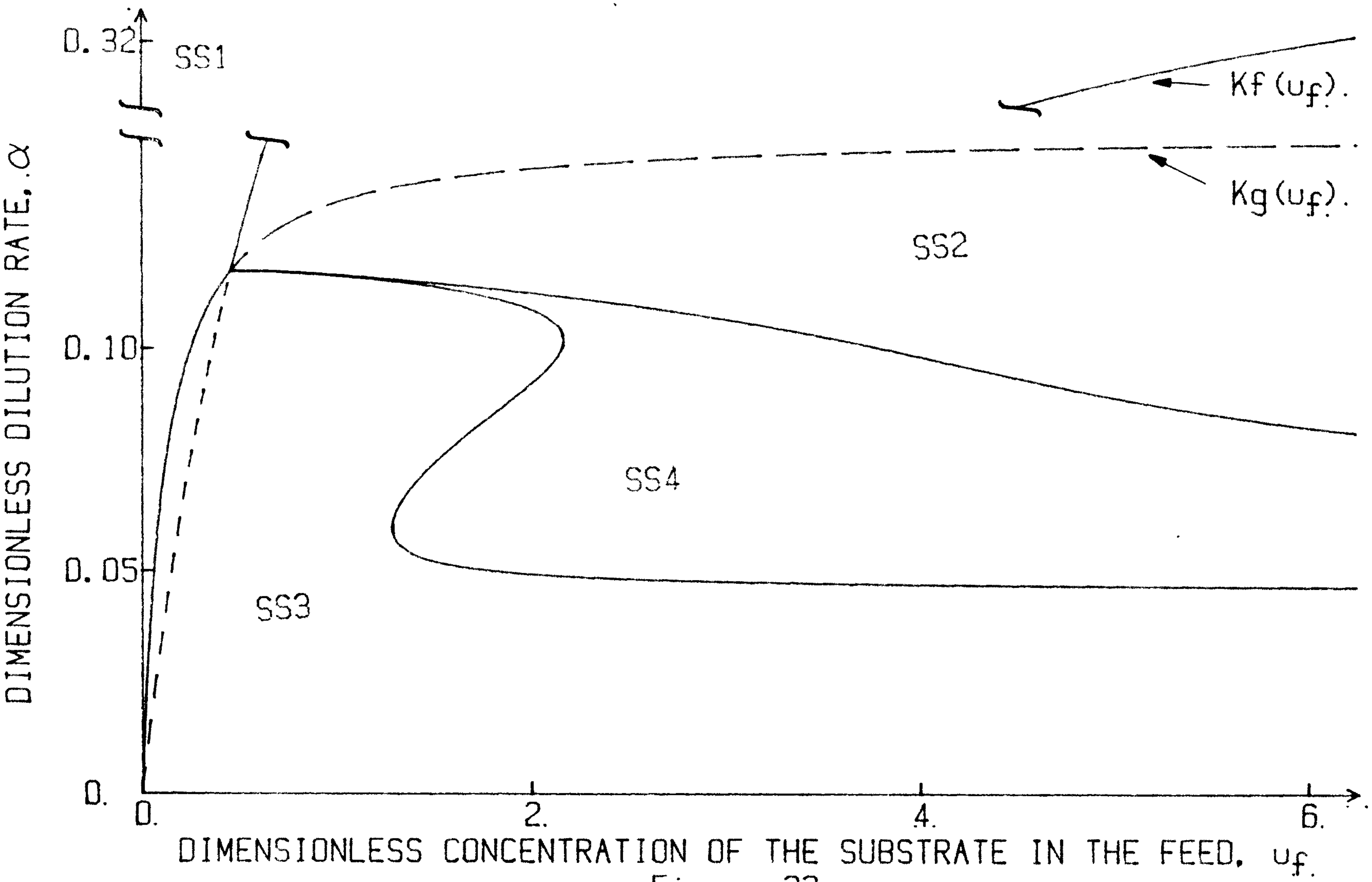

0.32
SS1
Kf (u_f).
Kg (u_f).
SS2
0.10
SS4
0.05
SS3
0.
0.
2.
4.
6.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 33.

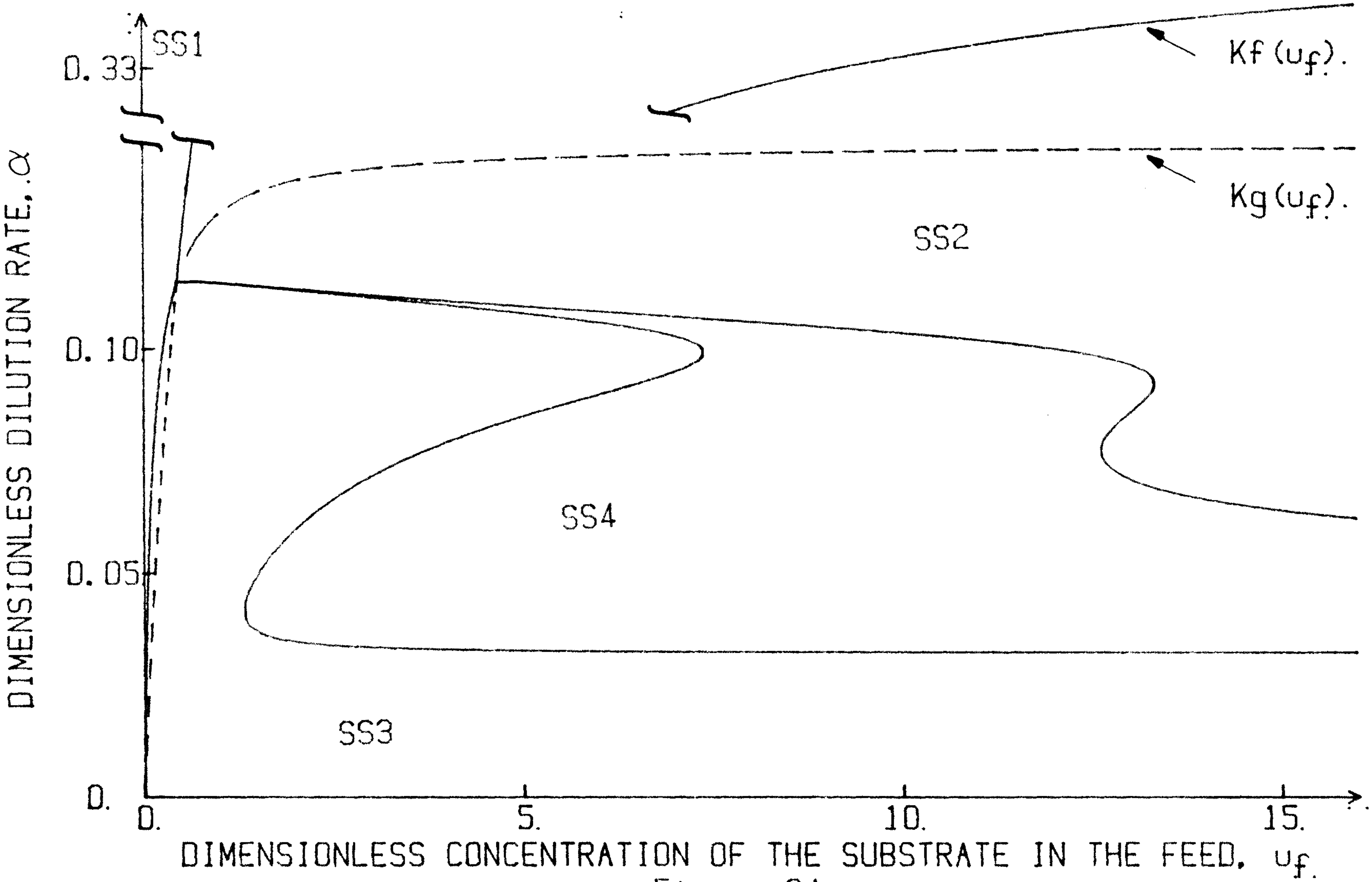
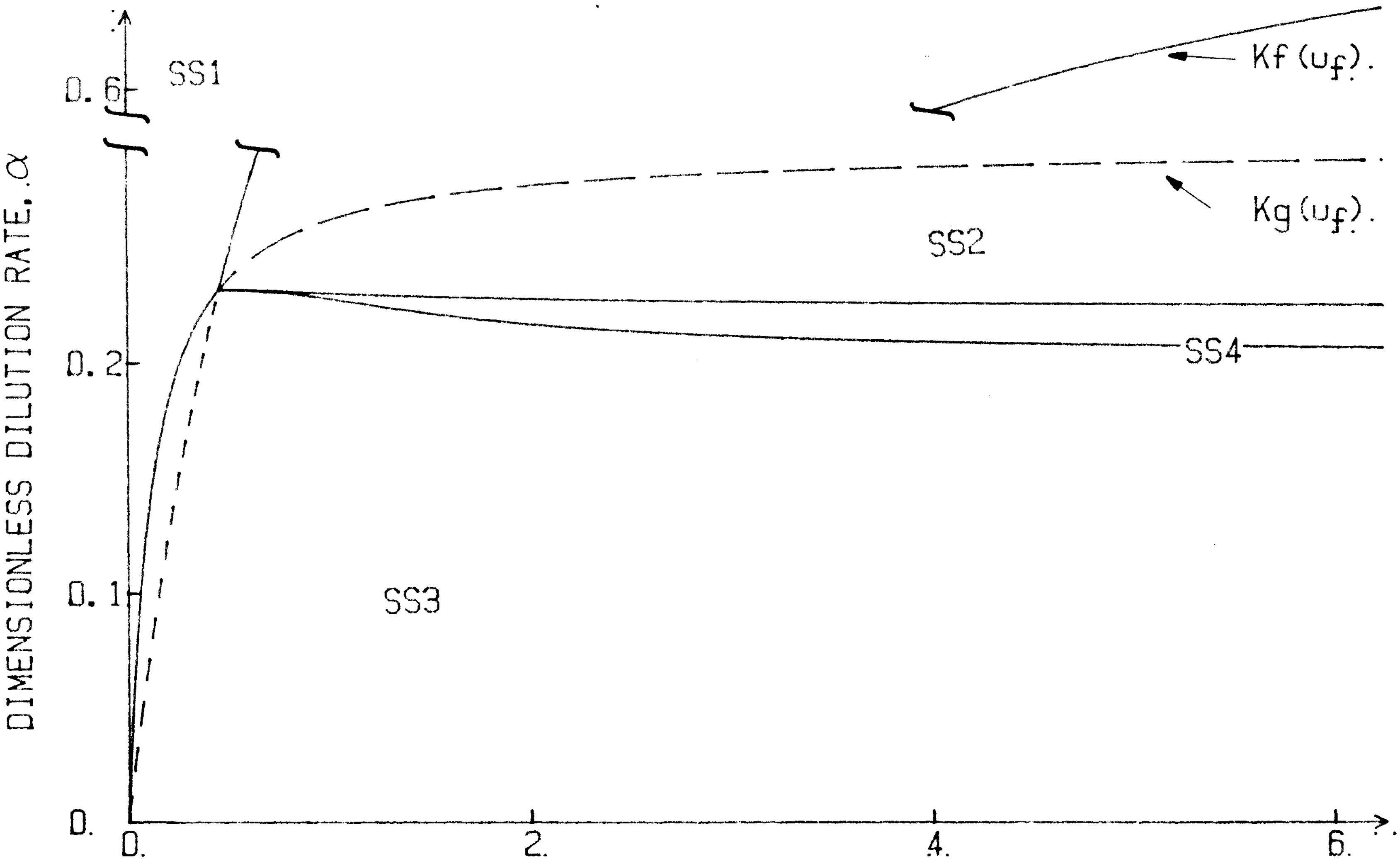

SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
0.33
0.10
0.05
0.
0.
5.
10.
15.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 34.



DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED. u_f.
Figure 35.

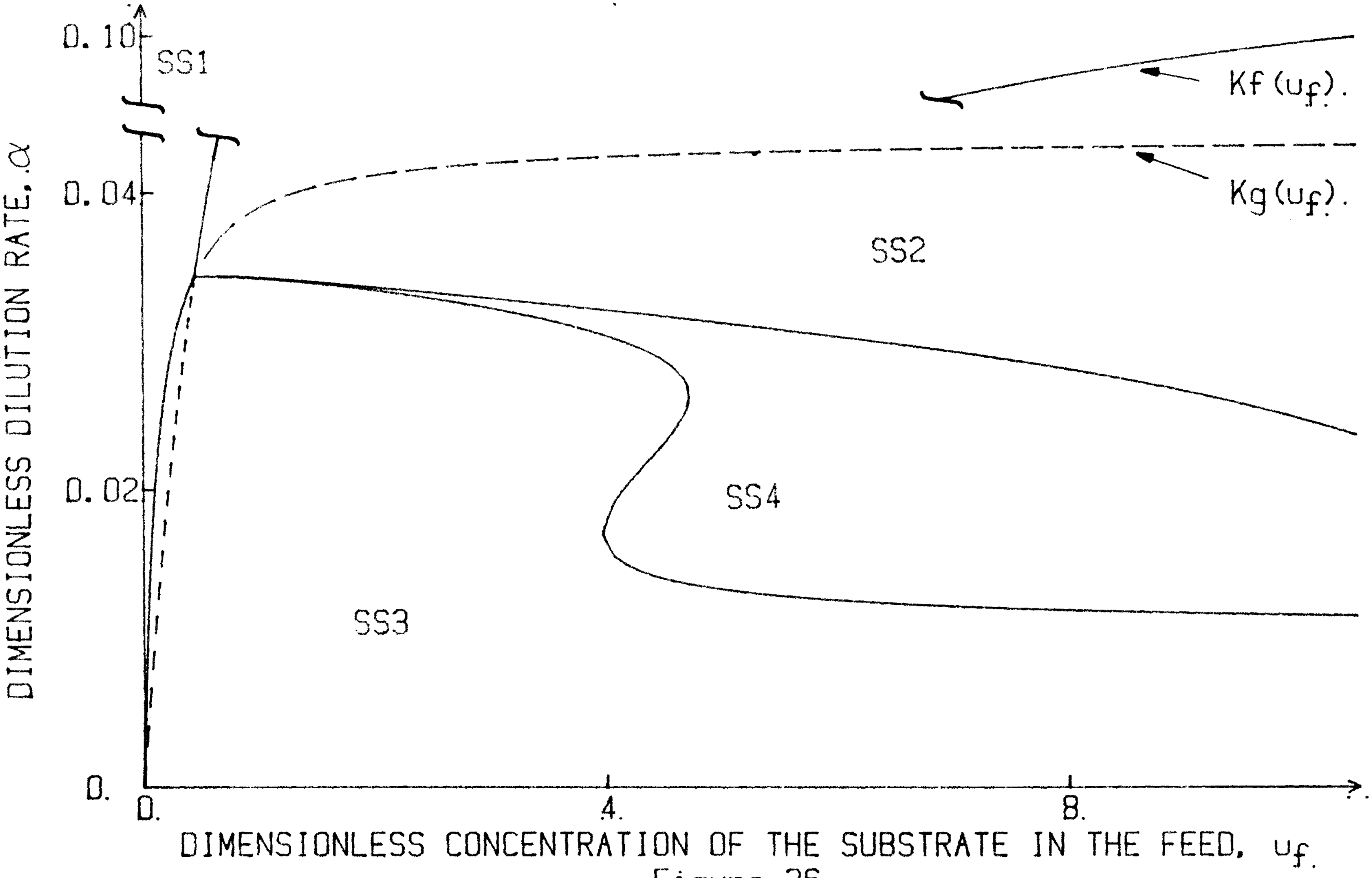

0.10
0.04
0.02
0.
0.
4.
8.
SS1
SS2
SS3
SS4
Kf (uf).
Kg (uf).
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, uf.

Figure 36.

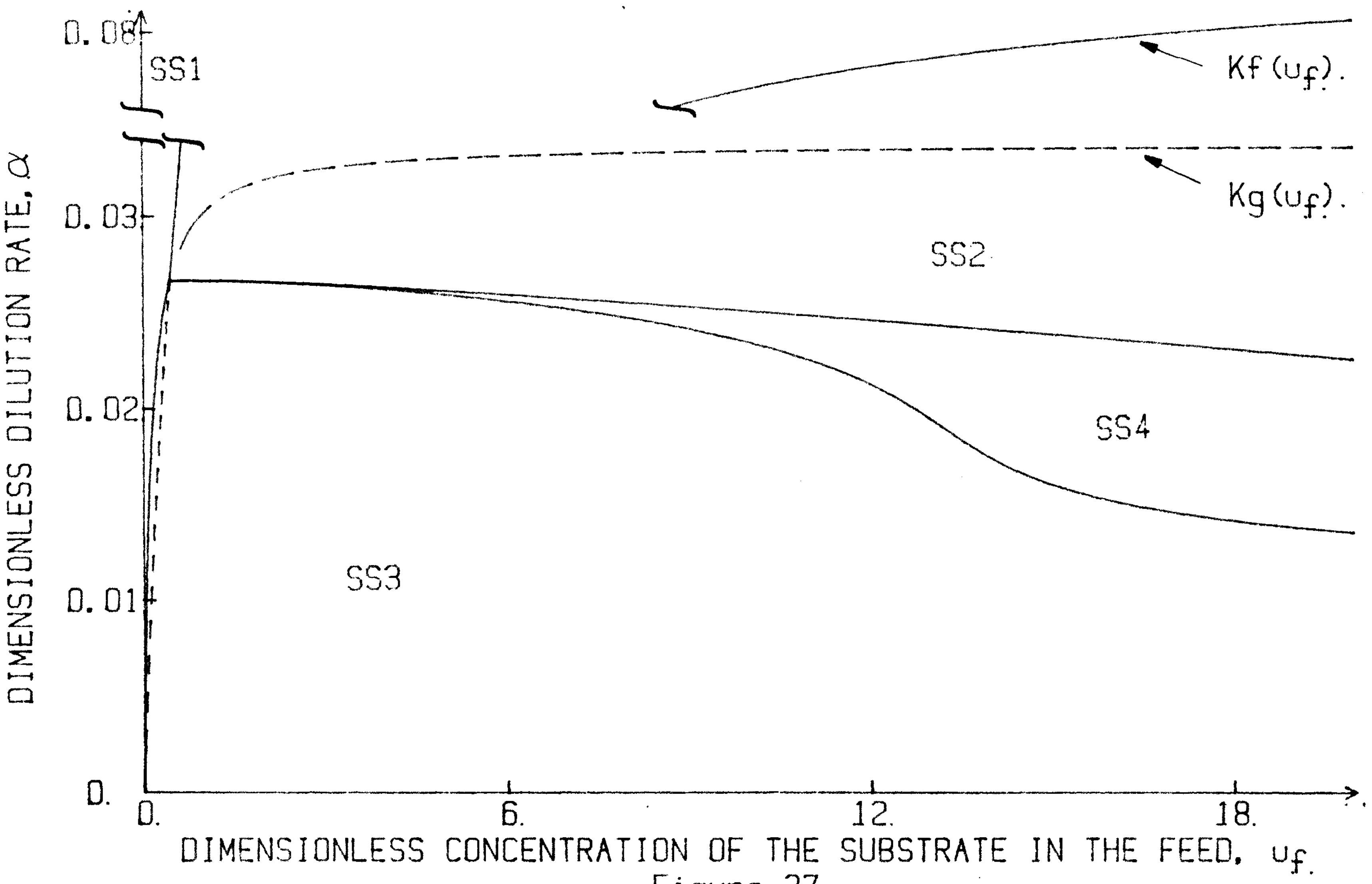
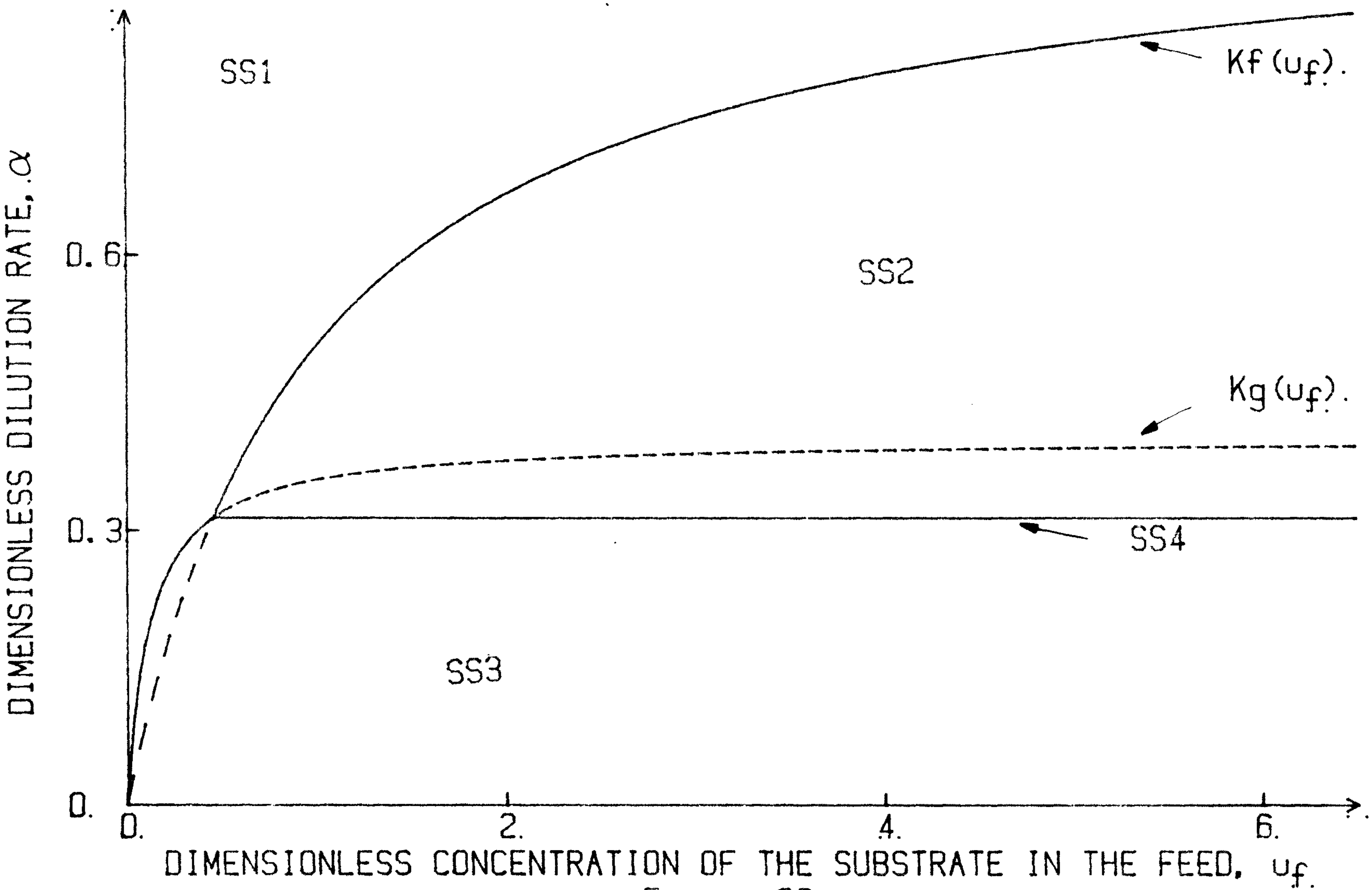

0.08
0.03
0.02
0.01
0.
0.
6.
12.
18.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
SS1
SS2
SS3
SS4
$Kf(u_f)$.
$Kg(u_f)$.

Figure 37.



SS1
SS2
SS3
SS4
Kf (u_f).
Kg (u_f).
DIMENSIONLESS DILUTION RATE, α
0.
0.3
0.6
0.
2.
4.
6.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 38.

IV ANALYSIS OF THE GENERAL SYSTEM

In this part the general system shown in Figure 1 (p.21) is discussed. The only difference between the general and the splitting system is that in the case of the general system the concentration of the rate-limiting substrate in the feed to the two vessels is not the same (i.e. $\eta \neq 1$). The two systems are highly similar and for the most part the analysis needs not to be repeated. It is the effect of the parameter η not being equal to unity that this part focuses on.

Mathematically, the system is described by equations (1.7) through (1.12) presented in part I of the thesis, and as it has been discussed there any two of the differential equations can be substituted by the stoichiometric relations (1.15) and (1.16). In fact, in studying this system equations (1.7), (1.8), (1.10), (1.11), (1.15) and (1.16) were used. Dynamically the system is again 4-dimensional and its Jacobian matrix, through which the local stability analysis of all possible steady states is investigated, is exactly the same as that of the splitting system (see pp.68-69). As a matter of fact the only difference between the splitting and the general system is in their stoichiometric relations, which of course become identical for $\eta=1$.

ANALYSIS OF SS1 (WASHOUT STEADY STATE)

This is the trivial steady state in which none of the two competitors survives, thus $x_i=y_i=0$, i=1, 2 while the values of u_1 and u_2 are given by the expressions:

$$u_1 = \frac{R(1+\eta\gamma)+1}{[R(\gamma+1)+1]}u_f = u_{1f}, \quad u_2 = \frac{1+\eta\gamma}{\gamma+1}u_f = u_{2f} \qquad (4.1)$$

It is clear from the expressions above that u_1 and u_2 will not be equal unless $\eta=1$ (splitting system) or $\gamma=0$ (non-splitting system). Hence it is only the general system which exhibits spatial heterogeneity when it is at the washout steady state.

The criteria for the (local) stability of SS1 are once again found by using Sevastyanov's lemma [29] since all off-diagonal elements of the Jacobian matrix are non-negative. The criteria are the following:

$$f_1 - [R(\gamma+1)+1]\alpha < 0 \qquad (4.2)$$

$$g_1 - [R(\gamma+1)+1]\alpha < 0 \qquad (4.3)$$

$$\beta[R(\gamma+1)+1](\gamma+1)\alpha^2 - \{\beta(R+1)(\gamma+1)f_1 + [R(\gamma+1)+1]f_2\}\alpha + f_1f_2 > 0 \qquad (4.4)$$

$$\beta[R(\gamma+1)+1](\gamma+1)\alpha^2 - \{\beta(R+1)(\gamma+1)g_1 + [R(\gamma+1)+1]g_2\}\alpha + g_1g_2 > 0 \qquad (4.5)$$

where f_i and g_i, i=1,2 are the functions f and g (dimensionless specific growth rates) evaluated at u_{if} which are given by (4.1). The difference between the conditions (4.2) through (4.5) and the conditions (3.9) through (3.12) is that in the latter set it is $f_1=f_2$ and $g_1=g_2$.

After some algebraic manipulations the criteria (4.2) through (4.5) can be combined into a single condition, namely:

$$\alpha > \max \{ \alpha_f , \alpha_g \} \tag{4.6}$$

where,

$$\alpha_f = \frac{\beta(R+1)(\gamma+1)f_1 + [R(\gamma+1)+1]f_2 + \Delta_f^{\frac{1}{2}}}{2\beta(\gamma+1)[R(\gamma+1)+1]}$$

$$\alpha_g = \frac{\beta(R+1)(\gamma+1)g_1 + [R(\gamma+1)+1]g_2 + \Delta_g^{\frac{1}{2}}}{2\beta(\gamma+1)[R(\gamma+1)+1]}$$

with,

$$\Delta_f = \{\beta(\gamma+1)f_1-[R(\gamma+1)+1]f_2\}^2+\beta^2R(R+2)(\gamma+1)^2f_1^2$$
$$+ 2\beta R(\gamma+1)[R(\gamma+1)+1]f_1f_2 > 0$$

and,

$$\Delta_g = \{\beta(\gamma+1)g_1-[R(\gamma+1)+1]g_2\}^2+\beta^2R(R+2)(\gamma+1)^2g_1^2$$
$$+ 2\beta R(\gamma+1)[R(\gamma+1)+1]g_1g_2 > 0$$

Because of the fact that $f_1 \neq f_2$ and $g_1 \neq g_2$ it can be easily seen that the expression (4.6) in terms of the parameters of the system is much more complicated than the corresponding expression for (3.13), (the complexity comes through Δ_f and Δ_g). This complexity presents the following problem: in the case of the splitting and the non-splitting systems considered earlier, if the f(u) and g(u) curves [or equivalently $f(u_f)$ and $g(u_f)$ curves] cross each other, it is obvious that the curves $Kf(u_f)$ and $Kg(u_f)$ cross each other as well; in the present case it is practically impossible to prove that the crossing of the $f(u_f)$ and $g(u_f)$ curves implies the crossing of the α_f and α_g curves although extensive numerical studies have indicated that this

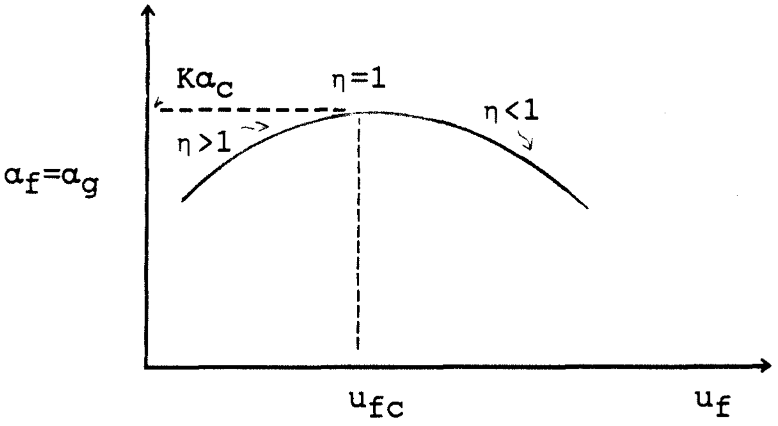


Figure 39: The locus of the crossing point of α_f and α_g as a function of u for various values of η

is so. The crossing point of $f(u_f)$ and $g(u_f)$ occurs at a value u_{fc} of u_f given by equation (2.28) and then $Kf(u_f)$ and $Kg(u_f)$ cross also at u_{fc} and their value is $K\alpha_c$ where α_c is given by equation (3.43), as it has been discussed in the previous parts of this thesis. In the case of the general system it has been observed that the crossing of the α_f and α_g curves occurs for a value of u_f less than u_{fc} if $\eta>1$ or for a value larger than u_{fc} if $\eta<1$. The relationship between the value of u_f at which the crossing occurs and the corresponding value of α_f and α_g at the crossing point is shown in Figure 39 from which it is interesting to observe that the maximum of α_f and α_g at the crossing point occurs for $\eta=1$. The diagram shown on Figure 39 is a qualitative one and it represents observations from numerical studies performed for the general system.

ANALYSIS OF SS2

SS2 is the steady state at which one of the two competing populations washes out of the system, namely $x_i>0$ and $y_i=0$, $i=1, 2$. The values of x_i and u_i, $i=1, 2$ are given as solution(s) of the system of equations (3.14), (3.15) and,

$$x_1 = u_{1f} - u_1 \tag{4.7}$$

$$x_2 = u_{2f} - u_2 \tag{4.8}$$

where u_{1f} and u_{2f} are the expressions given by (4.1). The relationship between u_1 and u_2 is that given by equation (3.21) while u_1 is given by the roots of the following cubic equation:

$$L_3u_1^3 + L_2u_1^2 + L_1u_1 + L_0 = 0 \tag{4.9}$$

where

$$L_3 = \{-[R(\gamma+1)+1]\alpha + 1\}C_1$$

$$L_2 = \{R(\gamma+1)A_1 - [R(\gamma+1)+1](C_1+D_1) + u_{1f}C_1$$
$$- R(\gamma+1)C_1(u_{2f}-u_{1f})\}\alpha + D_1 - u_{1f}C_1$$

$$L_1 = \{R(\gamma+1)(A_1+B_1) + u_{1f}(C_1+D_1) - [R(\gamma+1)+1]D_1$$
$$- R(\gamma+1)(C_1+D_1)(u_{2f}-u_{1f})\}\alpha - u_{1f}D_1$$
$$L_0 = [R(\gamma+1)B_1 + u_{1f}D_1 - D_1R(\gamma+1)(u_{2f}-u_{1f})]\alpha$$

After u_1 is found via (4.9) the values of x_1, x_2 and u_2 are easily calculated from equations (4.7), (4.8) and (3.21) respectively. SS2 will be meaningful if and only if $x_i>0$, and $0<u_i<u_{if}$, $i=1,2$.

As in the case of the splitting and the non-splitting system, SS2 in the general case does not exhibit multiplicity as numerical results indicate.

In the case of the non-splitting system it was proved that in a meaningful SS2 it is always $u_1>u_2$ while in the splitting system this is not necessarily true. It has been found numerically, that in the case of the general system as in the case of the splitting system the relationship between u_1 and u_2 is not always such that $u_1>u_2$.

In the case of the splitting system it was found that the relationship between u_1 and u_2 depends on the relation of the product of the parameters β and γ to unity [see relations (3.18) and (3.19)]. The same thing cannot be claimed for the general system. The numerical results were not conclusive in this case, it can be said though that the relationship between u_1 and u_2 depends on (among other things) the value of the parameter η.

The criterion for the (local) stability of SS2 is the one given by the relation (3.28). As it was discussed in part III, the stability criterion is always satisfied

If $\omega > \varphi$ and $\varphi < 1$

If $1 > \varphi > \omega$ and $u_c < \max\{u_1, u_2\}$

If $1 < \varphi < \omega$ and $u_c > \max\{u_1, u_2\}$

while (3.28) is never satisfied

If $\omega < \varphi$ and $\varphi > 1$

If $1 > \varphi > \omega$ and $u_c > \max\{u_1, u_2\}$

If $1 < \varphi < \omega$ and $u_c < \max\{u_1, u_2\}$

while for any other situation it cannot be concluded beforehand (or analytically) whether the criterion is satisfied or not.

ANALYSIS OF SS3

This steady state is symmetric to SS2 and it arises when $x_i=0$ and $y_i>0$, i=1, 2.

The value of u_1 in this case is given as a solution to the following cubic equation:

$$L_3' u_1^3 + L_2' u_1^2 + L_1' u_1 + L_0' = 0 \tag{4.10}$$

where,

$$L_3' = \{-[R(\gamma+1)+1]\alpha + \varphi\}C_1'$$

$$L_2' = \{R(\gamma+1)A_1' - [R(\gamma+1)+1](C_1'\omega+D_1') + u_{1f}C_1' - R(\gamma+1)C_1'(u_{2f}-u_{1f})\}\alpha + \varphi(D_1' - u_{1f}C_1')$$

$$L_1' = \{R(\gamma+1)(A_1'\omega+B_1') + u_{1f}(C_1'\omega+D_1') - [R(\gamma+1)+1]\omega D_1' - R(\gamma+1)(C_1'\omega+D_1')(u_{2f}-u_{1f})\}\alpha - \varphi u_{1f}D_1'$$

$$L_0' = \omega[R(\gamma+1)B_1' + u_{1f}D_1' - D_1'R(\gamma+1)(u_{2f}-u_{1f})]\alpha$$

with u_{1f} and u_{2f} given by the expressions (4.1), and A_1', B_1', C_1', D_1' given by the expressions after equation (3.29a) in part III.

Once u_1 is determined by solving equation (4.10) the value of u_2 is calculated via equation (3.29a) while y_1 and y_2 are given by the following equations

$$y_1 = u_{1f} - u_1$$

$$y_2 = u_{2f} - u_2$$

SS3, as its analogue SS2, does not exhibit multiplicity. The criterion for the stability of SS3 is given by (3.28) provided that g_i are substituted by f_i, $i=1,2$.

The eigenvalues of both SS2 and SS3 are always real hence no (damped) oscillatory phenomena are expected during transients, something confirmed via computer simulations.

ANALYSIS OF THE COEXISTENCE STEADY STATE (SS4)

The coexistence steady state arises when both competitors establish themselves in both chemostats. It is meaningful if and only if $x_i>0$, $y_i>0$ and $0<u_i<u_{if}$, $i=1,2$. The steady state equations in this case are equations (3.30) through (3.33) and

$$u_{1f} = x_1 + y_1 + u_1 \tag{4.11}$$

$$u_{2f} = x_2 + y_2 + u_2 \tag{4.12}$$

where u_{1f} and u_{2f} are given by the expressions (4.1).

In the analysis of SS4 for the splitting system it has been proved that a necessary condition for a meaningful coexistence steady state is that the specific growth rate curves f(u) and g(u) cross each other. The proof is based on equations (3.30) through (3.33) that are valid for the general case considered here as well. Hence, the necessity of the crossing of the f(u) and g(u) curves continues being a condition here and at this point one can conclude that this condition is necessary for coexistence in all configurations studied in the present thesis.

The value of u_1 is given as a solution to the quadratic (3.42) and once found, the value of u_2 can be calculated from the expression (3.44). As it was discussed in part III, the values of u_1 and u_2 are independent of the value of u_f and hence they are not affected by the value of the parameter η appearing in the general case. When u_1 and u_2 are known the values of the remaining four variables can be calculated from the following expressions:

$$x_1 = \frac{(u_{1f}-u_1)(\alpha-g_1)-[(u_{2f}-u_{1f})+(u_1-u_2)]R(\gamma+1)\alpha}{f_1 - g_1} \tag{4.13}$$

$$y_1 = \frac{[(u_{2f}-u_{1f})+(u_1-u_2)]R(\gamma+1)\alpha-(\alpha-f_1)x_1}{\alpha - g_1} \tag{4.14}$$

$$x_2 = \frac{[R(\gamma+1)+1]\alpha-f_1}{R(\gamma+1)\alpha}\, x_1 \tag{4.15}$$

$$y_2 = \frac{[R(\gamma+1)+1]\alpha-g_1}{R(\gamma+1)\alpha}\, y_1 \tag{4.16}$$

Observe that when $\eta=1$, $u_{1f}=u_{2f}$ and the expressions (4.13) through (4.16) reduce to the expressions (3.45) through (3.48) of the splitting system.

Since the values of u_1 and u_2 are independent of the parameter η, their relation to u_c will be exactly the same as in the case of the splitting system, namely:

if $\beta\gamma > 1$ then $u_2 > u_c > u_1$

if $\beta\gamma < 1$ then $u_1 > u_c > u_2$

The restrictions on the values of α given by (3.55) are still valid for the general system but in reality, as numerical results indicate, the range of values of α for coexistence is much more narrow than what conditions (3.55) indicate.

Numerical results indicate that α should be selected as following if one is to expect to get coexistence:

when $\beta\gamma > 1$ it must be $\dfrac{1}{\beta(\gamma+1)}\alpha_c < \alpha < K\alpha_c$

when $\beta\gamma < 1$ it must be $\dfrac{R+1}{R(\gamma+1)+1}\alpha_c < \alpha < K\alpha_c$

In the special case where $\beta\gamma=1$ and for $(u_f,\alpha)=(u_{fc}, K\alpha_c)$, it is $u_1=u_2$ as in the case of the splitting system. But, under the same conditions the values of x_i, y_i, $i=1,2$ are meaningless unless $\eta=1$. Hence if $\eta\neq1$ the general system does not lead to a homogeneous environment as the splitting system does when $\beta\gamma=1$.

From the numerical studies performed for the general system the following things have been observed:

If the values of u_1 and u_2 are such that $f_1>g_1$ and $f_2<g_2$, an increase in the value of η results in the following:

y_1, y_2 and y_2-y_1, increase while,
x_1, x_2 and x_2-x_1, decrease.

If the values of u_1 and u_2 are such that $f_1<g_1$ and $f_2>g_2$, an increase in the value of η results in the following:

y_1, y_2 and y_2-y_1, decrease while,
x_1, x_2 and x_2-x_1, increase.

The observations above, suggest that the parameter η can be used in order to affect and control the population balances (or their ratio) in order to achieve a desired populations distribution in the system.

The results of the (local) stability analysis, performed by using the Ruth-Hurwitz criteria, indicates that SS4 is stable if meaningful. Damped oscillations have never been observed during transients of the system, something which implies that the eigenvalues are real and negative whenever SS4 is meaningful.

The remarks made at the end of the analyses for the splitting and the non-splitting system are valid for the general system as well, namely the results of the local stability analysis hold also globally and SS1 through SS4 are mutually exclusive.

OPERATING DIAGRAMS AND THE EFFECT OF THE PARAMETERS

In this section some operating diagrams for the general system are presented. They are projections on the α-u_f plane of the actual 5-dimensional $(\alpha, u_f, R, \gamma, \eta)$ or 6-dimensional $(\alpha, u_f, R, \gamma, \eta, \beta)$ operating diagrams. The diagrams of the non-splitting system can be also viewed as diagrams of the general system for $\gamma=\eta=0$. The diagrams of the splitting system are also diagrams for the general system for $\eta=1$. In fact, the general and the splitting systems are very similar and the effects of the parameters β, R and γ for a fixed η are the same in both systems and their study is not repeated here. It is only the effect of the parameter η which is investigated and discussed in the present section. The values for the parameters φ and ω are 0.4 and 0.125, respectively, the same as those used for all the earlier presented diagrams.

The common features of all diagrams are the following:

—In most of the cases one can find a wide enough domain in the α-u_f plane in which coexistence occurs.

—The crossing point of the α_f and α_g curves is always a point on a boundary of the domain of coexistence. However this point is not $(u_{fc}, K\alpha_c)$ as in the cases of the two systems considered earlier.

—The upper bound of α values for coexistence is always $K\alpha_c$ as in the two systems considered earlier. The value of $\alpha=K\alpha_c$ is higher than the value of α at which the α_f and α_g curves cross each other. Hence, the domain of coexistence may extend above the point of crossing of the α_f and α_g curves (e.g. Figure 45) although this may not be obvious from the diagrams because for the parameters chosen, $K\alpha_c$ is very close to the α value at which $\alpha_f=\alpha_g$.

—The lower bound of α values for coexistence is

$$\alpha = \frac{1}{\beta(\gamma+1)}\,\alpha_c \qquad \text{when} \quad \beta\gamma > 1 \quad \text{and,}$$

$$\alpha = \frac{R+1}{R(\gamma+1)+1}\,\alpha_c \qquad \text{when} \quad \beta\gamma < 1$$

where $\alpha_c=0.314$ for $\varphi=0.4$ and $\omega=0.125$

The diagrams are such that starting from a point in the domain of coexistence they show that shift-up and shift-down experiments can cause the system to exhibit all possible kinds of behavior discussed in the cases of the splitting and non-splitting system.

The values of β, R and γ have been chosen so that one can compare the diagrams presented here with those presented for the splitting system (where $\eta=1$).

The diagrams are shown in Figures 40-54 and they can be divided in three categories:

1. $\beta\gamma < 1$ Figures 40-45

2. $\beta\gamma > 1$ Figures 46-53
3. $\beta\gamma = 1$ Figure 54

For the diagram shown in Figure 54 the values of the parameters are $R=0.1$, $\beta=0.5$, $\gamma=2.0$ and $\eta=3.0$. The interesting thing is that despite the fact that $\beta\gamma=1$ there is a domain (although very narrow in terms of the α values range) where coexistence occurs. This is a difference with the splitting system in which if $\beta\gamma=1$ the environment is spatially homogeneous and coexistence occurs for a discrete value of α only.

<u>Case I.</u> $\beta\gamma < 1$ (Figures 40-45)

For the diagrams shown in Figures 40 and 41 the value of η is 0.2 and 6.0, respectively while for both diagrams $R=0.1$, $\beta=0.1$ and $\gamma=0.2$. It is interesting to observe that as η increases the coexistence region shifts to higher u_f values. It can be also said that as η increases the domain of coexistence also increases not really in terms of the width of the range of α values but due to the fact that SS2 does not appear for low α values. For the diagrams shown in Figures 42 and 43 the value of η is 0.2 and 3.0, respectively, while for both cases $\beta=0.2$, $R=1.0$ and $\gamma=0.2$. Again it can be observed that as η increases the coexistence domain both increases and shifts to higher u_f values. It should be observed that in all diagrams of Figures 40-43 it is $\beta<1$. When $\beta>1$ as in the diagrams of Figures 44 and 45 where $\beta=1.5$, $R=0.1$, $\gamma=0.2$ and $\eta=0.2$ and 6.0, respectively, the results are disappointing as far as coexistence is concerned and this happens in all configurations examined in this study.

It was also observed that the value of η does not affect the shape of the domain of coexistence. From the diagrams shown previously it became obvious that changing R, γ or β the coexistence domain changed from the S-shaped type to the type where there is a domain at low α values and practically a curve at a higher α value. Such a change does not happen when η changes which implies that the shape of the domain of coexistence in the α-u_f plane is decided by all parameters but η.

Case II. $\beta\gamma > 1$ (Figures 46-53)

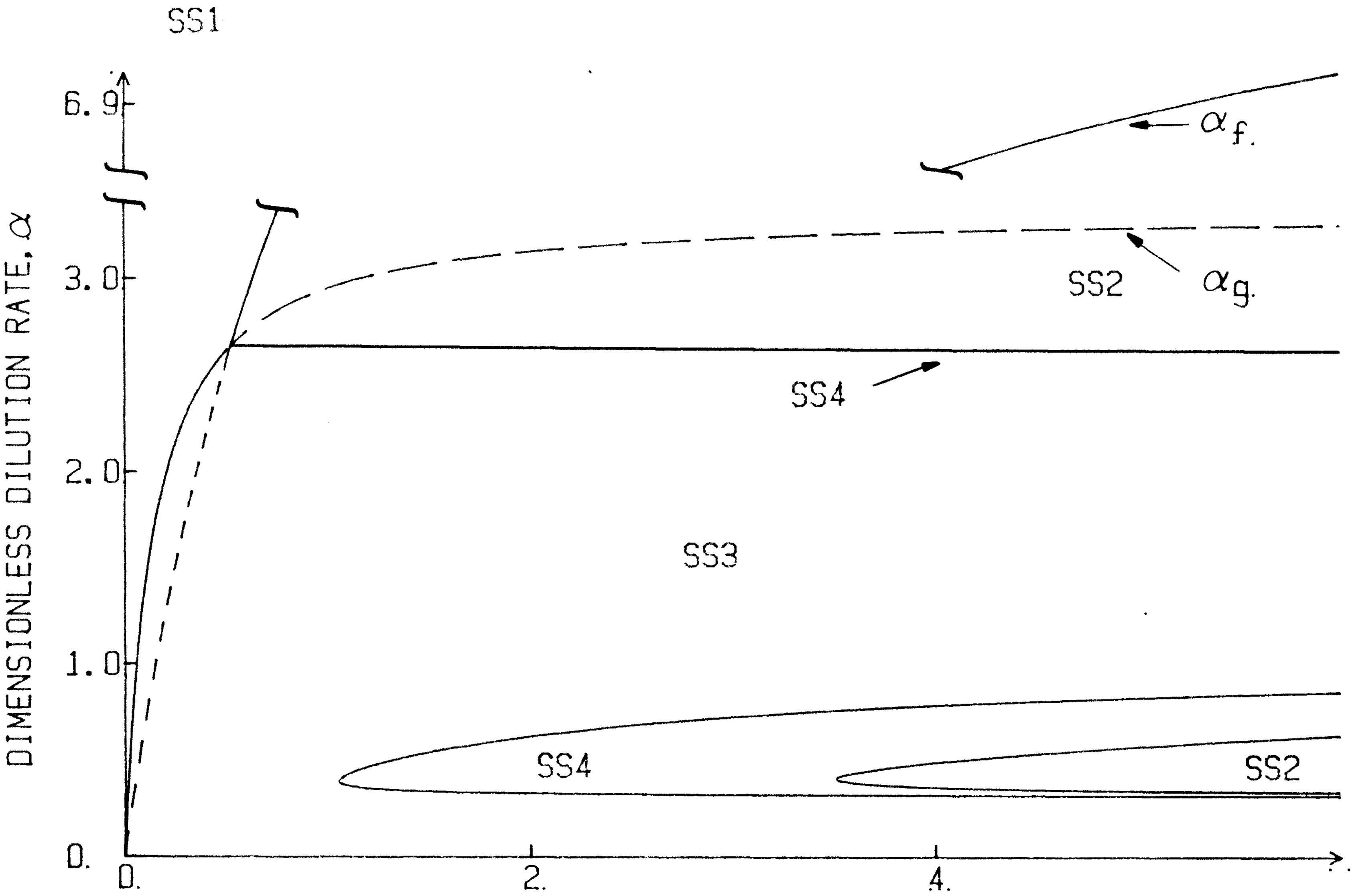
For the diagrams shown in Figures 46 and 47 the value of η is 0.2 and 3.0, respectively, while for both cases $R=0.1$, $\beta=0.6$ and $\gamma=20.0$. It can be observed that as η increases the domain of coexistence shifts to lower u_f values and its extent decreases in the sense that by increasing η, SS2 appears at low α values. In the diagrams of Figures 48 and 49 η is 0.2 and 6.0, respectively while $R=0.1$, $\beta=0.35$ and $\gamma=20.0$ in both cases. Again the domain of coexistence becomes smaller and it shifts to smaller u_f values. In all diagrams 46-49 it is $\beta<1$. It can be observed that the trend is opposite of that of diagrams 40-43 where $\beta<1$ and $\beta\gamma<1$. It can also be observed that the range of α values yielding coexistence when $\beta\gamma<1$ is much wider than that when $\beta\gamma>1$.

In the diagrams shown in Figures 50 to 53 it is $\beta>1$, actually in all of them it is $\beta=1.5$, also for all of them it is $R=0.1$. In the diagrams of Figures 50 and 51 the value of η is 0.2 and 3.0, respectively, while for both, $\gamma=20.0$. It can be observed that the trend is again for a decrease in the coexistence region and for a shift to smaller u_f values. These trends are reversed in Figures 52 and 53 for which η is 0.2 and 3.0, respectively, while in both $\gamma=1.0$. The only difference between Figures 50-51 and 52-53 is in the value of γ. It should be clearly stated that the range of α values for coexistence when $\beta>1$ is extremely small and sometimes even practically non-existing. Comparing the diagrams of Figures 44 and 45 with those of Figures 50 to 53 one can say that $\beta>1$ is not a good choice but if it has to be made it is better to have $\beta\gamma>1$ than $\beta\gamma<1$

One can conclude that the proper selections are $\beta<1$, $\beta\gamma<1$ and η at an intermediate value.

Table 3: Parameter Values used for the Operating Diagrams shown in Figures 40-54

Fig.No.	φ	ω	β	R	γ	η
40	0.4	0.125	0.1	0.1	0.2	0.2
41	"	"	"	"	"	6.0
42	"	"	0.2	1.0	0.2	0.2
43	"	"	"	"	"	3.0
44	"	"	1.5	0.1	0.2	0.2
45	"	"	"	"	"	6.0
46	"	"	0.6	0.1	20.0	0.2
47	"	"	"	"	"	3.0
48	"	"	0.35	0.1	20.0	0.2
49	"	"	"	"	"	6.0
50	"	"	1.5	0.1	20.0	0.2
51	"	"	"	"	"	3.0
52	"	"	1.5	0.1	1.0	0.2
53	"	"	"	"	"	3.0
54	"	"	0.5	0.1	2.0	3.0



SS1
6.9
3.0
2.0
1.0
0.
0.
2.
4.
α_f.
α_g.
SS2
SS4
SS3
SS4
SS2
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 40.

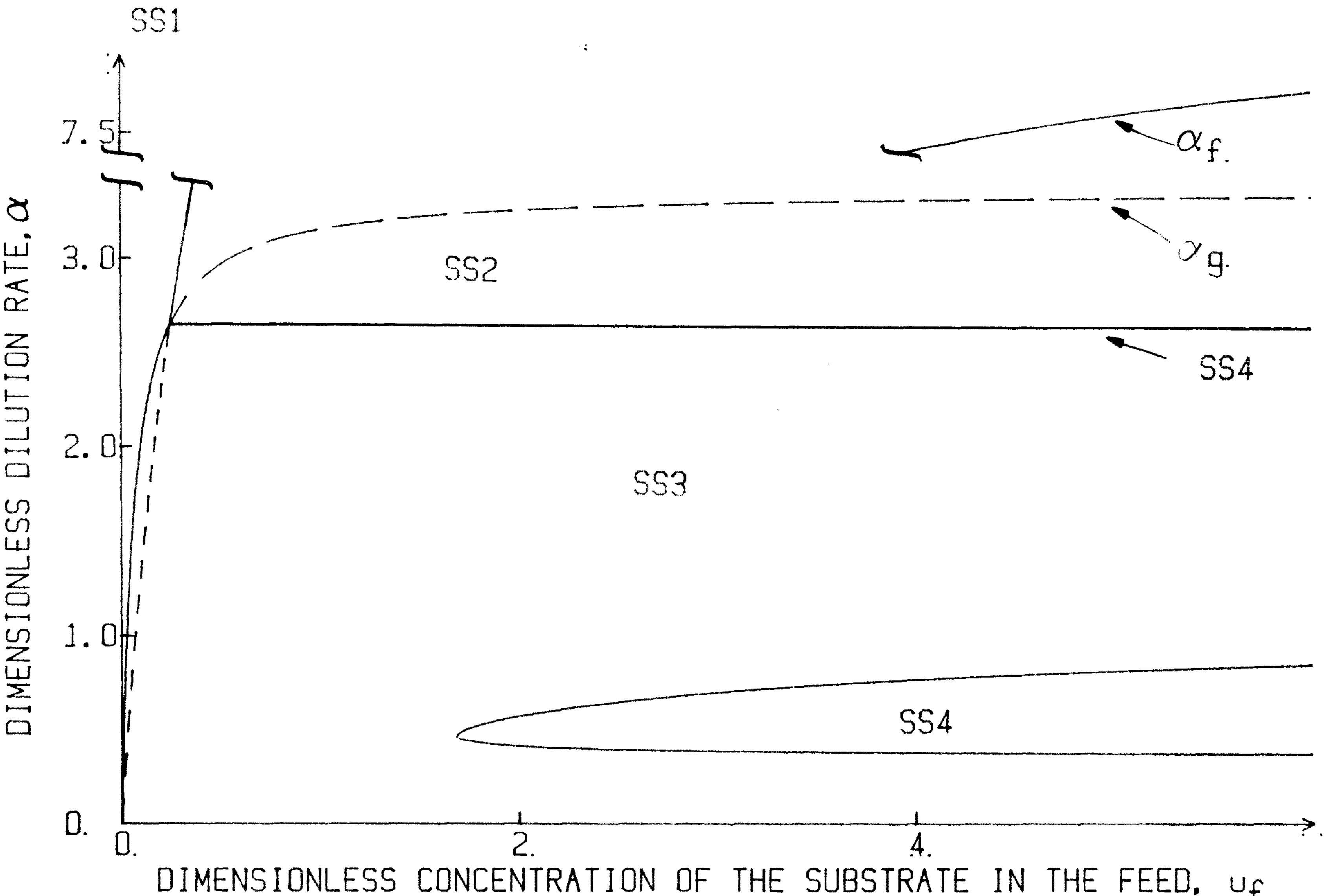

SS1
7.5
3.0
2.0
1.0
0.
DIMENSIONLESS DILUTION RATE, α
α_f.
α_g.
SS2
SS4
SS3
SS4
0.
2.
4.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 41.

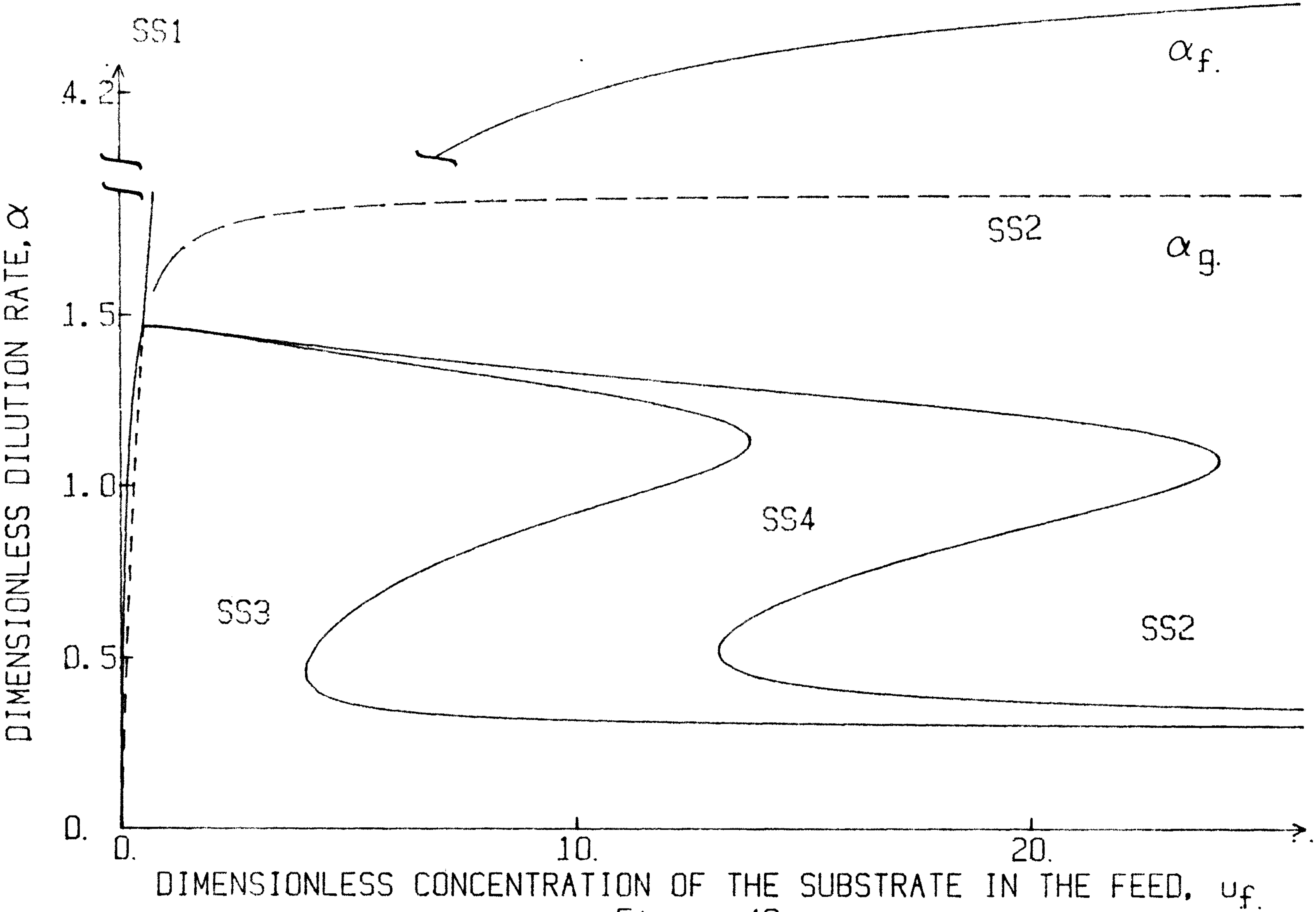

SS1
4.2
1.5
1.0
0.5
0.
α_f.
SS2
α_g.
SS4
SS3
SS2
0.
10.
20.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 42.

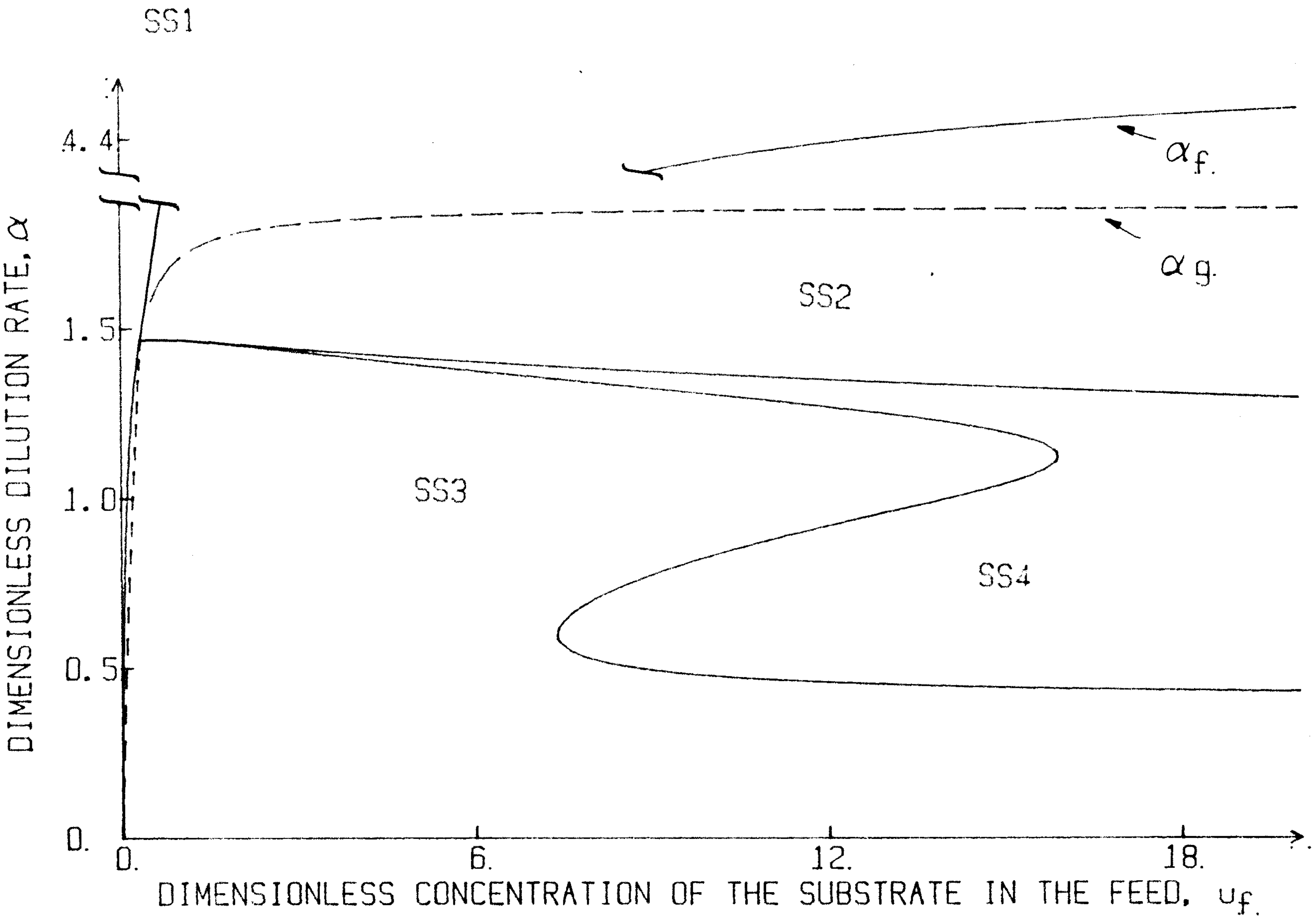

SS1
4.4
1.5
1.0
0.5
0.
DIMENSIONLESS DILUTION RATE, α
α f.
α g.
SS2
SS3
SS4
0.
6.
12.
18.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u f.

Figure 43.

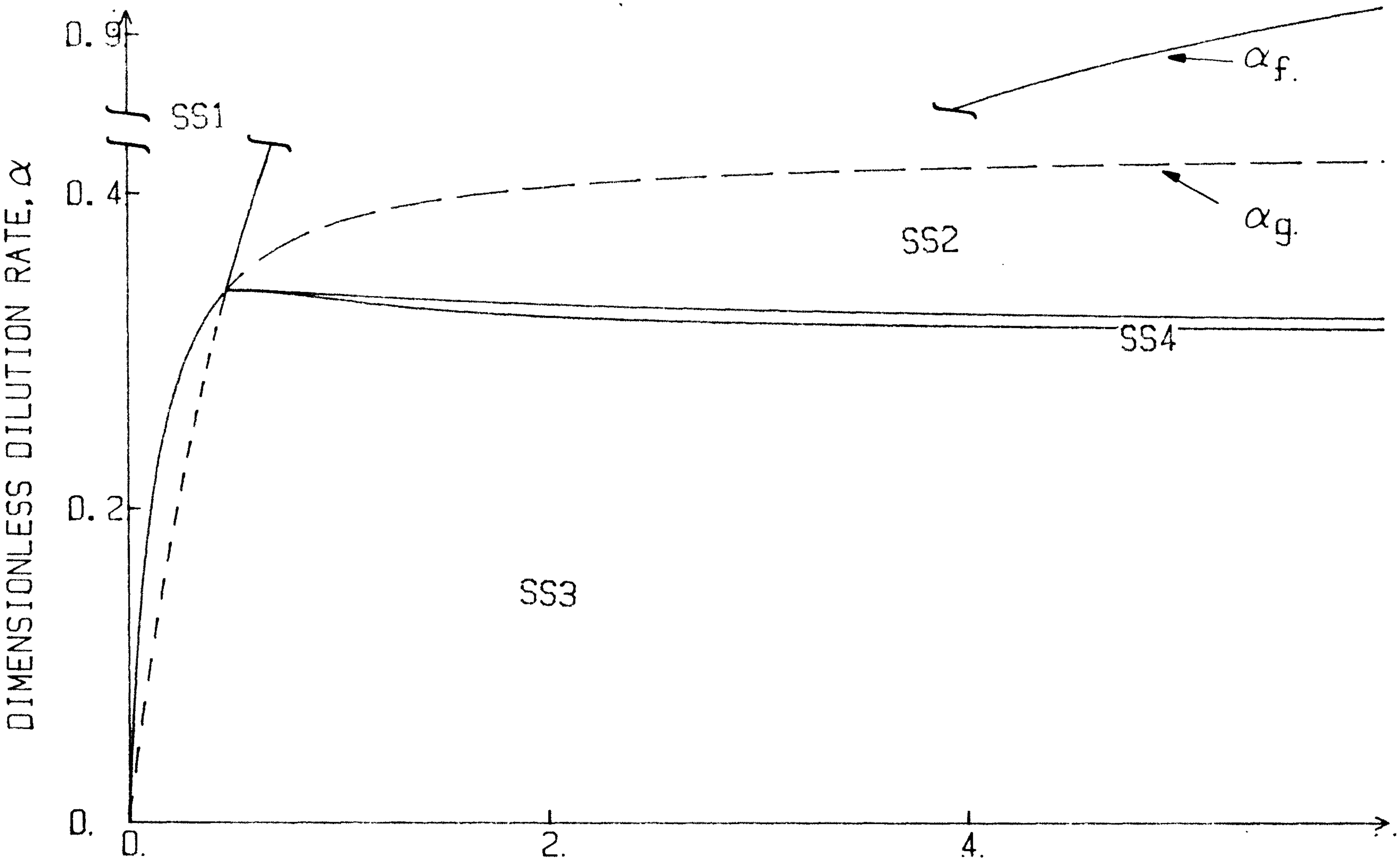

0.9
0.4
0.2
0.
0.
2.
4.
SS1
SS2
SS3
SS4
α_f.
α_g.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 44.

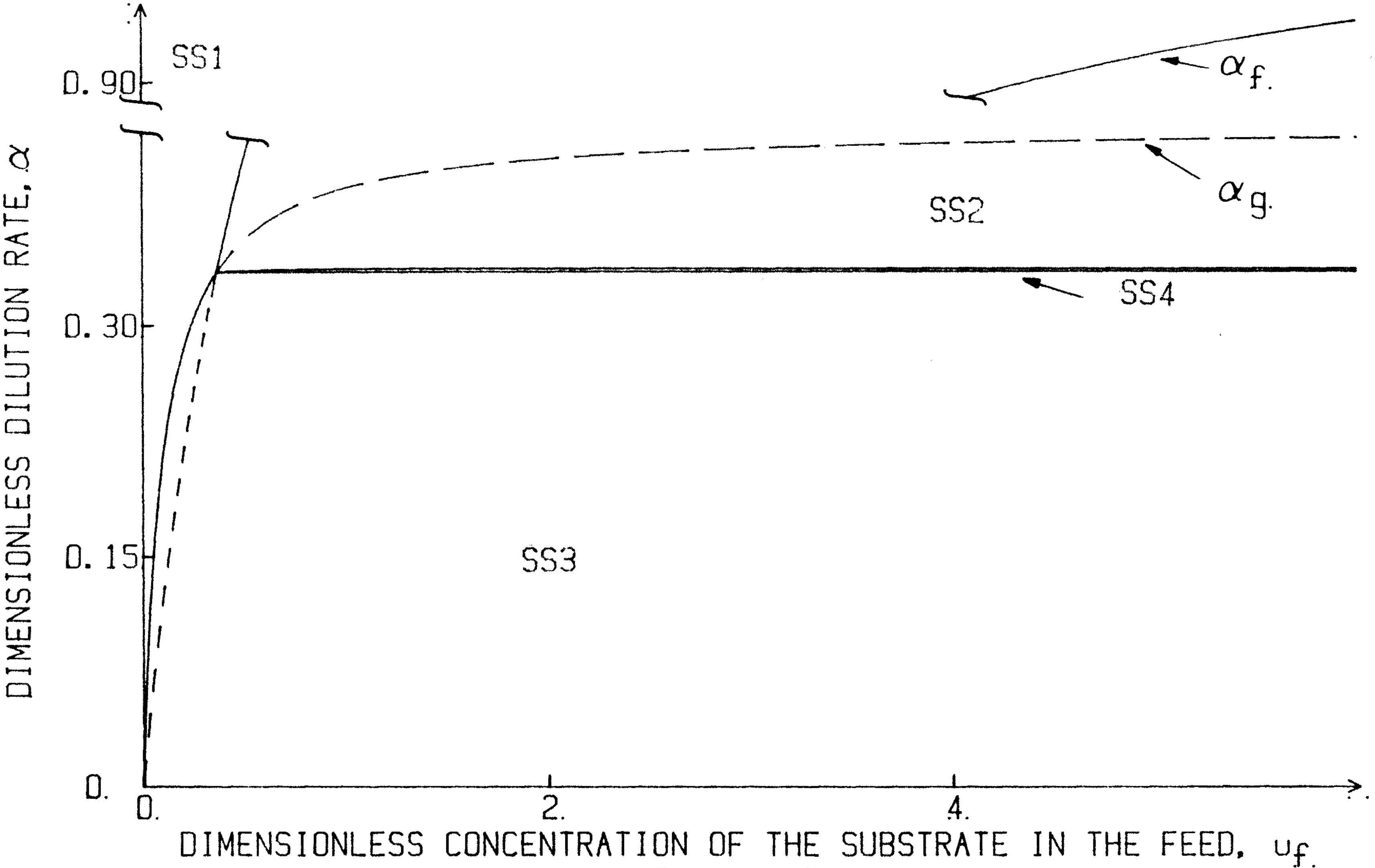

DIMENSIONLESS DILUTION RATE, α
0.90
0.30
0.15
0.
0.
2.
4.
SS1
SS2
SS3
SS4
α_f.
α_g.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 45.

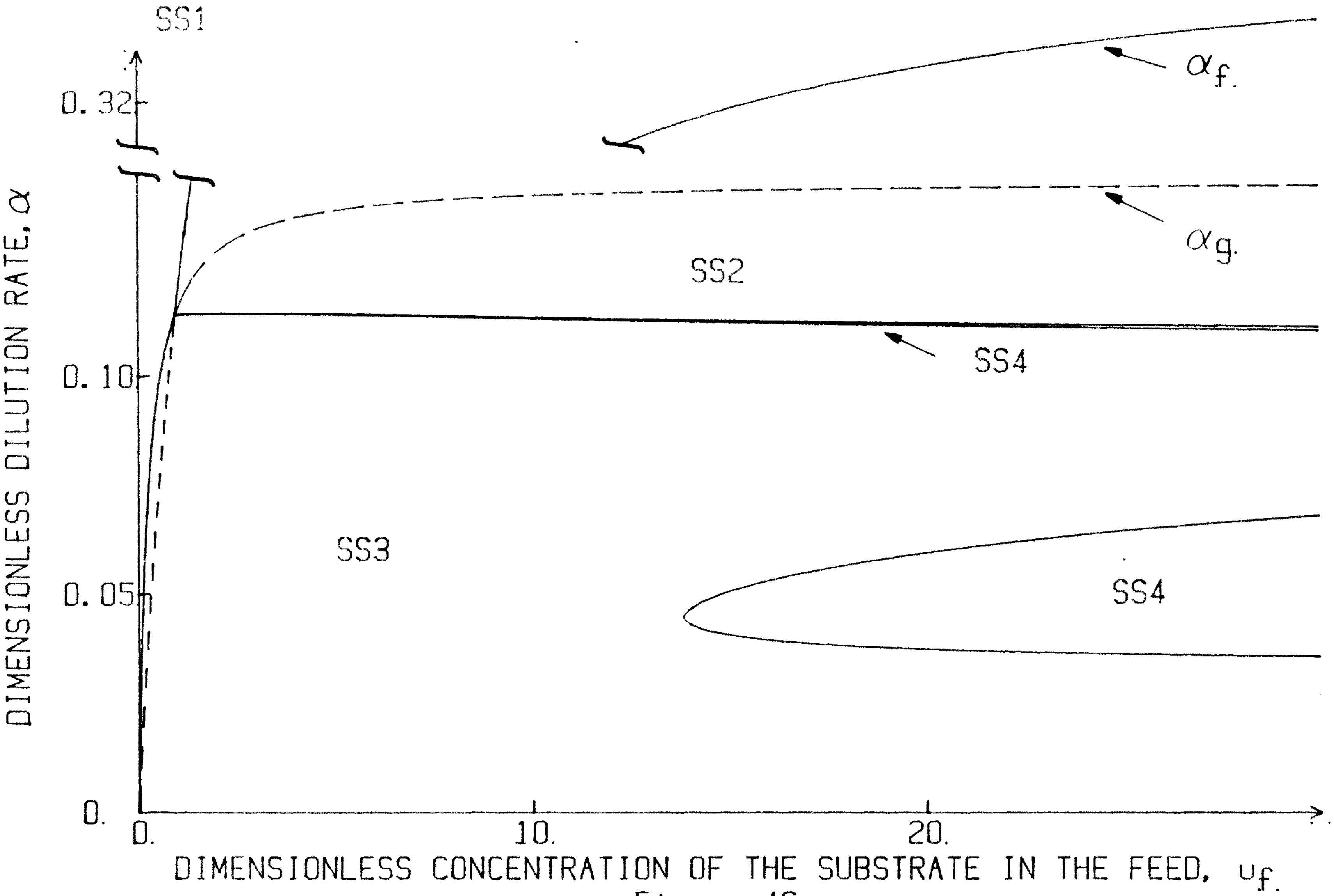

SS1
0.32
0.10
0.05
0.
DIMENSIONLESS DILUTION RATE, α
α_f.
α_g.
SS2
SS4
SS3
SS4
0.
10.
20.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 46.

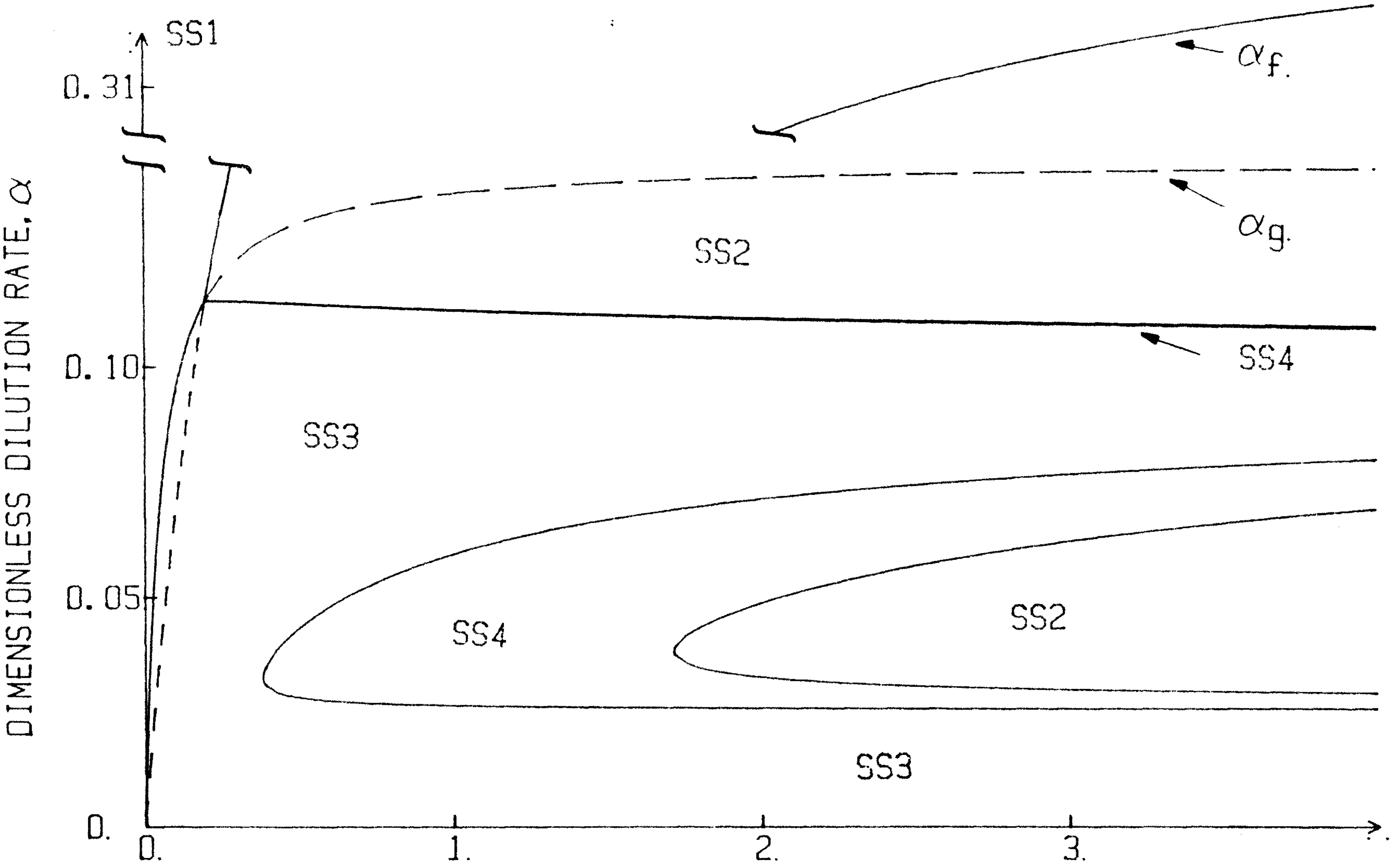

SS1
0.31
0.10
0.05
0.
DIMENSIONLESS DILUTION RATE, α
α_f.
α_g.
SS2
SS4
SS3
SS4
SS2
SS3
0.
1.
2.
3.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 47.

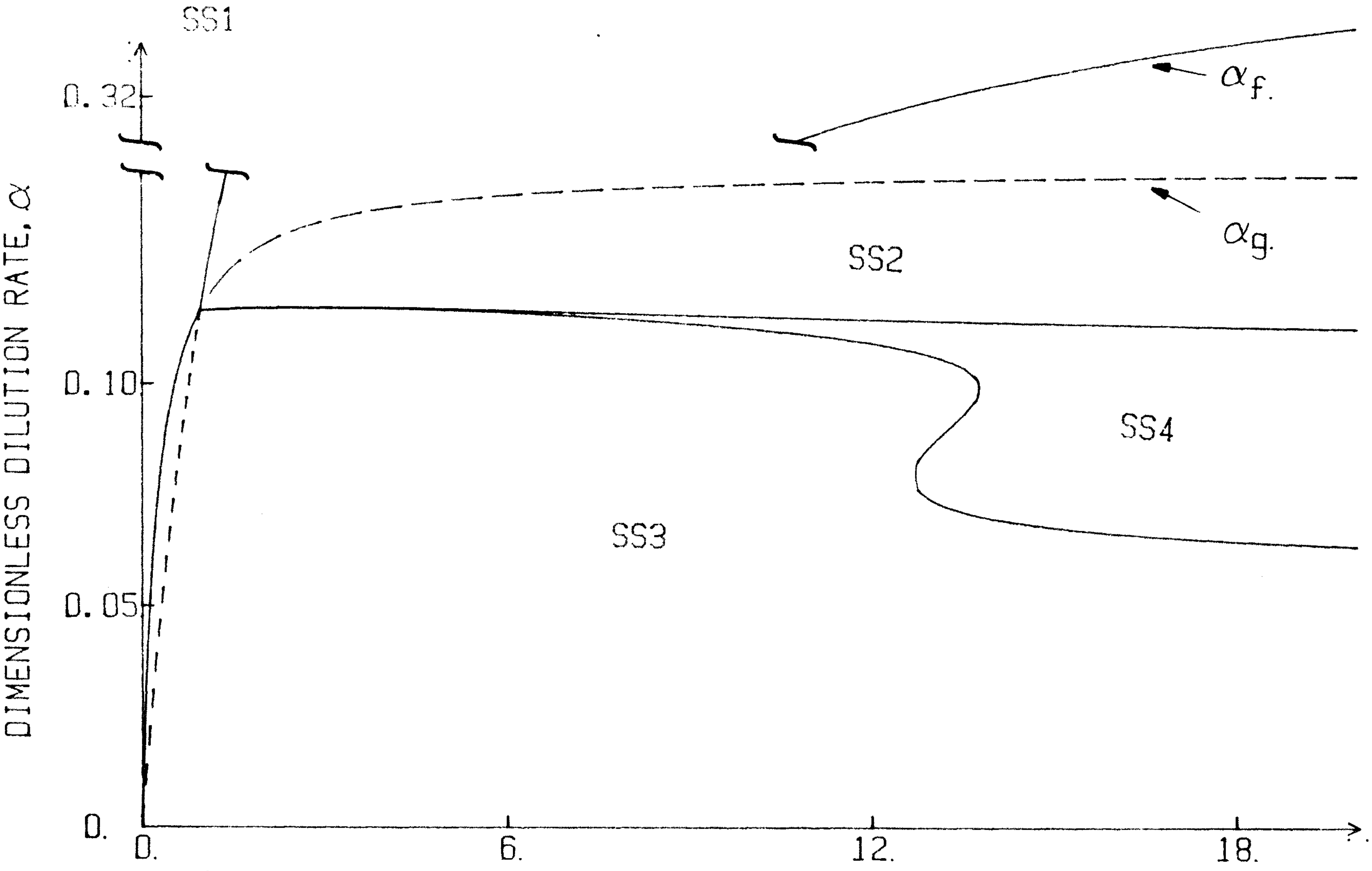
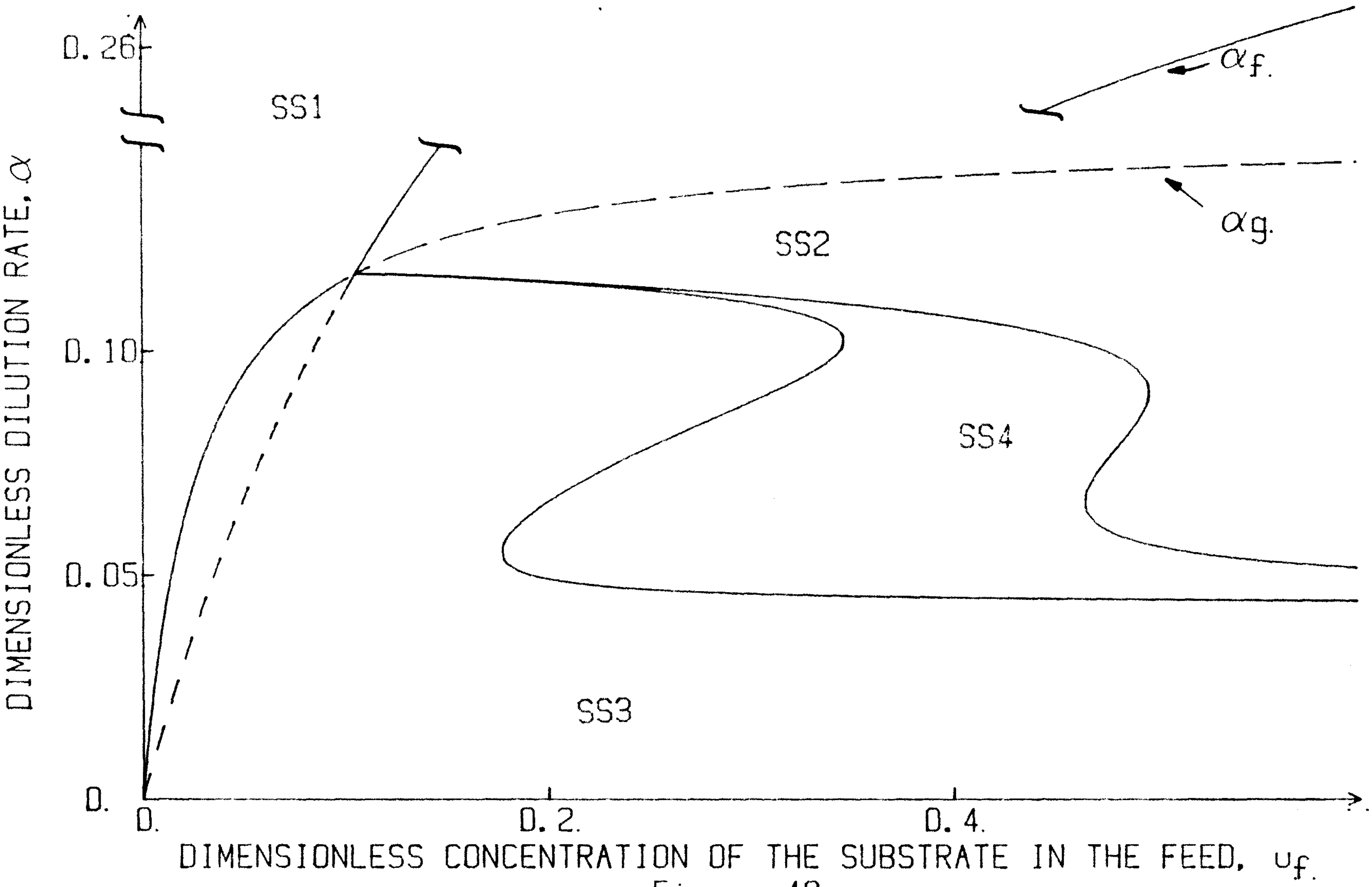

SS1
0.32
0.10
0.05
0.
DIMENSIONLESS DILUTION RATE, α
α_f.
α_g.
SS2
SS3
SS4
0.
6.
12.
18.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 48.



0. 26
0. 10
0. 05
0.
0.
0. 2.
0. 4.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
SS1
SS2
SS3
SS4
α_f.
α_g.

Figure 49.

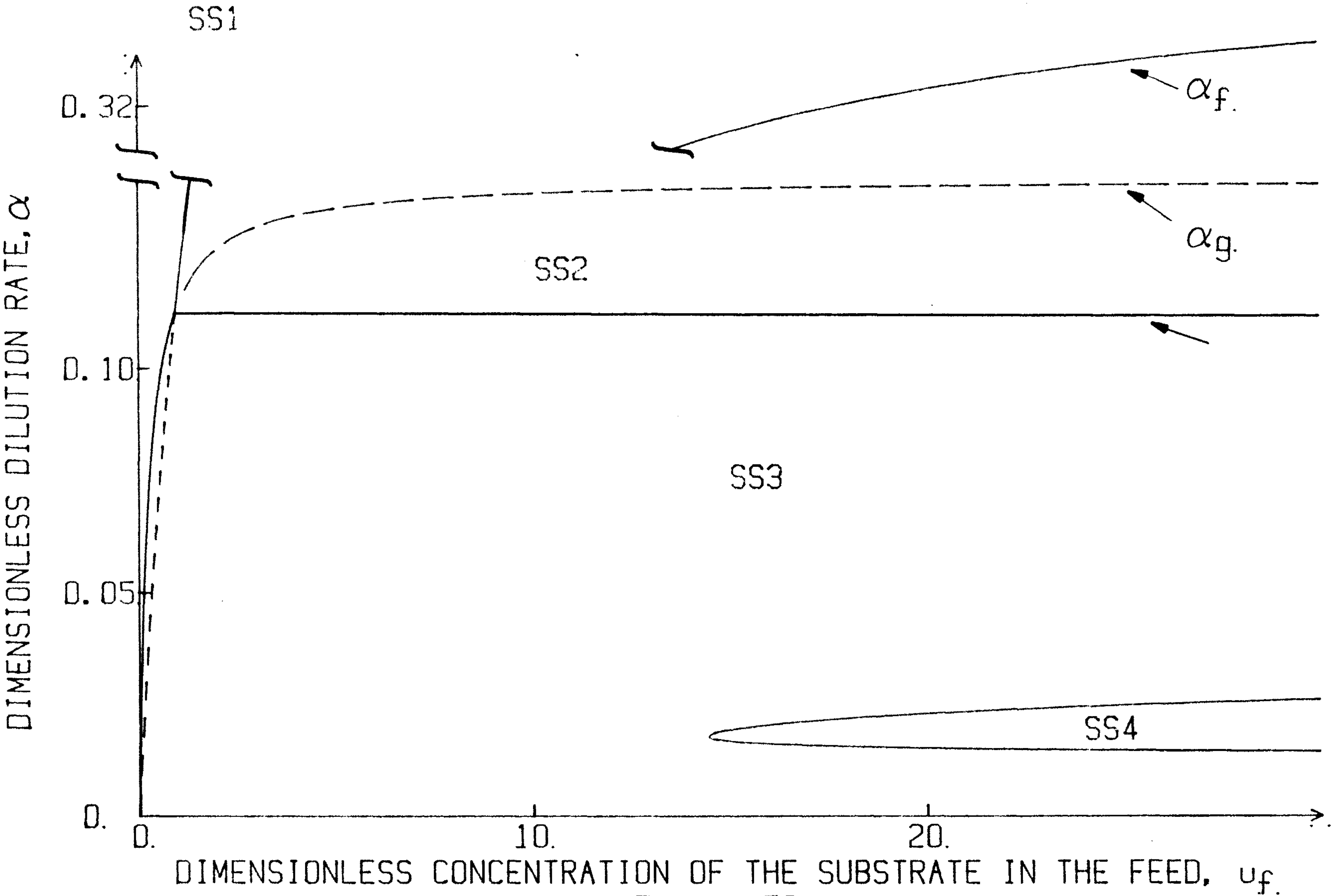

SS1
SS2
SS3
SS4
α_f.
α_g.
0.32
0.10
0.05
0.
0.
10.
20.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 50.

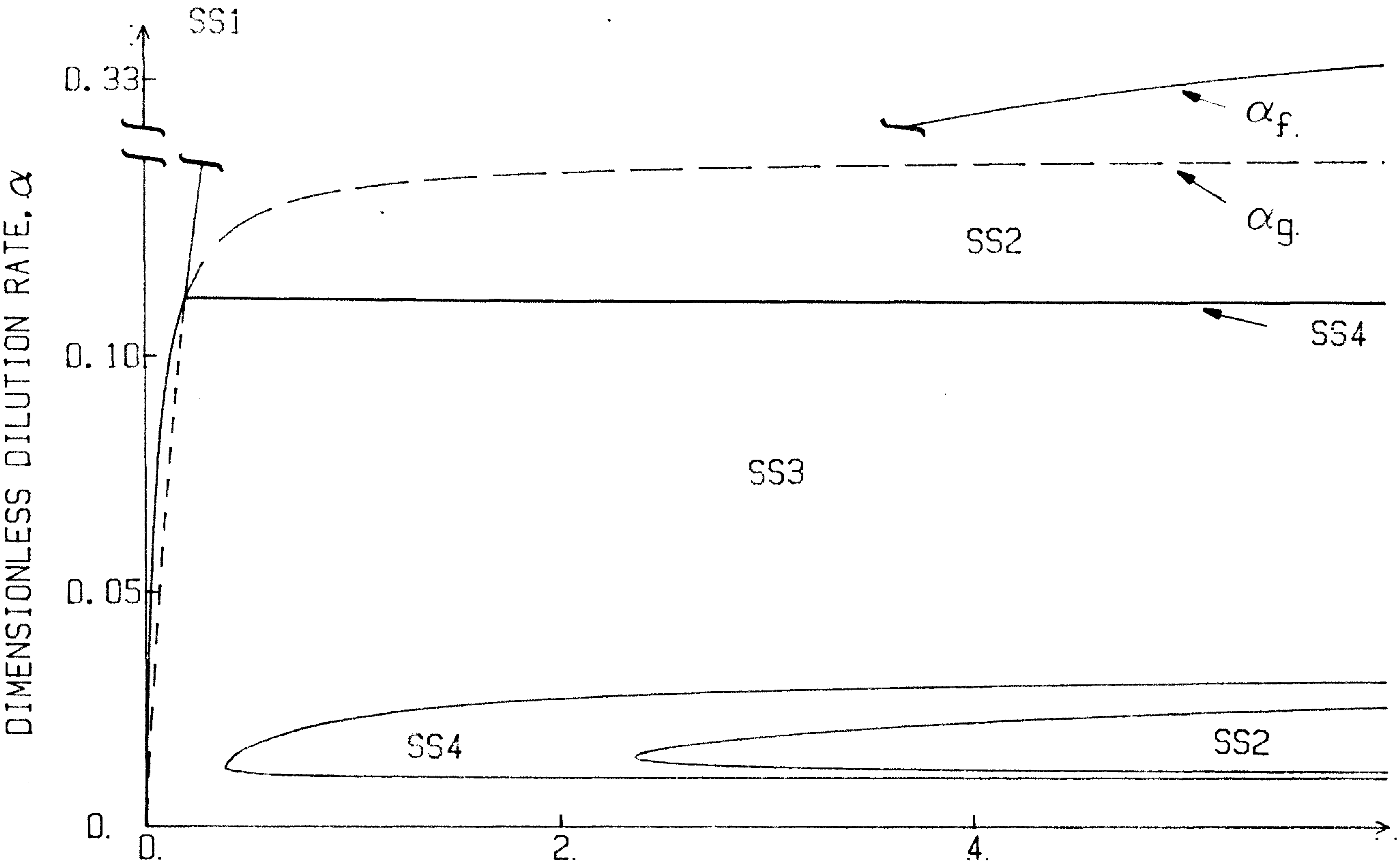

SS1
0.33
0.10
0.05
0.
0.
2.
4.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.
α_f.
α_g.
SS2
SS4
SS3
SS4
SS2

Figure 51.

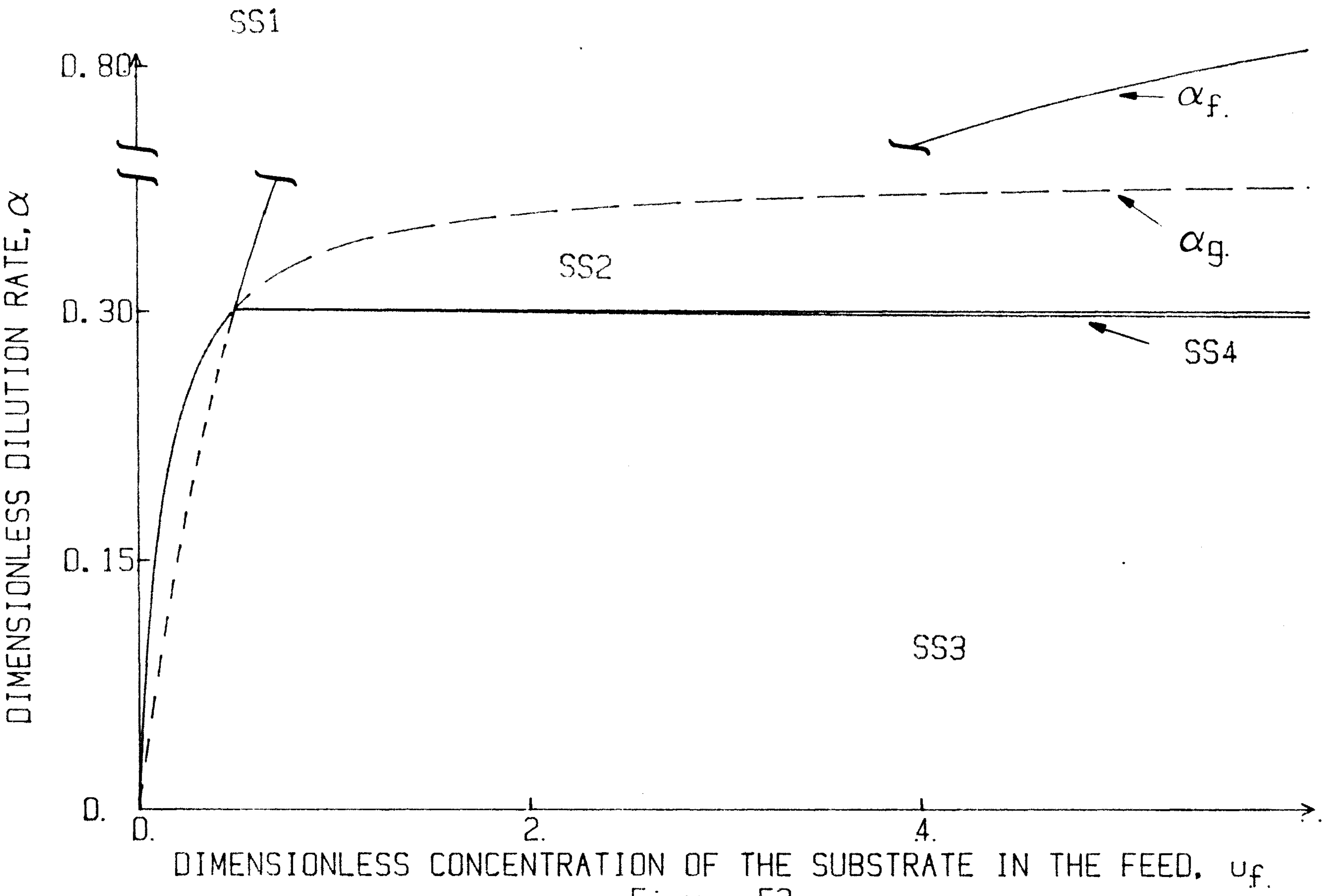

SS1
0.80
0.30
0.15
0.
DIMENSIONLESS DILUTION RATE, α
α_f.
α_g.
SS2
SS4
SS3
0.
2.
4.
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 52.

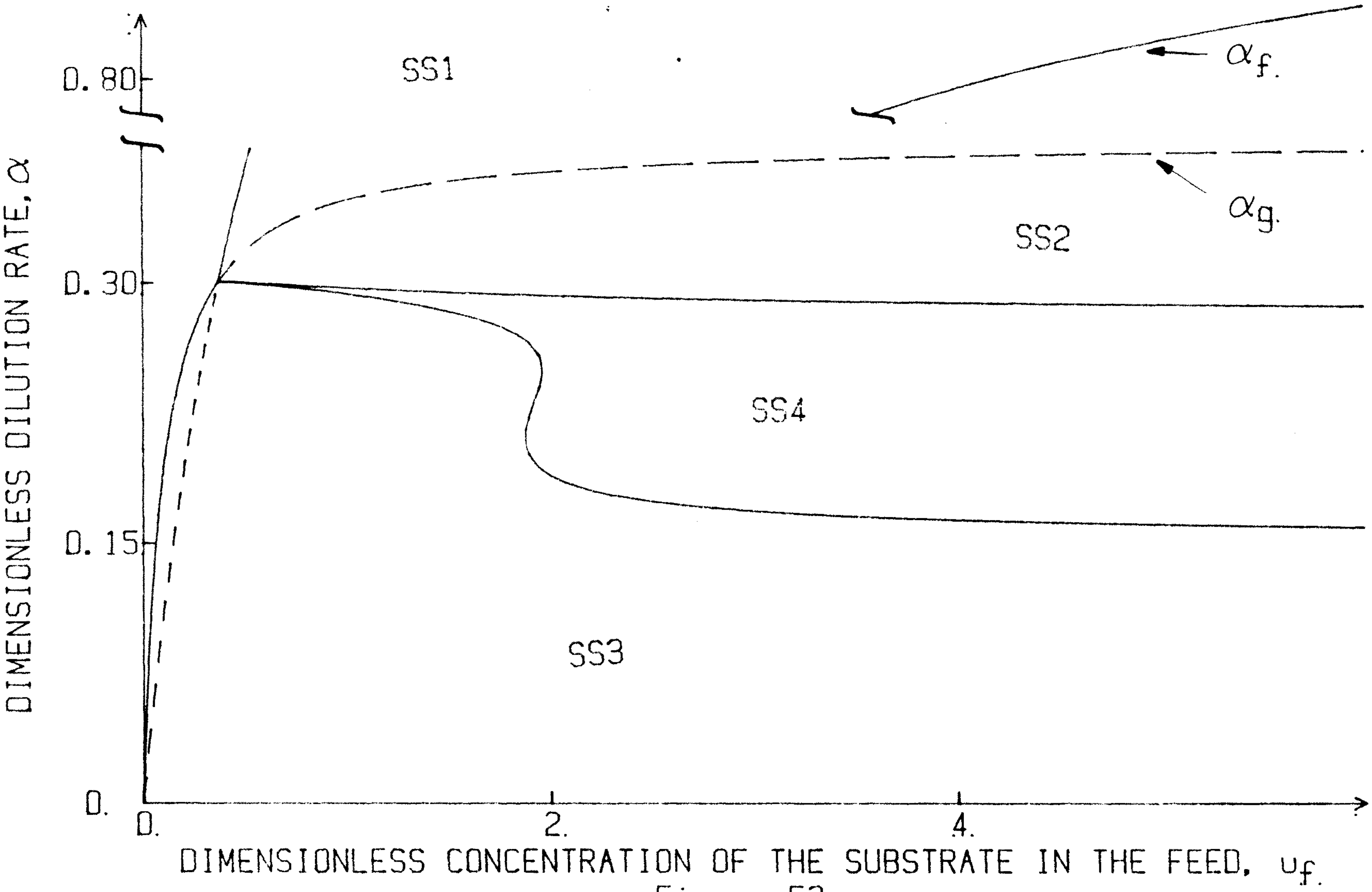

SS1
SS2
SS3
SS4
α_f.
α_g.
0.80
0.30
0.15
0.
0.
2.
4.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 53.

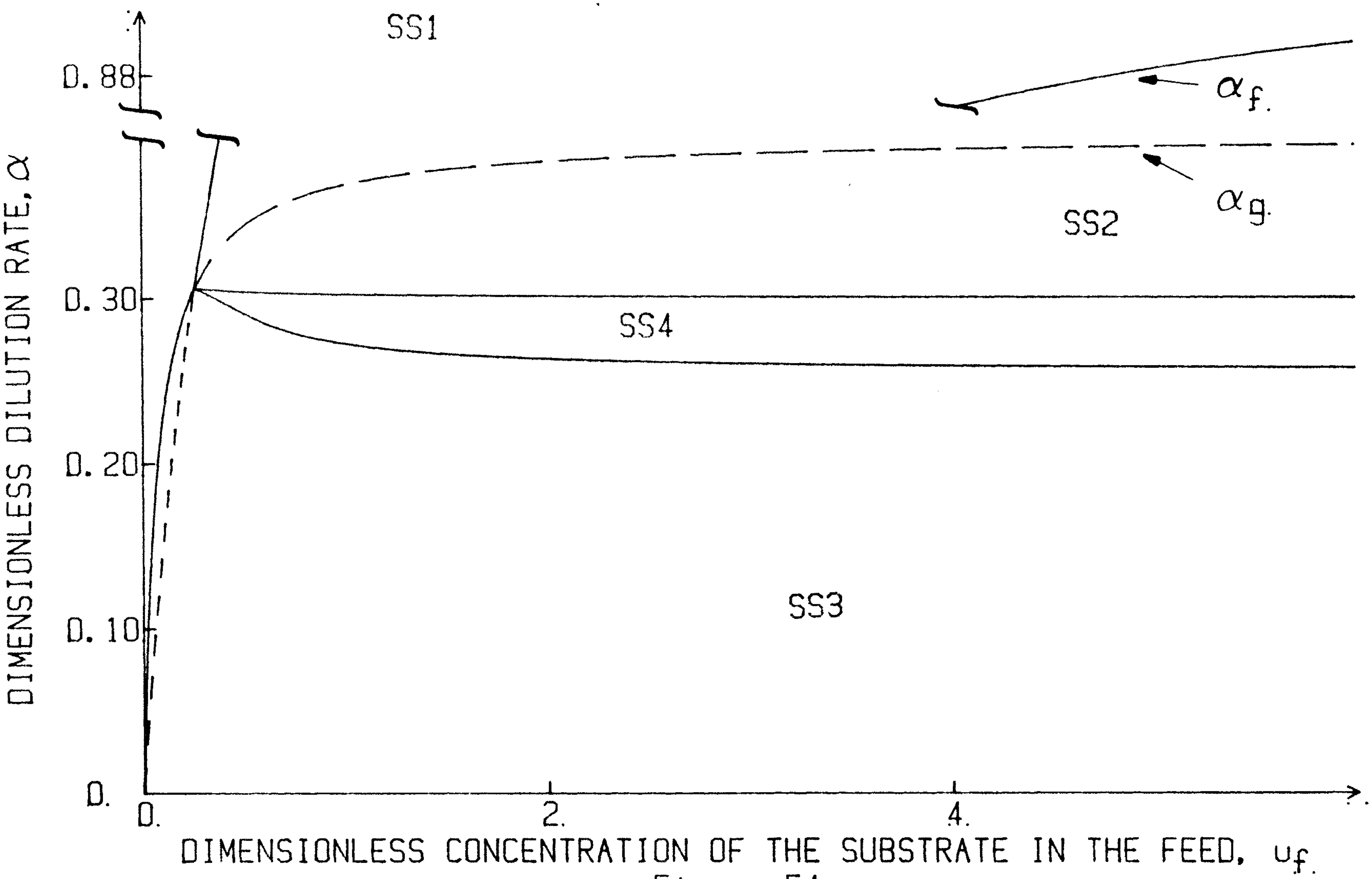

SS1
SS2
SS3
SS4
α_f.
α_g.
0.88
0.30
0.20
0.10
0.
0.
2.
4.
DIMENSIONLESS DILUTION RATE, α
DIMENSIONLESS CONCENTRATION OF THE SUBSTRATE IN THE FEED, u_f.

Figure 54.

DISCUSSION AND CONCLUSION

As it has been discussed in the beginning of this thesis, despite the predominance of pure culture techniques in the fermentation industry, there are reasons for which mixed culture techniques offer potential advantages and hence studying the dynamics as well as the ways for maintaining a culture of mixed species becomes important. Competition is a very common interaction between microbial populations and its simplest pattern is pure and simple competition. From the literature survey presented, one can see that it is impossible to maintain a mixed culture of pure and simple competitors in a steady state if the environment is homogeneous. However, in a homogeneous environment with properly varying inputs, pure and simple competitors can coexist in an oscillatory mode. Nevertheless steady state (or at least non-oscillatory) operation is usually preferable, and hence the investigation of possible steady state coexistence of pure and simple competitors becomes important.

The present study has shown that in a system of two interconnected chemostats, it is possible to get steady state coexistence of two pure and simple competitors. The idea for this thesis originated from a short communication published in the literature, but various aspects of the problem either not treated or even not mentioned there have been studied here.

The main necessary (but not sufficient) condition for coexistence is that the conditions in the two vessels must be different and such that in one vessel they favor the growth of one competitor and in the other vessel they favor the growth of the other competitor.

The interconnection of the two vessels is important because it implies that any species surviving in one reactor has to do so in the other as well. If the effluent of the first reactor goes into the second, but there is no recycle from the second to the first, then steady state coexistence may occur but it will be for the second chemostat only. In fact, if both reactors (without recycle) are initially inoculated with both species, and the conditions are picked in such a way that they favor the growth of species A in the first vessel and species B in the subsequent vessel, what will happen is that species A will exclude species B from the first vessel, but in the second vessel there will be coexistence, since species B will never be able to exclude species A (although B grows faster) due to the continuous inoculation of the second vessel with species A coming from the first vessel. This result though is not really optimal because in a sense, part of the volume of the system has to be underused (for growing one of the competing species). One wants to have the mixed culture in the entire volume used and thus, recycle becomes important and necessary. Furthermore, this general configuration provides further insight as to why coexistence occurs. Since coexistence proved to be possible, one can easily attribute it to the spatial heterogeneity of the environment. Spatial heterogeneities may arise in many other cases as well; for example due to incomplete mixing in a single reactor, due to the non-ideality of flow in a reactor or even in a distributed medium (e.g. a tubular reactor). Hence, the findings of the present study suggest that there are other reactor configurations that may lead to steady state coexistence, something which of course has to be investigated in future studies.

There are some (implicit or explicit) assumptions made in this study and they have to be stated here clearly.

(i) Each of the two reactors is assumed to be perfectly mixed. Hence each of the two subenvironments is homogeneous.

(ii) No cell attachment occurs on any solid surface, i.e. neither on the walls of the vessels or on the walls of the interconnecting tubes.

(iii) The tubes are assumed to be short enough or the flow fast enough, so that no growth occurs in them, and as a result the composition in the exit of one vessel is the same as the composition entering the following vessel.

(iv) It is also assumed that the rate-limiting substrate entering a vessel is the same as in the fresh medium, which implies that the maximum specific growth rate and the saturation constant of either population are the same in both vessels.

(v) The temperature in both vessels is assumed to be the same and not changing.

(vi) The competing species grow according to the Monod model.

Monod's model was used for two reasons: a very large number of populations are known to grow according to it, and it is the simplest model for expressing the specific growth rate. Since most of the existing expressions for the specific growth rate can under certain conditions reduce to the Monod expression, it is expected that any model for the specific growth rate will predict coexistence of two pure and simple competitors in a configuration of reactors like the ones considered here. This is only a statement concerning the qualitative and not the quantitative behavior of other models. Specific studies have to be performed. Nevertheless, in some cases like the Andrews

[24] substrate inhibition model, one should expect that under low concentrations and for comparable values of the model parameters, even the quantitative results will be the same (or analogous) with those obtained in this study with Monod's model.

The general configuration of the system involved two interconnected vessels being externally fed with nutrient medium containing the rate-limiting substrate at different concentration levels;this was called the general system. Two special cases of the general system were also studied in detail. The splitting system in which both reactors are externally fed at the same concentration level and the non-splitting system in which the externally fed medium goes in one reactor only. In all configurations it was found that there is a domain in the operating parameters space in which stable coexistence in a steady state occurs. Given the fact that in continuous operation each reactor must have an input and an output stream, analyzing the non-splitting system and showing that coexistence does occur the study provided an answer to the following question: given two reactors, how many additional streams are needed in order for the coexistence of two pure and simple competitors to be possible throughout the system? The answer is one, the recycle stream. Additional external streams are not needed although they may be desirable in order to extend the domain of coexistence in the parameters space. Furthermore, additional external streams with no recycle can never lead to coexistence throughout the system. For a configuration involving more than two vessels the findings of the present study suggest that two pure and simple competitors will be able to coexist in all vessels provided that they are properly interconnected (the answer to what is proper interconnection is not an obvious one) and that in some of the vessels one population grows faster while in the remaining vessels the other competitor has the advantage.

It should be emphasized that it is not the reactors configuration alone that makes coexistence possible. The type of organisms plays an important role also. That is if one of the two competing species grows faster than the other under all conditions then there is no reactors configuration leading to coexistence unless the slower growing population has another advantage, for example it exhibits wall attachment [28].

The model equations were written in a dimensionless form something which drastically reduced the number of parameters to eight from the thirteen appearing in the original dimensional equations. The eight parameters are ω, φ, β, α, u_f, R, γ and η. The type of the organisms and the identity of the rate-limiting substrate determine the values of ω and φ that were called system parameters (by system implying the physical one). The parameter β was called the design parameter since it stands for the ratio of the volumes of the two reactors. It is realized of course that in reality β stands for the ratio of the volumes of the culture in the two reactors rather than for the ratio of the physical volumes of the two vessels. Since usually a reactor is filled with liquid up to a certain extent so that the vessel does not overflow and so that sufficient room for effective mixing is allowed, if both vessels are filled at same percentage of their physical volume then β is indeed the ratio of the physical volumes of the two reactors. In any case though β is a parameter that is determined mainly by the design of the system. The parameter u_f is a dimensionless concentration of the externally fed substrate which is the actual concentration in the feed in the cases of the splitting and the non-splitting system; the recycle ratio is R; the ratio of the flow rates of the external feed streams is γ; the ratio of the concentrations of the rate-limiting substrate in the external feed streams is η. The parameter α stands for a dilution rate in the first vessel based on the external feed stream; it is not the actual dilution rate even though it is refereed to as such sometimes for simplicity (e.g. in labeling the y axis of the operating diagrams). In the case of the non-splitting system the number of parameters reduce further since $\gamma=\eta=0$. In the case of the splitting system, there is one parameter less than in the general case since it is $\eta=1$.

By using arguments similar to those of Aris and Humphrey [23] the dynamical dimension of the system was shown to be actually four instead of six. What this implies is that if the initial conditions in the two vessels are chosen in such a way that they satisfy the stoichiometric equations then the system is indeed 4-dimensional at all times; if the initial conditions are randomly chosen then the trajectories of the system very quickly (relative to the duration of the transients) fall on a 4-dimensional manifold of the 6-dimensional space. This reduction offers a substantial simplification for the analysis.

Despite the complexity of the system the local stability of all possible steady states was studied analytically. Furthermore, a number of conditions (sometimes both necessary and sufficient, sometimes only necessary) which need to be satisfied so that a possible steady state arises and is meaningful were also analytically derived. The results of the analysis provided a very good guidance for reducing the amount of numerical work and for judging if some features of the numerical results were general and expected or due to the values used for the parameters. The numerical results are presented in the form of operating diagrams, actually projections of them in the α-u_f plane. Although not presented, a large number of computer simulations (integration of the model equations) were performed in order to check if the results of the local stability analysis hold globally as well, and this was confirmed. The results of the simulations showed also that the system never exhibits any type of damped oscillatory behavior something which the analysis could not exclude only in the case of the coexistence steady state. The numerical results also revealed that none of the possible steady states exhibits any multiplicity and that all steady states are mutually exclusive.

It was found that in the case of the splitting system, if $\beta\gamma=1$ the environment becomes spatially homogeneous and hence if the specific growth rate curves have the proper mutual disposition (i.e. they cross each other), coexistence is only a mathematical possibility since it arises for a discrete value of α only. The results in this case are exactly the same as those of the single chemostat case.

An interesting finding (analytical result) is that in the coexistence steady state the values of the substrate concentrations are independent of the concentrations at which the substrate is supplied to the environment while this is not true for the biomass concentrations (or equivalently the population densities). Although the results of this study should be very cautiously (if at all) extended to the very complex ecological systems one could at least raise the following question. In many cases the judgement as to whether a chemical is dangerous (or harmful) for a liquid habitat or not, is based on the concentration level in that habitat. This, according to the aforementioned finding of this study, could be misleading since it could be possible that the concentration level of the chemical remains constant while the population densities change and possibly one (or some) of them decreases so much that it is practically extinct while one (or some) other population grows too much. If one relies on concentration measurements only (and does not monitor the population densities) he will not realize a catastrophy before it is too late. This could be a possible explanation for the situations where in marine habitats accepting water containing phosphorus from fertilizers an ubrupt and unexpected increase in the algal growth occurs. Again, the thoughts above are presented with a lot of reservation but one wonders if measurements of the concentration levels of the chemicals only, are safe or enough for environmental purposes.

The results of the analysis have indicated what are the ranges of α values that could lead to coexistence. These results proved to be much less strict for the α

values than what they should. This was expected to be so since they were derived on the basis that the values of the variables must be real. Further restrictions on the α values are needed so that $x_i>0$, $y_i>0$ and $0<u_i<u_{if}$, $i=1,2$ but these could not be analytically derived due to the complexity of the expressions. The results of the numerical studies have indicated that the upper bound of α values for coexistence is always $K\alpha_c$ while the lower bound of values of α for coexistence depends on the particular system. More specifically it was found that the lower bound is,

α_c	for the non-splitting system
$\dfrac{\alpha_c}{\beta\gamma}$	for the splitting system when $\beta\gamma>1$
α_c	for the splitting system when $\beta\gamma<1$
$\dfrac{\alpha_c}{\beta(\gamma+1)}$	for the general system when $\beta\gamma>1$
$\dfrac{R+1}{[R(\gamma+1)+1]}\,\alpha_c$	for the general system when $\beta g<1$

It was possible only for the boundary of the domain of SS1 in the α-u_f plane to be analytically derived. This boundary is formed by segments of the $Kf(u_f)$ and $Kg(u_f)$ curves for the splitting and the non-splitting systems while for the general system the boundary is formed by segments of the α_f and α_g curves. It was proved that the

$Kf(u_f)$ and $Kg(u_f)$ curves cross each other while the crossing of the α_f and α_g curves it was found numerically but an analytical proof as to whether they always have to cross was not possible to obtain. In all cases the crossing point of the $Kf(u_f)$ and $Kg(u_f)$ or the α_f and α_g curves is also a point on the boundary of the domain of coexistence. Except for the case of the general system, it was proved that this has to be so. Hence the crossing point of the two curves in all cases is a steady state bifurcation point.

When the recycle ratio becomes very large one expects that the environment tends towards homogeneity and hence coexistence must become very difficult (if not impossible) to get. The operating diagrams suggest that at low u_f values this is so. On the other hand, it was found that at large recycle ratios and large u_f values the model still predicts coexistence to be possible in a domain of the operating parameters space. This result is not really contradictory to the theory if one takes into account that very high u_f values are not necessarily physically possible and if they are one cannot talk about substrate limitation of the growth rate (the substrate is present in abundance) and hence competition does not really occur and there is nothing prohibiting the coexistence of species using a common substrate but not being rate-limited by it. In fact, at high concentrations of the substrate, Monod's model reduces to a constant and the original equations reduce to linear ones and it is obvious from them that the two populations do not interact. In reality though at very high u_f values it is certain that some other substrate becomes rate-limiting and the original formulation of the problem is no longer valid. Hence the results at very high u_f values of the present study are mathematical rather than possibly physical

The effects of the various parameters were discussed in detail in each one of the three parts of this thesis. Some of the general observations made are that in general it is preferable to choose a β such that it is $\beta<1$ along with $\beta\gamma<1$; if a $\beta>1$ is chosen after all it is better to at least also have $\beta\gamma>1$. More detailed observations are not repeated here. There is one thing which needs to be clarified at this point. By "preferable" those sets of parameters are characterized that result in a broad domain of coexistence in the α-u_f plane, and they are not necessarily optimal. The present study was not really on the optimal design and optimization in this case may have a number of different (and possibly conflicting) objectives such as high substrate utilization (low u_2), high biomass productivity, comparable population densities of the two species etc.. Because of the large number of parameters (up to six) the answer to the optimization problem is not expected to be either simple or unique (due to the large number of objectives).

From the foregoing discussion it is clear that it is repeated with emphasis that the results of coexistence refer to two competing species. An obvious question is if in the reactor configurations considered here it is possible to get coexistence of three or more species. The answer seems to be no but some work has to be done in order to really prove it.

Taking into consideration the fact that this study showed that whenever coexistence occurs each one of the competitors grows faster in one of the two vessels it suggests the following problem for study: Can three pure and simple competitors coexist in a steady state throughout a configuration of three interconnected vessels? This problem will be more complicated than the one solved here not only due to the increase in the number of equations but also due to a number of different possible recycle streams for interconnection. If coexistence proves to be possible one would be able to safely generalize for the case of n-species and it will be a proof to the claim made by ecologists that "one prevailing competitor per nitch (or patch) leads to an overall coexistence".

There is one more problem that the present study suggests. It is the problem of studying pure and simple competition in a tubular reactor (distributed medium). A tubular reactor requires in many cases a smaller volume in order to perform the same duty with a number of stirred tank reactors. There is little doubt that the existence of some recycle from the exit to the entrance will lead to coexistence under some conditions. The interesting thing will be to investigate if the recycle is necessary. Microorganisms are known to posses sensors for detecting the available nutrients and in some cases they exhibit chemotaxis, that is movement towards regions of high nutrient concentration. Chemotaxis will imply a movement of microorganisms towards the entrance of the tubular reactor and such a movement provides a degree of backmixing. The question is if the backmixing due to chemotaxis is enough to lead to coexistence in which case the recycle will prove to be not necessary even when there is plug flow.

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