ABSTRACT

Title of Thesis: Coexistence of Three Pure and Simple Competitors
in Four Interconnected Bioreactors

Ming Wu, Master of Science in Chemical Engineering, 1990

Thesis directed by: Dr. Basil C. Baltzis

It is known that a homogeneous environment having invariant inputs cannot allow for steady state coexistence of any number of pure and simple competitors. However, it has been proven that two pure and simple competitors can coexist at a steady state in two interconnected chemostats, if the conditions are such that they allow a different species to grow faster in each one of the two vessels. It has been also shown that three pure and simple competitors cannot coexist in three interconnected chemostats, even if the conditions are such that a different population could grow faster (have the competitive advantage) in each chemostat. The present study investigates theoretically whether the spatial heterogeneities created by four interconnected chemostats may lead to coexistence of three pure and simple competitors. Computer simulations indicate that there is the domain of coexistence of three species (XYZ) between domains of coexistence of two species. If the XYZ domain is between an XY and a YZ region, species Y grows faster than X and Z in two out of the four chemostats, for parameter values leading to XYZ coexistence. It is then concluded that spatial heterogeneities can lead to steady state coexistence of three pure and simple competitors. It is also concluded that N pure and simple competitors cannot coexist in N interconnected reactors; but one could speculate that if there are N competitors,

in order for them to coexist in an environment, this environment must be comprised of two subenvironments each one of which, should be able to maintain N-1 species. In configurations of chemostats then, it seems that one needs 2^{N-1} vessels. This is a necessary but not sufficient condition. The results for the three species system, are presented in two-dimensional operating diagrams and the effect of parameters on the behavior of the system, is studied to a certain extent.

COEXISTENCE OF THREE PURE AND SIMPLE COMPETITORS IN FOUR INTERCONNECTED BIOREACTORS

by

Ming Wu

Thesis submitted to the Faculty of the Graduate School of

the New Jersey Institute of Technology in partial fulfillment of

the requirements for the degree of

Master of Science in Chemical Engineering

1991

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ACKNOWLEDGMENTS

I am very grateful to my advisor, Dr. Basil C. Baltzis. Undoubtedly, without his guidance and helpful assistance, it would had been impossible for me to complete this research.

Special thanks should go to Mr. Cheng-Ming Kung for his valuable suggestions. Special thanks should also go to Dr. Lewandowski and Dr. Knox for their final correction of this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION

It is well known that microorganisms are agents that cause disease and spoil food. They also perform many functions that are beneficial to man. In nature, they are important geochemical agents which were involved in the formation of coal, oil, and some mineral deposits. In fact, the biosphere could not function without microorganisms, and the higher organisms, man included, could not exist as we know them. Today, microoganisms play a more and more important part in many industrial operations. It has been found that the activities of microorganisms have successful applications in quite a number of areas [9]. In biochemical engineering, they can be used to increase the value of raw materials. In sanitary or environmental engineering, they can be used to decompose sewage, solid, and industrial wastes. They can be also employed in ore and fuel processing in order to leach certain harmful or useful elements from their ore or remove pollutant-generating substances from fuel. Moreover, men might eventually employ microbial activities for bioconversion of solar energy.

Microbial populations must have chemicals and available energy in order to grow and proliferate. The chemicals provide them with elements (e.g., carbon, oxygen, nitrogen, sulfur, phosphorus) from which biological molecules are formed. Available energy is needed to synthesize these molecules and to maintain life. These common needs cause competition, which takes place in all but the simplest ecosystems.

Microoganisms can be divided into osmotrophic and phagotrophic organisms. Osmotrophic organisms (e.g., bacteria, yeasts, molds, and microalgae) obtain chemicals by molecule-by-molecule or ion-by-ion transfer of the chemicals across their cell membranes, while phagotrophic organisms (e.g., many protozoan populations) obtain chemicals by ingesting and digesting particulate 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 particulate matter, and populations of osmotrophic microorganisms are likely to compete for resources of chemicals. In designing a bioprocess then, one can apply the classical chemical reactor theories, but at the same time, microbial interactions have to be taken into account, if a mixed culture is involved. Mixed cultures which are composed of different types of microbial species can be used in certain industrial operations, notably, in wastewater treatment and the fermentation industry. Using mixed cultures in waste treatment seems necessary, since: (1) it is impossible that a single species can function over a wide range of environmental conditions; (2) it is non-economical to maintain a pure culture in an operation which involves large volumes. Some potential advantages for using mixed cultures in fermentations have been discussed by Fredrickson [7]. It should be also added that, what is characterized as a pure culture, may actually be a mixed one, due to mutations of the original strain.

It is well known that microbial populations inhabiting a common environment interact between one another in a number of different ways. Microbial interactions have been classified into: direct and indirect, positive and negative.

Additional important differences between organisms appear in the way they satisfy their needs for specific elements. The element most often considered is carbon.

Heterotrophic microorganisms which use organic compounds phagotrophically or osmotrophically in order to obtain carbon, will not interact (as far as carbon is concerned) with autotrophic microorganisms, which use carbon dioxide as their carbon source. But interactions between heterotrophs and autotrophs will arise, if they use common sources such as nitrogen, phosphorus, and so on. Microbial competition is an interaction which arises in all but the simplest ecosystems since it is the result of the common needs of microbial species for chemicals and available energy. According to Baltzis [2], of all microbial interactions, competition is the one which has been studied the most. But competition will not necessariy arise if two microorganisms use a common nutrient source. For example, two heterotrophic microorganisms which use a certain organic compound as a carbon and/or energy source, will not compete for it if this compound is present in abundance.

A rigorous definition of competion as well as a classification of its patterns has been given by Fredrickson and Stephanopoulos [8]. Two microbial populations compete for a resource ρ if and only if: (1) both populations use, but do not necessarily require ρ, and (2) resource ρ has a dynamical effect on at least one of the populations. Resource ρ has a dynamical effect on a population if its availability (concentration), at any time, has a significant effect on the net growth rate of the population.

In pure and simple competition which is the subject of the present thesis, there is only one nutrient competed for, and competition for this nutrient is the only interaction between the populations.

There are various patterns of microbial competition, and a classification of them, has been given by Baltzis [2].

The chemostat is a biological reactor. This is a well-stirred vessel which is continuously supplied by nutrient medium S. The culture volume in the vessel is kept constant by overflow of culture. Evidently, a steady state in which growth and reproduction of a population are exactly balanced by washout and other loss processes, is possible in the chemostat. Use of the chemostat is called continuous culture technique.

The topic of this thesis deals with the dynamics of pure and simple competition of three populations. It is known from the literature, that two or three microbial populations competing purely and simply for a common substrate in a single vessel which is spatially homogeneous, cannot-under any conditions-coexist in a steady state. However, Kung [17] has shown that two pure and simple competitors can coexist in configurations of two interconnected chemostats. On the other hand, Chang [5] has proven that it is impossible for three pure and simple competitors to coexist in three interconnected chemostats. The main question raised here, is whether or not three pure and simple competitors may coexist in configurations of four interconnected chemostats. This situation is the subject of the present study.

Chapter 2

LITERATURE REVIEW

The dynamics of a chemostat in which two populations of microorganisms grow competing for the same limiting nutrient has been examined by several researchers over the past years. The nonexistence of the coexistence steady state in a single vessel, has been amply demostrated by experiments. In fact, the notion that populations which simply compete for the same resource cannot coexist indefinitely in a habitat is sometimes stated as a basic ecological "law" called *Gause's principle* or *the competitive exclusion principle* [Hardin (12)].

A classic analysis of pure and simple competition in a chemostat with constant inputs was made by Powell [20]. He was interested in the ability of this apparatus to select one population over several initially present, and the basis of its selective power. The questions that his analysis answered were: Can the chemostat be operated with constant inputs so that two pure and simple competitors coexist? 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 experimentally or theoretically by many other researchers.

Jannasch [15] studied competition between *Escherichia coli* and a marine *Spirillum sp.* in a chemostat fed with lactate-supplemented seawater. He found that the density of *E. coli* declined toward zero if the dilution rate was low, whereas the density of

Spirillum sp. declined if the dilution rate was high.

Meers [19] performed experiments with a mixed culture of *Bacillus subtilis var. niger* and *Torula utilis* under magnesium-limiting conditions in a chemostat. His experiments show that *Bacillus subtilis* replaced the yeast at the higher dilution rate, but the reverse was true at the lower dilution rate. Coexistence was not found.

Harder and Veldkamp [11] investigated competition for lactate by two species of marine psychrophilic bacteria in a situation where the chemostat dilution rate and temperature were varied. At $-2°$C population O, an obligate psychrophile, excluded population F, a facultative psychrophile, at all dilution rates, and at 16°C population F excluded population O at all dilution rates. At 4°C and 10°C, however, the outcome of competition was dependent on the dilution rate; population O was excluded at low dilution rates and population F at high rates. These results, predicted in part from data on pure cultures, are important because they show whether or not a certain level of an externally imposed parameter confers a competitive advantage on a population, and if this advantage depends on the levels of the other parameters imposed.

Hansen and Hubbell [10] grew bacteria under tryptophan-limited conditions in a chemostat. Their conclusions are that coexsitence is impossible and that outcomes of competition can be predicted from pure culture data. Jost *et al.* [16] studied competition between *Escherichia coli* and *Azotobacter vinelandii* for glucose. They showed experimentally that the *E. coli* always won if only the two bacterial populations were present in a chemostat.

After considering the competition between two species, Powell [20] concluded that there are no operating conditions which lead to steady state coexistence and that the winner is determined by the ratio of the maximum specific growth-rate and the saturation constants of two species. The aforementioned two parameters appear in the Monod model, which Powell used to describe the specific growth-rate of the two populations. Using Monod's model, Hsu *et al.* [13] studied in a mathematically rigorous fashion the situation where n species compete for a single resource in a chemostat. They showed that under given conditions of operation no more than one population can survive in a steady state. Fredrickson and Stephanopoulos [8] in an excellent review paper concluded: (1) if the specific growth-rate curves of two populations do not cross each other at any positive value of the concentration of the substrate competed for, Powell's conclusion stands as stated above. (2) if the specific growth-rate curves cross each other, the winner is determined by the operating conditions (e.g., the concentration of a limiting nutrient and dilution rate). There is a unique value of dilution rate at which steady state coexistence of two populations is predicted, if the specific growth rate curves cross each other. In practice, however, a physical parameter such as a chemostat dilution rate, will always exhibit random variations with time, and the variations may even be biased. Stephanopoulos *et al.* [23] modeled the random fluctuations in the dilution rate as white noise and showed that one competitor will be excluded from the chemostat if the intensity of the noise in dilution rate and the bias of mean of dilution rate are not both zero. Moreover, they showed that there is a finite probability that either population may be excluded. If the intensity of the noise and the magnitude of the bias are both small, then the drift toward exclusion of a population will be slow, but it will always occur. In fact, the aforementioned results have been extended to any number of pure and simple competitors.

From the discussion above and without proper caution, one could generalize and claim that pure and simple competitors cannot coexist. In 1961, however, Hutchinson [14] first challenged the "*competitive exclusion principle*" and pointed out that the "principle" cannot be a general ecological law. He examined planktonic algae which require essentially the same nutrients from a commonly held resource pool. Classical ecological competition theory predicted that, under idealized conditions, the species best able to acquire and use the limiting resource should displace all other competitors. If this prediction were correct, lakes and oceans should contain few species of algae. But marine and fresh water usually contain more than 30 species of phytoplankton in apparent competitive coexistence within any small amount of water. Hutchinson termed this discrepancy between nature and theoretical prediction the "*paradox of the plankton*". Many theories have been proposed to explain this. One class of explanations emphasizes that the spatial complexity and temporal variability of nature are a violation of the idealized conditions assumed in classic theory. A second class, stresses the possibility that differing mortality rates, from differential grazing and settling, may minimize interspecific competition. Another theory hypothesizes that, even under idealized conditions, coexistence should be possible if species differ in their ability to acquire and utilize a resource.

Aris and Humphrey [1] studied the case in which the resource competed for has negative (inhibitory or toxic) effect on the growth of the competitors, especially when its concentration is high; in this situation, coexistence occurs only for discrete values of the chemostat dilution rate, and thus again it cannot be practically realized.

Stephanopoulos *et al.* [24] analyzed a periodically forced chemostat and examined the possibility of coexistence of two pure and simple competitors. They found that coexistence is in fact possible, in the form of sustained oscillations. Nonetheless, the exit of the unit will carry high substrate concentrations for part of the cycle, something totally undesirable especially in situations in which the substrate is a toxic or hazardous substance which is to undergo biodegradation in the process unit. Stephanopoulos and Fredrickson [22] showed that if two pure and simple competitors compete for the same resource in two interconnected chemostats, both of which are externally fed with sterile medium, steady state coexistence (in both vessels) may occur provided that the specific growth rate curves of the two competitors have a crossing-point.

Jost *et al.* [16] showed experimentally that the competition of *Escherichia coli* and *Azotobacter vinelandii* for glucose (in which the *E. coli* always won if only the two bacterial populations were present) ended in coexistence when the ciliate *Tetrahymena pyriforms*, which preys upon both kinds of bacteria, was present. Baltzis and Fredrickson [4] proved that coexistence limit cycles (sustained oscillations) do not occur in non-predator-prey systems. But, after studying a food chain involving two pure and simple competitors, competing for a substrate produced in a chemostat by the growth of a host population, they found that the two competitors as well as the host can coexist in a limit cycle under some operating conditions. The difference between the food-chain and non-food-chain systems is not due to the presence of a third population, since such a presence does not change the competition pattern but rather, it is the character of the substrate competed for.

Baltzis and Fredrickson [3] studied theoretically the case where two microbial populations compete for a single resource in a chemostat but one of them exhibits attachment to the walls. They used the Topiwala-Hamer model and a model which assumes that the attachment of microbial cells to the solid surfaces is a reversible process. They found that the first model does not allow the population that exhibits wall attachment to wash out from the chemostat, in contrast to the second model (which nevertheless reduces to the first one in the limit). They showed that in most cases, and for both models, the two competitors can coexist in a stable steady state for a wide range of the operating parameters space. Because of the attachment of the cells to the walls, the environment is no longer homogeneous. Therefore, the coexistence of two pure and simple competitors in a steady state, can be attributed to the spatially heterogeneous environment, as in the study of Stephanopoulos and

Fredrickson [22], dicussed before (two coupled chemostats).

It now becomes clear that pure and simple competitors in a spatially inhomogeneous environment may under certain conditions coexist in a steady state.

Pure and simple competition between two populations in configurations of two interconnected chemostats has been extensively studied by Kung and Baltzis [18]. They considered three possible configurations: (1) external input into one of the vessels only, (2) external inputs into both vessels with medium having the same concentration of the rate-limiting substrate, and (3) external inputs into both vessels with medium having a different composition, at least as far as the substrate competed for is concerned. They showed that it is possible to get steady state coexistence of two competitors, regardless of the way the medium is fed to the system. According to their arguments, 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 existence of a recycle stream is important because it implies that any species surviving in one reactor has to do so in the other as well; hence, if coexistence occurs it occurs throughout the system. If the effluent of the first reactor goes into the second but there is no recycle, 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 a steady state of coexistence will be reached, since species B will never be able to exclude species A despite the growth advantage due to the continuous inoculation of the second vessel with species A coming from the first vessel. Obviously, the configuration without recycle can lead to coexistence (in the second vessel) of two species even in the case where the specific growth rate curves of the two populations do not cross each other, provided that in the first vessel one has a pure culture of the slower growing species. In fact, in the latter case, the recycle stream would exclude coexistence anywhere in the system. On the other hand, the authors argue that if the specific growth curves cross each other and one is interested in a mixed culture, the absence of recycle is a suboptimal choice in the sense that part of the volume of the system is underused.

The possibility of coexistence of three microbial populations competing purely and simply in configurations of three interconnected chemostats has been investigated by Chang and Baltzis [6]. Via computer simulations, they showed that under any conditions no more than two populations can survive in a steady state with the exception of some discrete values of the design and operating parameters, at which three populations can coexist. It should be emphasized that for all practical purposes, coexistence is impossible since even when it is predicted to occur at some specific value(s) of the dilution rate, operation at a constant value of a physical parameter is impossible even with a perfect control device; the dilution rate will always exhibit random variations with time. By computer simulations, they also found that there are conditions under which the dynamical response (transients) of the system is so slow that although one population will be eventually washed out, a mixed culture of three competitors can be maintained (in an unsteady state) in the system for a considerable amount of time.

From the above review, some questions about possible extensions and generalizations have been raised. For example, is it possible for three pure and simple competitors to coexist in four interconnected chemostat? How many recycle streams are needed? How do the design and operating parameters affect the outcome of three competitors? The present study is directed at answering the foregoing questions.

Chapter 3

MATHEMATICAL DESCRIPTION OF THE GENERAL SYSTEM

3.1 Configuration of the General System

As was dicussed in the literature review, it has become clear that pure and simple competitors competing for a single rate-limiting nutrient which is not biologically renewable within the system, cannot coexist in a steady state. In addition, it is well known that except for one of the competitors, the other competitors under any conditions will wash out. It has been also shown that spatial heterogeneities can lead to coexistence of pure and simple competitors. One can conclude that pure and simple competition of two populations in a spatially homogeneous environment leads to exclusion of one of the competitors if all inputs to the competitive system are time-invariant. But, steady state coexistence of two pure and simple competitors can occur if one uses configurations of two interconnected chemostats (i.e., a spatially heterogeneous environment), even in cases where the inputs are time invariant. The necessary (but not sufficient) condition for coexistence is for each one of the competitors to have the growth advantage in one of the chemostats. Although an ideal chemostat is well mixed and hence spatially homogeneous, the system of two interconnected chemostats is spatially inhomogeneous since it can be viewed as a system of two homogeneous subenvironments where different conditions prevail. The question whether or not three pure and simple competitors can coexist in a steady state in configurations of three interconnected chemostats has been answered negatively.

The problem which is investigated in the present thesis is an extension of the study of competition of three species mentioned above. The main question here is whether three pure and simple competitors can coexist in a steady state throughout a system of four interconnected chemostats. The choice of four vessels is based on the following idea: the four vessels can be viewed as a system of two subenvironments, each one of which, consists of two reactors. It is known that two reactors can sustain two populations. Suppose that one has three populations X, Y, Z. If a pair of species (say X any Y) can survive in a pair of vessels, and in the other two reactors another pair of species (say Y and Z) can survive, by coupling all four vessels one should get coexistence of all three species.

The most general configuration of the system under investigation is shown in Figure 3.1. In the general case, each vessel has four inputs one of which consists of externally fed substrate (which is competed for), while the other three are fractions of effluents of the other three vessels. Each one of the four vessels is perfectly mixed. No cell attachment occurs on any solid surface, i.e., neither on the walls of the vessels nor on the walls of the interconnecting tubes. The tubes are assumed to be short enough or the flow fast enough, so that no growth occurs in them, and as a resut the composition of a stream in the exit of one vessel is the same as the composition of the same stream at the entrance of the vessel to which it is fed. The rate-limiting substrate exiting from a vessel is the same (from the structural point of view) as that in the fresh medium. The temperature in all vessels is the same and not changing.

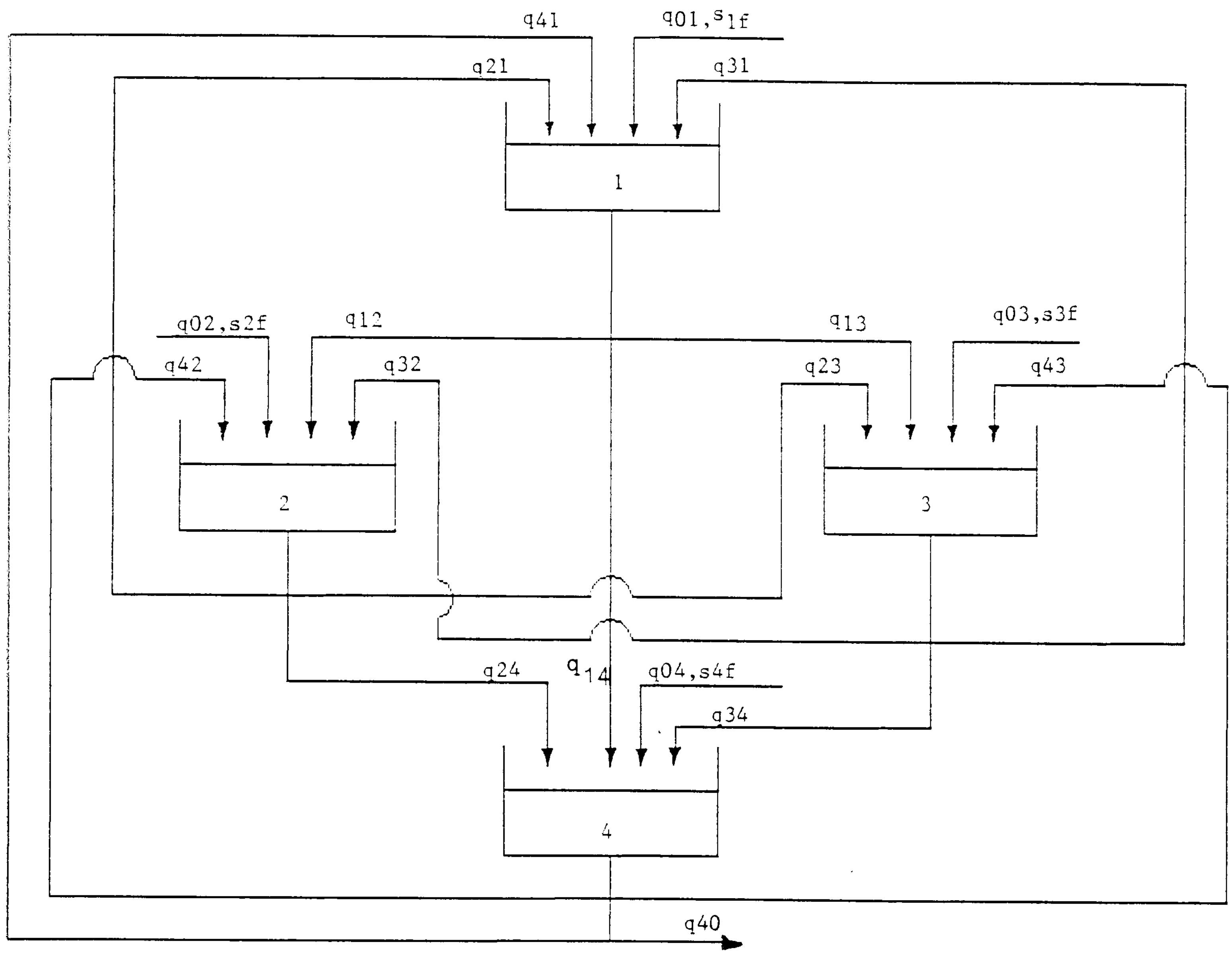


Figure 3.1: General Configuration of Four Interconnected Chemostats

3.2 Model Equations

In the general case, three populatitions A, B, and C, with biomass concentrations a, b, and c, respectively, are considered. In order then to completely describe the system, one needs four mass balances for each vessel, three of which are for the biomass of the three populations and one is for the rate-limiting substrate, S. These equations are as follows:

Chemostat 1

$$V_1\frac{da_1}{dt} = q_{21}a_2 + q_{31}a_3 + q_{41}a_4 + V_1\mu_1(s_1)a_1 - (q_{12} + q_{13} + q_{14})a_1 \tag{3.1}$$

$$V_1\frac{db_1}{dt} = q_{21}b_2 + q_{31}b_3 + q_{41}b_4 + V_1\mu_2(s_1)b_1 - (q_{12} + q_{13} + q_{14})b_1 \tag{3.2}$$

$$V_1\frac{dc_1}{dt} = q_{21}c_2 + q_{31}c_3 + q_{41}c_4 + V_1\mu_3(s_1)c_1 - (q_{12} + q_{13} + q_{14})c_1 \tag{3.3}$$

$$\begin{aligned} V_1\frac{ds_1}{dt} &= q_{01}s_{1f} + q_{21}s_2 + q_{31}s_3 + q_{41}s_4 - V_1[\frac{1}{Y_1}\mu_1(s_1)a_1 + \\ &\quad \frac{1}{Y_2}\mu_2(s_1)b_1 + \frac{1}{Y_3}\mu_3(s_1)c_1] - (q_{12} + q_{13} + q_{14})s_1 \end{aligned} \tag{3.4}$$

Chemostat 2

$$V_2\frac{da_2}{dt} = q_{12}a_1 + q_{32}a_3 + q_{42}a_4 + V_2\mu_1(s_2)a_2 - (q_{21} + q_{23} + q_{24})a_2 \tag{3.5}$$

$$V_2\frac{db_2}{dt} = q_{12}b_1 + q_{32}b_3 + q_{42}b_4 + V_2\mu_2(s_2)b_2 - (q_{21} + q_{23} + q_{24})b_2 \tag{3.6}$$

$$V_2\frac{dc_2}{dt} = q_{12}c_1 + q_{32}c_3 + q_{42}c_4 + V_2\mu_3(s_2)c_2 - (q_{21} + q_{23} + q_{24})c_2 \tag{3.7}$$

$$V_2\frac{ds_2}{dt} = q_{02}s_{2f} + q_{12}s_1 + q_{32}s_3 + q_{42}s_4 - V_2[\frac{1}{Y_1}\mu_1(s_2)a_2 + \frac{1}{Y_2}\mu_2(s_2)b_2 + \frac{1}{Y_3}\mu_3(s_2)c_2] - (q_{21} + q_{23} + q_{24})s_2 \quad (3.8)$$

Chemostat 3

$$V_3\frac{da_3}{dt} = q_{13}a_1 + q_{23}a_2 + q_{43}a_4 + V_3\mu_1(s_3)a_3 - (q_{31} + q_{32} + q_{34})a_3 \quad (3.9)$$

$$V_3\frac{db_3}{dt} = q_{13}b_1 + q_{23}b_2 + q_{43}b_4 + V_3\mu_2(s_3)b_3 - (q_{31} + q_{32} + q_{34})b_3 \quad (3.10)$$

$$V_3\frac{dc_3}{dt} = q_{13}c_1 + q_{23}c_2 + q_{43}c_4 + V_3\mu_3(s_3)c_3 - (q_{31} + q_{32} + q_{34})c_3 \quad (3.11)$$

$$V_3\frac{ds_3}{dt} = q_{03}s_{3f} + q_{13}s_1 + q_{23}s_2 + q_{43}s_4 - V_3[\frac{1}{Y_1}\mu_1(s_3)a_3 + \frac{1}{Y_2}\mu_2(s_3)b_3 + \frac{1}{Y_3}\mu_3(s_3)c_3] - (q_{31} + q_{32} + q_{34})s_3 \quad (3.12)$$

Chemostat 4

$$V_4\frac{da_4}{dt} = q_{14}a_1 + q_{24}a_2 + q_{34}a_3 + V_4\mu_1(s_4)a_4 - (q_{41} + q_{42} + q_{43} + q_{40})a_4 \quad (3.13)$$

$$V_4\frac{db_4}{dt} = q_{14}b_1 + q_{24}b_2 + q_{34}b_3 + V_4\mu_2(s_4)b_4 - (q_{41} + q_{42} + q_{43} + q_{40})b_4 \quad (3.14)$$

$$V_4\frac{dc_4}{dt} = q_{14}c_1 + q_{24}c_2 + q_{34}c_3 + V_4\mu_3(s_4)c_4 - (q_{41} + q_{42} + q_{43} + q_{40})c_4 \quad (3.15)$$

$$V_4\frac{ds_4}{dt} = q_{04}s_{4f} + q_{14}s_1 + q_{24}s_2 + q_{34}s_3 - V_4[\frac{1}{Y_1}\mu_1(s_4)a_4 + \frac{1}{Y_2}\mu_2(s_4)b_4 + \frac{1}{Y_3}\mu_3(s_4)c_4] - (q_{41} + q_{42} + q_{43} + q_{40})s_4 \quad (3.16)$$

Where,

a_i, b_i, c_i: biomass concentration of species A, B, C respectively in chemostat i, i=1,...,4.

s_i and s_f: concentration of the rate-limiting substrate in vessel i, and in the externally fed medium to vessel i, respectively.

V_i: working volume of vessel i.

q_{0i}: volumetric flowrate of the externally fed medium to vessel i.

Y_j: yield coefficient of species j on the rate-limiting substrate (assumed constant).

q_{ik}: volumetric flowrate of the stream originating from chemostat i and fed to chemostat k.

q_{40}: volumetric flowrate of the system's exit.

$\mu_j(s_i)$: specific growth rate of species j evaluated at the conditions prevailing in tank i; for this study, it is assumed to be given by Monod's model:

$$\mu_j(s_i) = \frac{\mu_{mj} s_i}{K_j + s_i}$$

With,

μ_{mj}: maximum specific growth rate of species j.

K_j: saturation constant of species j.

By introducing the following dimensionless quantities:

$$x_i = \frac{a_i}{Y_1 K_1} \qquad y_i = \frac{b_i}{Y_2 K_1} \qquad z_i = \frac{c_i}{Y_3 K_1} \qquad u_i = \frac{s_i}{K_1} \qquad i = 1, 2, 3, 4$$

$$u_f = \frac{s_{1f}}{K_1} \qquad \alpha = \frac{q_{01}}{V_1 \mu_{m1}} \qquad \theta_{lm} = \frac{q_{lm}}{V_1 \mu_{m1}} \qquad l, m = 1, 2, 3, 4 \quad l \neq m$$

$$\theta_{40} = \frac{q_{40}}{V_1\mu_{m1}} \qquad \beta = \frac{V_1}{V_2} \qquad \beta_1 = \frac{V_1}{V_3} \qquad \beta_2 = \frac{V_1}{V_4} \qquad \tau = t\mu_{m1}$$

$$\varphi_1 = \frac{\mu_{m2}}{\mu_{m1}} \qquad \varphi_2 = \frac{\mu_{m3}}{\mu_{m1}} \qquad \omega_1 = \frac{K_2}{K_1} \qquad \omega_2 = \frac{K_3}{K_1} \qquad \gamma = \frac{q_{02}}{q_{01}}$$

$$\gamma_1 = \frac{q_{03}}{q_{01}} \qquad \gamma_2 = \frac{q_{04}}{q_{01}} \qquad \eta = \frac{s_{2f}}{s_{1f}} \qquad \eta_1 = \frac{s_{3f}}{s_{1f}} \qquad \eta_2 = \frac{s_{4f}}{s_{1f}}$$

the equations described above, can be written in dimensionless form as follows:

Chemostat 1

$$\frac{dx_1}{d\tau} = \theta_{21}x_2 + \theta_{31}x_3 + \theta_{41}x_4 + f(u_1)x_1 - (\theta_{12} + \theta_{13} + \theta_{14})x_1 \tag{3.17}$$

$$\frac{dy_1}{d\tau} = \theta_{21}y_2 + \theta_{31}y_3 + \theta_{41}y_4 + g(u_1)y_1 - (\theta_{12} + \theta_{13} + \theta_{14})y_1 \tag{3.18}$$

$$\frac{dz_1}{d\tau} = \theta_{21}z_2 + \theta_{31}z_3 + \theta_{41}z_4 + h(u_1)z_1 - (\theta_{12} + \theta_{13} + \theta_{14})z_1 \tag{3.19}$$

$$\begin{aligned}\frac{du_1}{d\tau} = {} & \alpha u_f + \theta_{21}u_2 + \theta_{31}u_3 + \theta_{41}u_4 - [f(u_1)x_1 + g(u_1)y_1 + \\ & h(u_1)z_1] - (\theta_{12} + \theta_{13} + \theta_{14})u_1\end{aligned} \tag{3.20}$$

Chemostat 2

$$\frac{dx_2}{d\tau} = \beta\theta_{12}x_1 + \beta\theta_{32}x_3 + \beta\theta_{42}x_4 + f(u_2)x_2 - \beta(\theta_{21} + \theta_{23} + \theta_{24})x_2 \tag{3.21}$$

$$\frac{dy_2}{d\tau} = \beta\theta_{12}y_1 + \beta\theta_{32}y_3 + \beta\theta_{42}y_4 + g(u_2)y_2 - \beta(\theta_{21} + \theta_{23} + \theta_{24})y_2 \tag{3.22}$$

$$\frac{dz_2}{d\tau} = \beta\theta_{12}z_1 + \beta\theta_{32}z_3 + \beta\theta_{42}z_4 + h(u_2)z_2 - \beta(\theta_{21} + \theta_{23} + \theta_{24})z_2 \tag{3.23}$$

$$\begin{aligned}\frac{du_1}{d\tau} &= \alpha\beta\gamma\eta u_f + \beta\theta_{12}u_1 + \beta\theta_{32}u_3 + \beta\theta_{42} - [f(u_2)x_2 + g(u_2)y_2 + \\ &\quad h(u_2)z_2] - \beta(\theta_{21} + \theta_{23} + \theta_{24})u_2 \end{aligned}\tag{3.24}$$

Chemostat 3

$$\frac{dx_3}{d\tau} = \beta_1\theta_{13}x_1 + \beta_1\theta_{23}x_2 + \beta_1\theta_{43}x_4 + f(u_3)x_3 - \beta_1(\theta_{31} + \theta_{32} + \theta_{34})x_3 \tag{3.25}$$

$$\frac{dy_3}{d\tau} = \beta_1\theta_{13}y_1 + \beta_1\theta_{23}y_2 + \beta_1\theta_{43}y_4 + g(u_3)y_3 - \beta_1(\theta_{31} + \theta_{32} + \theta_{34})y_3 \tag{3.26}$$

$$\frac{dz_3}{d\tau} = \beta_1\theta_{13}z_1 + \beta_1\theta_{23}z_2 + \beta_1\theta_{43}z_4 + h(u_3)z_3 - \beta_1(\theta_{31} + \theta_{32} + \theta_{34})z_3 \tag{3.27}$$

$$\begin{aligned}\frac{du_3}{d\tau} &= \alpha\beta_1\gamma_1\eta_1 u_f + \beta_1\theta_{13}u_1 + \beta_1\theta_{23}u_2 + \beta_1\theta_{43}u_4 - [f(u_3)x_3 + g(u_3) \\ &\quad y_3 + h(u_3)z_3] - \beta_1(\theta_{31} + \theta_{32} + \theta_{34})u_3\end{aligned}\tag{3.28}$$

Chemostat 4

$$\begin{aligned}\frac{dx_4}{d\tau} &= \beta_2\theta_{14}x_1 + \beta_2\theta_{24}x_2 + \beta_2\theta_{34}x_3 + f(u_4)x_4 - \beta_2(\theta_{40} + \theta_{41} + \theta_{42} + \\ &\quad \theta_{43})x_4\end{aligned}\tag{3.29}$$

$$\begin{aligned}\frac{dy_4}{d\tau} &= \beta_2\theta_{14}y_1 + \beta_2\theta_{24}y_2 + \beta_2\theta_{34}y_3 + g(u_4)y_4 - \beta_2(\theta_{40} + \theta_{41} + \theta_{42} + \\ &\quad \theta_{43})y_4\end{aligned}\tag{3.30}$$

$$\begin{aligned}\frac{dz_4}{d\tau} &= \beta_2\theta_{14}z_1 + \beta_2\theta_{24}z_2 + \beta_2\theta_{34}z_3 + h(u_4)z_4 - \beta_2(\theta_{40} + \theta_{41} + \theta_{42} + \\ &\quad \theta_{43})z_4\end{aligned}\tag{3.31}$$

$$\begin{aligned}\frac{du_4}{d\tau} &= \alpha\beta_2\gamma_2\eta_2 u_f + \beta_2\theta_{14}u_1 + \beta_2\theta_{24}u_2 + \beta_2\theta_{34}u_3 - [f(u_4)x_4 + \\ &\quad g(u_4)y_4 + (u_4)z_4] - \beta_2(\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})u_4\end{aligned}\tag{3.32}$$

Where,

$$f(u_i) = \frac{u_i}{1+u_i} \qquad g(u_i) = \frac{\varphi_1 u_i}{\omega_1 + u_i} \qquad h(u_i) = \frac{\varphi_2 u_i}{\omega_2 + u_i}$$

Since the working volume V_j of vessel j is assumed to remain constant at all times, and the density to be constant throughout the system, one can write the following relations among flow rates:

$$\begin{aligned}
\theta_{12} &= \{I_1[R_5(R_2+R_3)+(R_4+1)(R_2+R_3+1)]+I_2[R_4+R_2(R_4+R_5+1)] \\
&\quad +I_3[R_2R_5+R_4(R_2+R_3+1)]\}I && (3.33) \\
\theta_{23} &= \{I_1[R_5(R_0+1)+R_4+1]+I_2[(R_0+R_1+1)(R_5+1)+R_4(R_1+1)]+ \\
&\quad I_3[R_4+R_5(R_0+R_1+1)]\}I && (3.34) \\
\theta_{34} &= \{I_1[R_0(R_2+R_3+1)+1]+I_2[R_0(R_2+1)+R_1+1]+ \\
&\quad I_3[(R_0+R_1)(R_2+R_3+1)+R_3+1]\}I && (3.35) \\
\theta_{13} &= R_0\theta_{12} && (3.36) \\
\theta_{14} &= R_1\theta_{12} && (3.37) \\
\theta_{21} &= R_2\theta_{23} && (3.38) \\
\theta_{24} &= R_3\theta_{23} && (3.39) \\
\theta_{31} &= R_4\theta_{34} && (3.40) \\
\theta_{32} &= R_5\theta_{34} && (3.41) \\
\theta_{40} &= (\gamma+\gamma_1+\gamma_2+1)\alpha && (3.42) \\
\theta_{41} &= R_8(\gamma+\gamma_1+\gamma_2+1)\alpha && (3.43) \\
\theta_{42} &= R_6(R_8+1)(\gamma+\gamma_1+\gamma_2+1)\alpha && (3.44) \\
\theta_{43} &= R_7(R_8+1)(\gamma+\gamma_1+\gamma_2+1)\alpha && (3.45)
\end{aligned}$$

With,

$$I_1 = R_8(\gamma + \gamma_1 + \gamma_2 + 1) + 1$$

$$I_2 = R_6(R_8 + 1)(\gamma + \gamma_1 + \gamma_2 + 1) + \gamma$$

$$I_3 = R_7(R_8 + 1)(\gamma + \gamma_1 + \gamma_2 + 1) + \gamma_1$$

$$I = \frac{\alpha}{R_3(R_4 + 1) + R_5[R_1(R_2 + R_3) + R_3(R_0 + 1)] + (R_2 + R_3 + 1)[R_0 + R_1(R_4 + 1)] + 1}$$

Where,

$$R_0 = \frac{q_{13}}{q_{12}} \qquad R_1 = \frac{q_{14}}{q_{12}} \qquad R_2 = \frac{q_{21}}{q_{23}}$$

$$R_3 = \frac{q_{24}}{q_{23}} \qquad R_4 = \frac{q_{31}}{q_{34}} \qquad R_5 = \frac{q_{32}}{q_{34}}$$

$$R_6 = \frac{q_{42}}{q_{40} + q_{41}} \qquad R_7 = \frac{q_{43}}{q_{40} + q_{41}} \qquad R_8 = \frac{q_{41}}{q_{40}}$$

3.3 Dimensional Reduction of The Model

Although the system is described by 16 differential equations, by using arguments similar to those of Aris and Humphrey [1], one can show that the system is actually a 12-dimensional one, due to the existence of four stoichiometric equations.

By adding equations (3.17) through (3.20), (3.21) through (3.24), (3.25) through (3.28), and (3.29) through (3.32), one gets

$$\begin{aligned}\frac{d(x_1 + y_1 + z_1 + u_1)}{d\tau} &= \alpha u_f + \theta_{21}(x_2 + y_2 + z_2 + u_2) + \theta_{31}(x_3 + y_3 + z_3 u_3) \\ &\quad + \theta_{41}(x_4 + y_4 + z_4 + u_4) - (\theta_{12} + \theta_{13} + \theta_{14})(x_1 + y_1 \\ &\quad + z_1 + u_1) \qquad (3.46)\\ \frac{d(x_2 + y_2 + z_2 + u_2)}{d\tau} &= \alpha\beta\gamma\eta u_f + \beta\theta_{12}(x_1 + y_1 + z_1 + u_1) + \\ &\quad \beta\theta_{32}(x_3 + y_3 + z_3 + u_3) + \beta\theta_{42}(x_4 + y_4 + z_4 + u_4) -\end{aligned}$$

$$\beta(\theta_{21}+\theta_{23}+\theta_{24})(x_2+y_2+z_2+u_2) \quad (3.47)$$

$$\begin{aligned}
\frac{d(x_3+y_3+z_3+u_3)}{d\tau} &= \alpha\beta_1\gamma_1\eta_1 u_f + \beta_1\theta_{13}(x_1+y_1+z_1+u_1) + \\
&\quad \beta_1\theta_{23}(x_2+y_2+z_2+u_2) + \beta_1\theta_{43}(x_4+y_4+z_4+u_4) - \\
&\quad \beta_1(\theta_{31}+\theta_{32}+\theta_{34})(x_3+y_3+z_3+u_3) \qquad (3.48)
\end{aligned}$$

$$\begin{aligned}
\frac{d(x_4+y_4+z_4+u_4)}{d\tau} &= \alpha\beta_2\gamma_2\eta_2 u_f + \beta_2\theta_{14}(x_1+y_1+z_1+u_1) + \\
&\quad \beta_2\theta_{24}(x_2+y_2+z_2+u_2) + \beta_2\theta_{34}(x_3+y_3+z_3+u_3) - \\
&\quad \beta_2(\theta_{40}+\theta_{41}+\theta_{42}+\theta_{43})(x_4+y_4+z_4+u_4) \qquad (3.49)
\end{aligned}$$

If one defines

$$w_1 = x_1+y_1+z_1+u_1-v_1 \qquad (3.50)$$

$$w_2 = x_2+y_2+z_2+u_2-v_2 \qquad (3.51)$$

$$w_3 = x_3+y_3+z_3+u_3-v_3 \qquad (3.52)$$

$$w_4 = x_4+y_4+z_4+u_4-v_4 \qquad (3.53)$$

Where,

$$v_1 = (k_1\gamma\eta + k_2\gamma_1\eta_1 + k_3\gamma_2\eta_2 + k_4)k \qquad (3.54)$$

$$v_2 = (k_5\gamma\eta + k_6\gamma_1\eta_1 + k_7\gamma_2\eta_2 + k_8)k \qquad (3.55)$$

$$v_3 = (k_9\gamma\eta + k_{10}\gamma_1\eta_1 + k_{11}\gamma_2\eta_2 + k_{12})k \qquad (3.56)$$

$$v_4 = (k_{13}\gamma\eta + k_{14}\gamma_1\eta_1 + k_{15}\gamma_2\eta_2 + k_{16})k \qquad (3.57)$$

With,

$$\begin{aligned}
k &= \frac{\alpha u_f}{k^*} \\
k^* &= \theta_{40}[(\theta_{12}+\theta_{13})(\theta_{23}\theta_{34}+\theta_{24}\theta_{32}) + (\theta_{21}+\theta_{24})(\theta_{14}\theta_{32}+\theta_{13}\theta_{34}+\theta_{14}\theta_{31}+\theta_{14}\theta_{34}) + \\
&\quad (\theta_{31}+\theta_{34})(\theta_{12}\theta_{24}+\theta_{14}\theta_{23})] \\
k_1 &= (\theta_{40}+\theta_{41}+\theta_{42}+\theta_{43})[\theta_{21}(\theta_{31}+\theta_{32})+\theta_{21}\theta_{34}+\theta_{23}\theta_{31}] + \theta_{24}[\theta_{31}(\theta_{41}+\theta_{43})+
\end{aligned}$$

$$\theta_{41}(\theta_{32} + 2\theta_{34})]$$

$$k_2 = (\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})[\theta_{31}(\theta_{21} + \theta_{23}) + \theta_{21}\theta_{32}] + (\theta_{40} + \theta_{41} + \theta_{43})\theta_{24}\theta_{31} + \theta_{21}\theta_{34}(\theta_{41} + \theta_{42}) + \theta_{41}[\theta_{24}(\theta_{32} + \theta_{34}) + \theta_{23}\theta_{34}]$$

$$k_3 = (\theta_{31} + \theta_{32} + \theta_{34})[\theta_{41}(\theta_{21} + \theta_{24}) + \theta_{21}\theta_{42}] + \theta_{43}[\theta_{21}(\theta_{31} + \theta_{32}) + \theta_{31}(\theta_{23} + \theta_{24})] + \theta_{23}[\theta_{31}(\theta_{41} + \theta_{42}) + \theta_{34}\theta_{41}]$$

$$k_4 = \theta_{23}[(\theta_{31} + \theta_{34})(\theta_{40} + \theta_{41}) + \theta_{31}(\theta_{42} + \theta_{43})] + (\theta_{31} + \theta_{32} + \theta_{34})[(\theta_{21} + \theta_{24})(\theta_{40} + \theta_{41} + \theta_{21}\theta_{42}] + \theta_{43}[\theta_{31}(\theta_{21} + \theta_{24}) + \theta_{21}\theta_{32}]$$

$$k_5 = (\theta_{31} + \theta_{32} + \theta_{34})[\theta_{14}(\theta_{40} + \theta_{42}) + \theta_{12}(\theta_{40} + \theta_{41} + \theta_{42})] + \theta_{13}[\theta_{40}(\theta_{32} + \theta_{34}) + \theta_{32}(\theta_{41} + \theta_{42} + \theta_{43})] + \theta_{43}[\theta_{32}(\theta_{12} + \theta_{14}) + \theta_{12}\theta_{31}]$$

$$k_6 = (\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})[\theta_{32}(\theta_{12} + \theta_{13}) + \theta_{12}\theta_{31}] + \theta_{42}[\theta_{14}(\theta_{31} + \theta_{34}) + \theta_{13}\theta_{34}] + \theta_{14}\theta_{32}(\theta_{40} + \theta_{42} + \theta_{43}) + \theta_{12}\theta_{34}(\theta_{41} + \theta_{42})$$

$$k_7 = \theta_{42}[\theta_{14}(\theta_{31} + \theta_{32}) + \theta_{12}\theta_{32}] + \theta_{42}(\theta_{32} + \theta_{34})(\theta_{12} + \theta_{13} + \theta_{14}) + \theta_{12}\theta_{31}(\theta_{42} + \theta_{43}) + \theta_{13}\theta_{32}(\theta_{41} + \theta_{42}) + \theta_{12}\theta_{41}(\theta_{31} + \theta_{32} + \theta_{34})$$

$$k_8 = (\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})[\theta_{12}(\theta_{31} + \theta_{32}) + \theta_{13}\theta_{32}] + \theta_{42}[\theta_{14}(\theta_{31} + \theta_{34}) + \theta_{13}\theta_{34}] + \theta_{12}\theta_{34}(\theta_{40} + \theta_{41} + \theta_{43}) + \theta_{14}\theta_{32}(\theta_{42} + \theta_{43})$$

$$k_9 = (\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})[\theta_{23}(\theta_{12} + \theta_{13}) + \theta_{13}\theta_{21}] + \theta_{24}[\theta_{43}(\theta_{12} + \theta_{13}) + \theta_{13}\theta_{41}] + \theta_{14}\theta_{43}(\theta_{21} + \theta_{23} + \theta_{24}) + \theta_{23}\theta_{14}(\theta_{40} + \theta_{42})$$

$$k_{10} = \theta_{23}[\theta_{12}(\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43}) + \theta_{14}\theta_{42}] + \theta_{13}(\theta_{21} + \theta_{23})(\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43}) + \theta_{14}(\theta_{40} + \theta_{43})(\theta_{21} + \theta_{23} + \theta_{24}) + \theta_{13}\theta_{24}(\theta_{40} + \theta_{41} + \theta_{43}) + \theta_{12}\theta_{24}(\theta_{40} + \theta_{43})$$

$$k_{11} = (\theta_{21} + \theta_{23} + \theta_{24})[\theta_{43}(\theta_{13} + \theta_{14}) + \theta_{13}\theta_{41}] + \theta_{42}[\theta_{23}(\theta_{12} + \theta_{13} + \theta_{14}) + \theta_{13}\theta_{21}] + \theta_{12}[\theta_{43}(\theta_{23} + \theta_{24}) + \theta_{23}\theta_{14}]$$

$$k_{12} = (\theta_{40} + \theta_{41} + \theta_{42} + \theta_{42})[\theta_{13}(\theta_{21} + \theta_{23}) + \theta_{12}\theta_{23}] + \theta_{14}[\theta_{23}(\theta_{42} + \theta_{43}) + \theta_{21}\theta_{43}] +$$

$$
\begin{aligned}
& \theta_{24}\theta_{43}(\theta_{12}+\theta_{13}+\theta_{14})+\theta_{13}\theta_{24}(\theta_{40}+\theta_{41}) \\
k_{13} &= (\theta_{31}+\theta_{32}+\theta_{34})[\theta_{24}(\theta_{12}+\theta_{14})+\theta_{14}\theta_{21}]+\theta_{23}[\theta_{34}(\theta_{12}+\theta_{13}+\theta_{14})+\theta_{14}\theta_{31}]+ \\
& \theta_{13}[\theta_{24}(\theta_{32}+\theta_{34})+\theta_{21}\theta_{34}] \\
k_{14} &= (\theta_{21}+\theta_{23}+\theta_{24})[\theta_{34}(\theta_{13}+\theta_{14})+\theta_{14}\theta_{31}]+\theta_{32}[\theta_{24}(\theta_{12}+\theta_{13}+\theta_{14})+\theta_{14}\theta_{21}]+ \\
& \theta_{12}[\theta_{34}(\theta_{23}+\theta_{24})+\theta_{24}\theta_{31}] \\
k_{15} &= \theta_{31}[\theta_{14}(\theta_{21}+\theta_{23}+\theta_{24})+\theta_{12}\theta_{24}]+(\theta_{12}+\theta_{13}+\theta_{14})[\theta_{34}(\theta_{23}+\theta_{24})+\theta_{24}\theta_{32}]+ \\
& \theta_{21}[\theta_{34}(\theta_{13}+\theta_{14})+\theta_{14}\theta_{32}] \\
k_{16} &= (\theta_{31}+\theta_{32}+\theta_{34})[\theta_{14}(\theta_{21}+\theta_{24})+\theta_{12}\theta_{24}]+\theta_{23}[\theta_{14}(\theta_{31}+\theta_{34})+\theta_{12}\theta_{34}]+ \\
& \theta_{13}[\theta_{34}(\theta_{21}+\theta_{23}+\theta_{24})+\theta_{24}\theta_{32}]
\end{aligned}
$$

then, equations (3.46) through (3.49) can be written as follows:

$$\frac{dw_1}{d\tau} = -(\theta_{12}+\theta_{13}+\theta_{14})w_1+\theta_{21}w_2+\theta_{31}w_3+\theta_{41}w_4 \tag{3.58}$$

$$\frac{dw_2}{d\tau} = \beta\theta_{12}w_1-\beta(\theta_{21}+\theta_{23}+\theta_{24})w_2+\beta\theta_{32}w_3+\beta\theta_{42}w_4 \tag{3.59}$$

$$\frac{dw_3}{d\tau} = \beta_1\theta_{13}w_1+\beta_1\theta_{23}w_2-\beta_1(\theta_{31}+\theta_{32}+\theta_{34})w_3+\beta_1\theta_{43}w_4 \tag{3.60}$$

$$\frac{dw_4}{d\tau} = \beta_2\theta_{14}w_1+\beta_2\theta_{24}w_2+\beta_2\theta_{34}w_3-\beta_2(\theta_{40}+\theta_{41}+\theta_{42}+\theta_{43})w_4 \tag{3.61}$$

The Jacobian matrix for the system of eqns. (3.58) through (3.61) is the following:

$$J = \begin{bmatrix} J_{1,1} & J_{1,2} & J_{1,3} & J_{1,4} \\ J_{2,1} & J_{2,2} & J_{2,3} & J_{2,4} \\ J_{3,1} & J_{3,2} & J_{3,3} & J_{3,4} \\ J_{4,1} & J_{4,2} & J_{4,3} & J_{4,4} \end{bmatrix}$$

Where,

$$J_{1,1} = -(\theta_{12}+\theta_{13}+\theta_{14})$$

$$
\begin{aligned}
J_{1,2} &= \theta_{21} \\
J_{1,3} &= \theta_{31} \\
J_{1,4} &= \theta_{41} \\
J_{2,1} &= \beta\theta_{12} \\
J_{2,2} &= -\beta_1(\theta_{21} + \theta_{23} + \theta_{24}) \\
J_{2,3} &= \beta\theta_{32} \\
J_{2,4} &= \beta\theta_{42} \\
J_{3,1} &= \beta_1\theta_{13} \\
J_{3,2} &= \beta_1\theta_{23} \\
J_{3,3} &= -\beta_1(\theta_{31} + \theta_{32} + \theta_{34}) \\
J_{3,4} &= \beta_1\theta_{43} \\
J_{4,1} &= \beta_2\theta_{14} \\
J_{4,2} &= \beta_2\theta_{24} \\
J_{4,3} &= \beta_2\theta_{34} \\
J_{4,4} &= -\beta_2(\theta_{40} + \theta_{41} + \theta_{42} + \theta_{43})
\end{aligned}
$$

It is clear then, that all but the diagonal elements of the Jacobian matrix, J, are positive. By using *Sevastyanov's lemma* [21], the conditions under which the eigenvalues of the matrix are negative or complex with negative real parts, are the following:

$$J_{1,1} < 0$$

$$\begin{vmatrix} J_{1,1} & J_{1,2} \\ J_{2,1} & J_{2,2} \end{vmatrix} > 0$$

$$\begin{vmatrix} J_{1,1} & J_{1,2} & J_{1,3} \\ J_{2,1} & J_{2,2} & J_{2,3} \\ J_{3,1} & J_{3,2} & J_{3,3} \end{vmatrix} < 0$$

$$\begin{vmatrix} J_{1,1} & J_{1,2} & J_{1,3} & J_{1,4} \\ J_{2,1} & J_{2,2} & J_{2,3} & J_{2,4} \\ J_{3,1} & J_{3,2} & J_{3,3} & J_{3,4} \\ J_{4,1} & J_{4,2} & J_{4,3} & J_{4,4} \end{vmatrix} > 0$$

Numerically, it can be shown that the eigenvalues of the Jacobian matrix are indeed real and negative, i.e., the conditions above are satisfied. Using the arguments of Aris and Humphrey, one can say, then, that $w_1 = w_2 = w_3 = w_4 = 0$ and use at all times the following four stoichiometric equations:

$$x_1 + y_1 + z_1 + u_1 = v_1 \tag{3.62}$$

$$x_2 + y_2 + z_2 + u_2 = v_2 \tag{3.63}$$

$$x_3 + y_3 + z_3 + u_3 = v_3 \tag{3.64}$$

$$x_4 + y_4 + z_4 + u_4 = v_4 \tag{3.65}$$

Due to the existence of the four stoichiometric equations, for computer simulations one needs to integrate any twelve of the sixteen equations (3.17) through (3.32), substituting for the remaining four, the algebraic relations (3.62) through (3.65); this greatly reduces the amount of computer time needed for the simulations.

3.4 Possible Steady States

There are eight possible steady states for the system considered here.

SS-0: $x_i = y_i = z_i = 0$, i=1, 2, 3, 4

All three populations wash out from the system.

SS-X: $x_i > 0$, $y_i = z_i = 0$, i=1, 2, 3, 4

SS-Y: $y_i > 0$, $x_i = z_i = 0$, i=1, 2, 3, 4

SS-Z: $z_i > 0$, $x_i = y_i = 0$, i=1, 2, 3, 4

Any one population survives in the system and its competitors wash out.

SS-XY: $x_i > 0$, $y_i > 0$, $z_i = 0$, i=1, 2, 3, 4

SS-YZ: $y_i > 0$, $z_i > 0$, $x_i = 0$, i=1, 2, 3, 4

SS-XZ: $x_i > 0$, $z_i > 0$, $y_i = 0$, i=1, 2, 3, 4

Any two populations survive in the system, while the third population is washed out.

SS-XYZ: $x_i > 0$, $y_i > 0$, $z_i > 0$, i=1, 2, 3, 4

All three populations coexist in a steady state.

As mentioned before, because of the interconnection of chemostats, if one population establishes itself in the system, it should survive in all four vessels.

3.5 Specific Growth- Rate Curves

The so-called specific growth-rate of a microbial population, implies the growth-rate of a unit amount of biomass of the population. Kung and Baltzis [18] have shown that the mutual disposition of the specific growth-rate curves of the two populations has a critical effect on the possibility of coexistence. Chang and Baltzis [6] have shown that the disposition of the specific growth-rate curves of the three populations has again a determining role on outcome of competition.

The specific growth-rates of the three populations can be expressed as follows:

$$f(u) = \frac{u}{1+u} \qquad g(u) = \frac{\varphi_1 u}{\omega_1 + u} \qquad h(u) = \frac{\varphi_2 u}{\omega_2 + u}$$

Without loss of generality, due to symmetry, one can assume:

$$\lim_{u\to\infty} f(u) > \lim_{u\to\infty} g(u) > \lim_{u\to\infty} h(u)$$

or

$$1 > \varphi_1 > \varphi_2$$

There are eight possible dispositions of the f(u), g(u) and h(u) curves which are shown in Figure 3.2.

The conditions under which each situation arises are as follows:

case 1: $\varphi_2 < \varphi_1 < 1$; $\varphi_1 < \omega_1$; $\varphi_2\omega_1 < \varphi_1\omega_2$

case 2: $\varphi_2 < \varphi_1 < 1$; $\omega_1 < \varphi_1$; $\varphi_2 < \omega_2$

case 3: $\varphi_2 < \varphi_1 < 1$; $\varphi_1 < \omega_1$; $\varphi_2 < \omega_2$; $\varphi_1\omega_2 < \varphi_2\omega_1$

case 4: $\varphi_2 < \varphi_1 < 1$; $\omega_1 < \varphi_1$; $\omega_2 < \varphi_2$; $\varphi_2\omega_1 < \varphi_1\omega_2$

case 5: $\varphi_2 < \varphi_1 < 1$; $\varphi_1 < \omega_1$; $\varphi_2 < \omega_2$

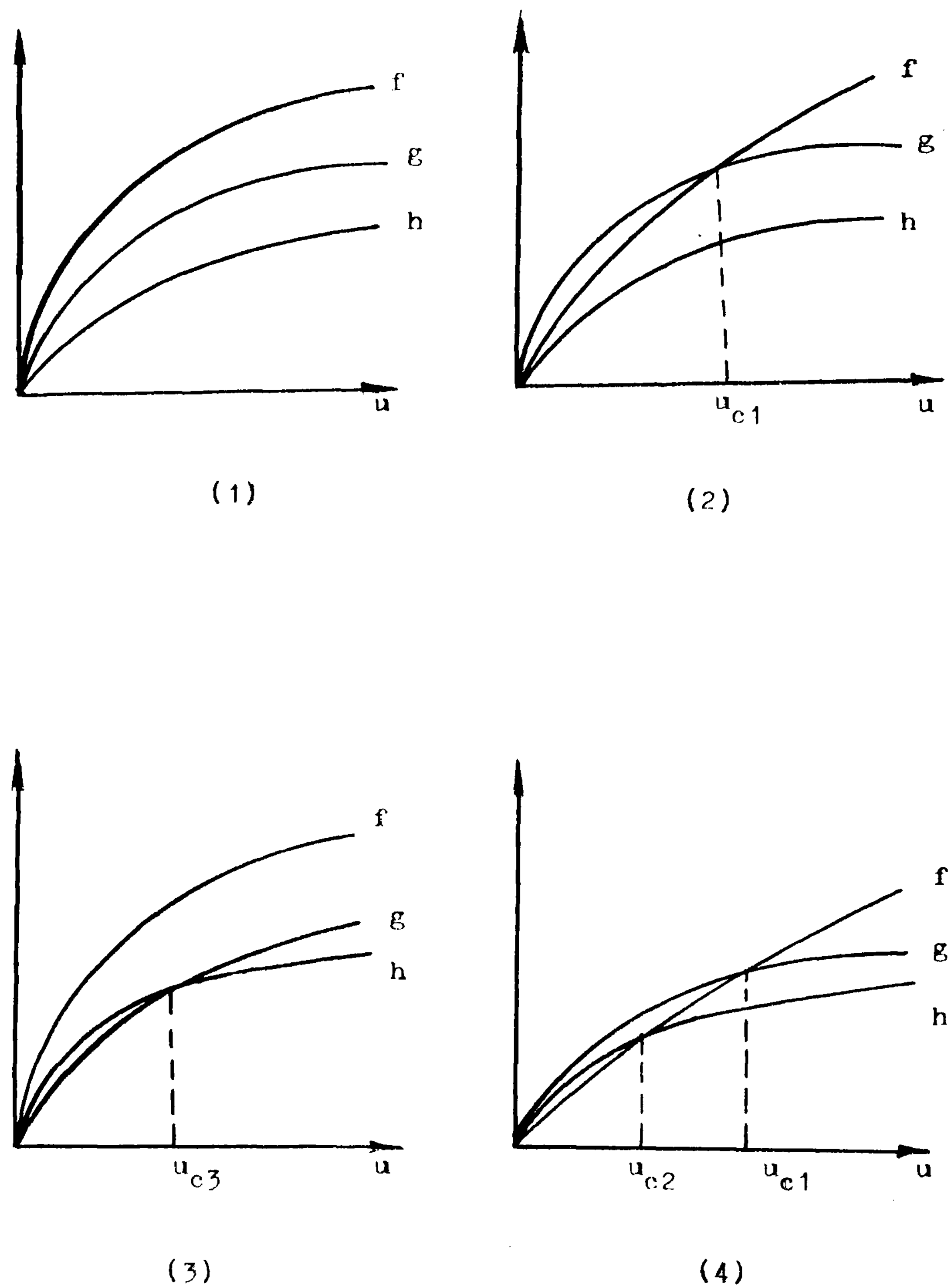
case 6: $\varphi_2 < \varphi_1 < 1$; $\omega_1 < \varphi_1$; $\omega_2 < \varphi_2$; $\varphi_1\omega_2 < \varphi_2\omega_1$

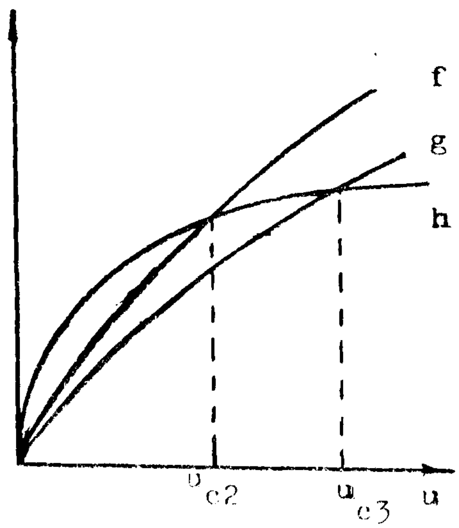
case 7: $\varphi_2 < \varphi_1 < 1$; $\omega_1 < \varphi_1$; $\omega_2 < \varphi_2$; $\varphi_1\omega_2 < \varphi_2\omega_1$; $\varphi_1 - \omega_1 + \varphi_2\omega_1 < \varphi_2 - \omega_2 + \varphi_1\omega_2$

case 8: $\varphi_2 < \varphi_1 < 1$; $\omega_1 < \varphi_1$; $\omega_2 < \varphi_2$; $\varphi_1\omega_2 < \varphi_2\omega_1$; $\varphi_1 - \omega_1 + \varphi_2\omega_1 = \varphi_2 - \omega_2 + \varphi_1\omega_2$

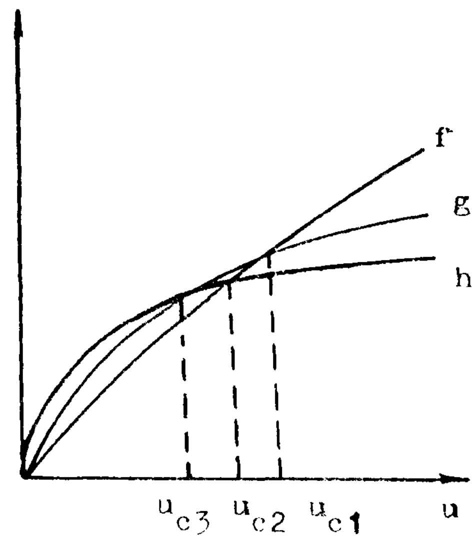
It is emphasized that coexistence of three species is impossible unless there is pair-wise crossing of the three specific growth-rate curves. Moreover, only case 6 may lead to coexistence, since it is the only case where each species can have the competitive advantage (depending on the conditions prevailing in a particular environment) over its competitors. It should be added that the disposition of the f(u), g(u) and h(u) curves depends on the type of the competing species and the substrate competed for (i.e., φ_1, φ_2, ω_1, and ω_2).

Figure 3.2: The Dispositions of the Specific Grow-Rate Curves

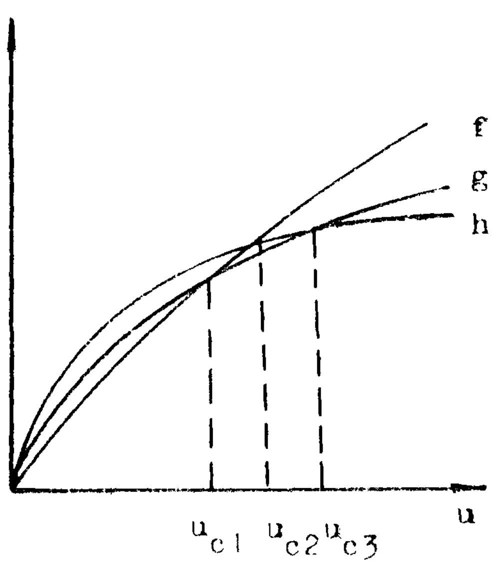




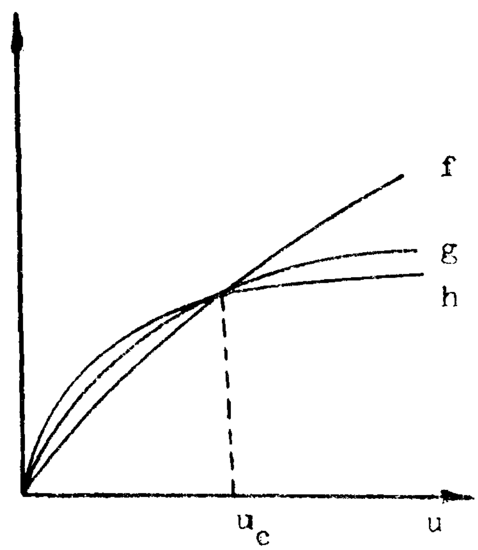
(5)



(6)



(7)



(8)

Chapter 4

ANALYSIS OF A SPECIAL CONFIGURATION

A special configuration of the four interconnected chemostats is shown in Figure 4.1. In this particular case, there are only two external feed streams into the system (namely, into vessel 1 and vessel 3) and there are no direct interconnections between vessels 1 and 3, or between vessels 1 and 4. This configuration constitutes a coupling of two, 2-vessel systems. Each two-vessel system viewed alone is identical to the system considered by Kung [17].

4.1 Model Equations

In this case, the general equations (3.17) through (3.22) reduce to the following:

$$\frac{dx_1}{d\tau} = [f(u_1) - \theta_{12}]x_1 + \theta_{21}x_2 \tag{4.1}$$

$$\frac{dy_1}{d\tau} = [g(u_1) - \theta_{12}]y_1 + \theta_{21}y_2 \tag{4.2}$$

$$\frac{dz_1}{d\tau} = [h(u_1) - \theta_{12}]z_1 + \theta_{21}z_2 \tag{4.3}$$

$$\frac{du_1}{d\tau} = \alpha u_f + \theta_{21}u_2 - \theta_{12}u_1 - [f(u_1)x_1 + g(u_1)y_1 + h(u_1)z_1] \tag{4.4}$$

$$\frac{dx_2}{d\tau} = \beta\theta_{12}x_1 + [f(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20})]x_2 + \beta\theta_{42}x_4 \tag{4.5}$$

$$\frac{dy_2}{d\tau} = \beta\theta_{12}y_1 + [g(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20})]y_2 + \beta\theta_{42}y_4 \tag{4.6}$$

$$\frac{dz_2}{d\tau} = \beta\theta_{12}z_1 + [h(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20})]z_2 + \beta\theta_{42}z_4 \tag{4.7}$$

$$\frac{du_2}{d\tau} = \beta\theta_{12}u_1 + \beta\theta_{42}u_4 - [f(u_2)x_2 + g(u_2)y_2 + h(u_2)z_2] - \beta(\theta_{21} + \theta_{23} + \theta_{20})u_2 \tag{4.8}$$

$$\frac{dx_3}{d\tau} = \beta_1\theta_{23}x_2 + [f(u_3) - \beta_1\theta_{34}]x_3 + \beta_1\theta_{43}x_4 \tag{4.9}$$

$$\frac{dy_3}{d\tau} = \beta_1\theta_{23}y_2 + [f(u_3) - \beta_1\theta_{34}]y_3 + \beta_1\theta_{43}y_4 \tag{4.10}$$

$$\frac{dz_3}{d\tau} = \beta_1\theta_{23}z_2 + [h(u_3) - \beta_1\theta_{34}]z_3 + \beta_1\theta_{43}z_4 \tag{4.11}$$

$$\frac{du_3}{d\tau} = \alpha\beta_1\gamma_1\eta_1 u_f + \beta_1\theta_{23}u_2 + \beta_1\theta_{43}u_4 - [f(u_3)x_3 + g(u_3)y_3 + h(u_3)z_3] - \beta_1\theta_{34}u_3 \tag{4.12}$$

$$\frac{dx_4}{d\tau} = \beta_2\theta_{34}x_3 + [f(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})]x_4 \tag{4.13}$$

$$\frac{dy_4}{d\tau} = \beta_2\theta_{34}y_3 + [g(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})]y_4 \tag{4.14}$$

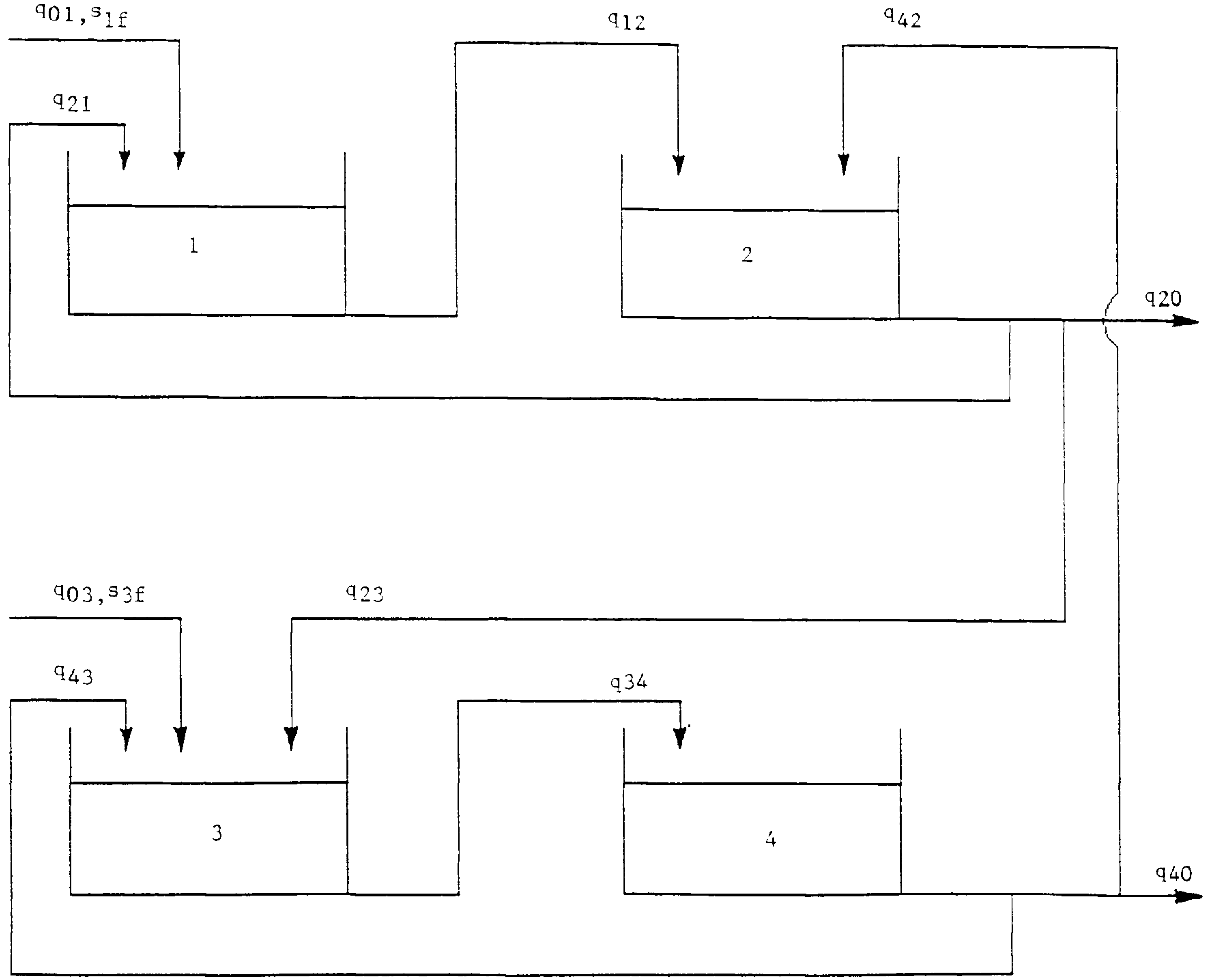


Figure 4.1: Special Configuration of Four Interconnected Chemostats

$$\frac{dz_4}{d\tau} = \beta_2\theta_{34}z_3 + [h(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})]z_4 \tag{4.15}$$

$$\frac{du_4}{d\tau} = \beta_2\theta_{34}u_3 - [f(u_4)x_4 + g(u_4)y_4 + h(u_4)z_4] - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})u_4 \tag{4.16}$$

With,

$$\theta_{12} = \frac{R_1(R_3+1) + R_2R_3(\gamma_1+1) + R_2 + 1}{R_1(R_3+1)+1}\alpha \tag{4.17}$$

$$\theta_{23} = \frac{R_3(\gamma_1+1)+1}{R_1(R_3+1)+1}\alpha \tag{4.18}$$

$$\theta_{34} = \frac{(R_4+R_3+1)[\gamma_1(R_1+1)+1]}{R_1(R_3+1)+1}\alpha \tag{4.19}$$

$$\theta_{40} = \frac{\gamma_1(R_1+1)+1}{R_1(R_3+1)+1}\alpha \tag{4.20}$$

$$\theta_{20} = R_1\theta_{23} \tag{4.21}$$

$$\theta_{21} = R_2\theta_{23} \tag{4.22}$$

$$\theta_{42} = R_3\theta_{40} \tag{4.23}$$

$$\theta_{43} = R_4\theta_{40} \tag{4.24}$$

Again, one can write the stoichiometric relations as in the previous section. Namely,

$$x_1 + y_1 + z_1 + u_1 = v_1 \tag{4.25}$$

$$x_2 + y_2 + z_2 + u_2 = v_2 \tag{4.26}$$

$$x_3 + y_3 + z_3 + u_3 = v_3 \tag{4.27}$$

$$x_4 + y_4 + z_4 + u_4 = v_4 \tag{4.28}$$

Where,

$$v_1 = \frac{\theta_{21}\theta_{42}(\gamma_1\eta_1 + 1) + \theta_{21}\theta_{40} + \theta_{40}(\theta_{23} + \theta_{20}) + \theta_{20}\theta_{42}}{\theta_{12}[\theta_{40}(\theta_{23} + \theta_{20}) + \theta_{20}\theta_{42}]}\alpha u_f \tag{4.29}$$

$$v_2 = \frac{\theta_{42}(\gamma_1\eta_1 + 1) + \theta_{40}}{\theta_{40}(\theta_{23} + \theta_{20}) + \theta_{20}\theta_{42}}\alpha u_f \tag{4.30}$$

$$v_3 = \frac{(\theta_{43} + \theta_{42} + \theta_{40})[(\theta_{23} + \theta_{20})\gamma_1\eta_1 + \theta_{23}]}{\theta_{34}[\theta_{40}(\theta_{23} + \theta_{20}) + \theta_{20}\theta_{42}]}\alpha u_f \tag{4.31}$$

$$v_4 = \frac{(\theta_{23} + \theta_{20})\gamma_1\eta_1 + \theta_{23}}{\theta_{40}(\theta_{23} + \theta_{20}) + \theta_{20}\theta_{42}}\alpha u_f \tag{4.32}$$

Dynamically speaking, the system now can be described by the four stoichiometric relations along with any twelve of the differential equations (4.1) through (4.16). In the present study, equations (4.4), (4.8), (4.12), and (4.16) were substituted for by the stoichiometric relations (4.25), (4.26), (4.27), and (4.28), respectively.

The local stability of any steady state depends on the eigenvalues of a 12×12 Jacobian matrix. The Jacobian (stability) matrix for this system is the following:

$$J_1 = \begin{bmatrix} A_1 & A_2 & A_3 & A_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ B_1 & B_2 & B_3 & 0 & B_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ C_1 & C_2 & C_3 & 0 & 0 & C_4 & 0 & 0 & 0 & 0 & 0 & 0 \\ D_1 & 0 & 0 & D_2 & D_3 & D_4 & 0 & 0 & 0 & D_5 & 0 & 0 \\ 0 & E_1 & 0 & E_2 & E_3 & E_4 & 0 & 0 & 0 & 0 & E_5 & 0 \\ 0 & 0 & F_1 & F_2 & F_3 & F_4 & 0 & 0 & 0 & 0 & 0 & F_5 \\ 0 & 0 & 0 & G_1 & 0 & 0 & G_2 & G_3 & G_4 & G_5 & 0 & 0 \\ 0 & 0 & & 0 & H_1 & 0 & H_2 & H_3 & H_4 & 0 & H_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & I_1 & I_2 & I_3 & I_4 & 0 & 0 & I_5 \\ 0 & 0 & 0 & 0 & 0 & 0 & J_1 & 0 & 0 & J_2 & J_3 & J_4 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & K_1 & 0 & K_2 & K_3 & K_4 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & L_1 & L_2 & L_3 & L_4 \end{bmatrix}$$

Where,

$A_1 = f(u_1) - \theta_{12} - x_1 F(u_1)$ $\qquad$ $A_2 = -x_1 F(u_1)$

$A_3 = -x_1 F(u_1)$ $\qquad$ $A_4 = \theta_{21}$

$B_1 = -y_1 G(u_1)$ $\qquad$ $B_2 = g(u_1) - \theta_{12} - y_1 G(u_1)$

$B_3 = -y_1 G(u_1)$ $\qquad$ $B_4 = \theta_{21}$

$C_1 = -z_1 H(u_1)$ $\qquad$ $C_2 = -z_1 H(u_1)$

$C_3 = h(u_1) - \theta_{12} - z_1 H(u_1)$ $\qquad$ $C_4 = \theta_{21}$

$D_1 = \beta\theta_{12}$ $\qquad$ $D_2 = f(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20}) - x_2 F(u_2)$

$D_3 = -x_2 F(u_2)$ $\qquad$ $D_4 = -x_2 F(u_2)$

$D_5 = \beta\theta_{42}$ $\qquad$ $E_1 = \beta\theta_{12}$

$E_2 = -y_2 G(u_2)$ $\qquad$ $E_3 = g(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20}) - y_2 G(u_2)$

$E_4 = -y_2 G(u_2)$ $\qquad$ $E_5 = \beta\theta_{42}$

$F_1 = \beta\theta_{12}$ $\qquad$ $F_2 = -z_2 H(u_2)$

$F_3 = -z_2 H(u_2)$ $\qquad$ $F_4 = h(u_2) - \beta(\theta_{21} + \theta_{23} + \theta_{20}) - z_2 H(u_2)$

$F_5 = \beta\theta_{42}$ $\qquad$ $G_1 = \beta_1\theta_{43}$

$G_2 = f(u_3) - \beta_1\theta_{34} - x_3 F(u_3)$ $\qquad$ $G_3 = -x_3 F(u_3)$

$G_4 = -x_3 F(u_3)$ $\qquad$ $G_5 = \beta_1\theta_{43}$

$H_1 = \beta_1\theta_{23}$ $\qquad$ $H_2 = -y_3 G(u_3)$

$H_3 = g(u_3) - \beta_1\theta_{34} - y_3 G(u_3)$ $\qquad$ $H_4 = -y_3 G(u_3)$

$H_5 = \beta_1\theta_{23}$ $\qquad$ $I_1 = \beta_1\theta_{23}$

$I_2 = -z_3 H(u_3)$ $\qquad$ $I_3 = z_3 H(u_3)$

$I_4 = h(u_3) - \beta_1\theta_{34} - z_3 H(u_3)$ $\qquad$ $I_5 = \beta_1\theta_{43}$

$J_1 = \beta_2\theta_{34}$ $\qquad$ $J_2 = f(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40}) - x_4 F(u_4)$

$J_3 = -x_4 F(u_4)$ $\qquad$ $J_4 = -x_4 F(u_4)$

$K_1 = \beta_2\theta_{34}$ $\qquad$ $K_2 = -y_4 G(u_4)$

$K_3 = g(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40}) - y_4 G(u_4)$ $\qquad$ $K_4 = -y_4 G(u_4)$

$L_1 = \beta_2\theta_{34}$ $\qquad$ $L_2 = -z_4 H(u_4)$

$L_3 = -z_4 H(u_4)$ $\qquad$ $L_4 = h(u_4) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40}) - z_4 H(u_4)$

With,

$$f(u_i) = \frac{u_i}{1+u_i} \qquad F(u_i) = \frac{1}{(1+u_i)^2}, \qquad i = 1,2,3,4$$

$$g(u_i) = \frac{\varphi_1 u_i}{\omega_1 + u_i} \qquad G(u_i) = \frac{\varphi_1 \omega_1}{(\omega_1 + u_i)^2}, \qquad i = 1,2,3,4$$

$$h(u_i) = \frac{\varphi_2 u_2}{\omega_2 + u_2} \qquad H(u_i) = \frac{\varphi_2 \omega_2}{(\omega_2 + u_i)^2}, \qquad i = 1,2,3,4$$

When at the steady state, the derivatives are zero. Then, equations (4.1) through (4.3), (4.5) through (4.7), (4.9) through (4.11) and, (4.13) through (4.15) as well as the stoichiometric relations (4.25) through (4.28) must be simultaneously satisfied. From this point on, it is assumed that both vessels 1 and 3 are fed with medium of identical composition, and this leads to the following system of algebraic equations.

Bioreactor 1

$$\begin{aligned} \{[R_1(R_3+1)+1]f(u_1) &- [R_1(R_3+1)+R_2R_3(\gamma_1+1)+R_2+1]\alpha\}x_1 + \\ R_2[R_3(\gamma_1+1)+1]\alpha x_2 &= 0 \end{aligned} \tag{4.33}$$

$$\begin{aligned} \{[R_1(R_3+1)+1]g(u_1) &- [R_1(R_3+1)+R_2R_3(\gamma_1+1)+R_2+1]\alpha\}y_1 + \\ R_2[R_3(\gamma_1+1)+1]\alpha y_2 &= 0 \end{aligned} \tag{4.34}$$

$$\begin{aligned} \{[R_1(R_3+1)+1]h(u_1) &- [R_1(R_3+1)+R_2R_3(\gamma_1+1)+R_2+1]\alpha\}z_1 + \\ R_2[R_3(\gamma_1+1)+1]\alpha z_2 &= 0 \end{aligned} \tag{4.35}$$

Bioreactor 2

$$\begin{aligned} \beta \;\; &[R_1(R_3+1)+R_2R_3(\gamma_1+1)+R_2+1]\alpha x_1 + \{[R_1(R_3+1)+1]f(u_2) - \\ \beta \;\; &(R_2+R_1+1)[R_3(\gamma_1+1)+1]\alpha\}x_2 + \beta R_3[\gamma_1(R_1+1)+1]\alpha x_4 = 0 \end{aligned} \tag{4.36}$$

$$\beta \;\; [R_1(R_3+1)+R_2R_3(\gamma_1+1)+R_2+1]\alpha y_1 + \{[R_1(R_3+1)+1]g(u_2) -$$

$$\beta \quad (R_2 + R_1 + 1)[R_3(\gamma_1 + 1) + 1]\alpha\}y_2 + \beta R_3[\gamma_1(R_1 + 1) + 1]\alpha y_4 = 0 \tag{4.37}$$

$$\beta \quad [R_1(R_3 + 1) + R_2R_3(\gamma_1 + 1) + R_2 + 1]\alpha z_1 + \{R_1(R_3 + 1) + 1]h(u_2) -$$

$$\beta \quad (R_2 + R_1 + 1)[R_3(\gamma_1 + 1) + 1]\alpha\}z_2 + \beta R_3[\gamma_1(R_1 + 1) + 1]\alpha z_4 = 0 \tag{4.38}$$

Bioreactor 3

$$\beta_1 \quad [R_3(\gamma_1 + 1) + 1]\alpha x_2 + \{[R_1(R_3 + 1) + 1]f(u_3) -$$

$$\beta_1 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}x_3 + \beta_1 R_4[\gamma_1(R_1 + 1) + 1]\alpha x_4 = 0 \tag{4.39}$$

$$\beta_1 \quad [R_3(\gamma_1 + 1) + 1]\alpha y_2 + \{[R_1(R_3 + 1) + 1]g(u_3) -$$

$$\beta_1 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}y_3 + \beta_1 R_4[\gamma_1(R_1 + 1) + 1]\alpha y_4 = 0 \tag{4.40}$$

$$\beta_1 \quad [R_3(\gamma_1 + 1) + 1]\alpha z_2 + \{[R_1(R_3 + 1) + 1]h(u_3) -$$

$$\beta_1 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}z_3 + \beta_1 R_4[\gamma_1(R_1 + 1) + 1]\alpha z_4 = 0 \tag{4.41}$$

Bioreactor 4

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha x_3 + \{[R_1(R_3 + 1) + 1]f(u_4) -$$

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}x_4 = 0 \tag{4.42}$$

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha y_3 + \{[R_1(R_3 + 1) + 1]g(u_4) -$$

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}y_4 = 0 \tag{4.43}$$

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha z_3 + \{[R_1(R_3 + 1) + 1]h(u_4) -$$

$$\beta_2 \quad (R_4 + R_3 + 1)[\gamma_1(R_1 + 1) + 1]\alpha\}z_4 = 0 \tag{4.44}$$

Stoichiometric Relations

$$x_1 + y_1 + z_1 + u_1 = u_f \tag{4.45}$$

$$x_2 + y_2 + z_2 + u_2 = u_f \tag{4.46}$$

$$x_3 + y_3 + z_3 + u_3 = u_f \tag{4.47}$$

$$x_4 + y_4 + z_4 + u_4 = u_f \tag{4.48}$$

4.2 Analysis of SS-0

This is the total wash-out steady state (i.e., $x_i = y_i = z_i = 0$, $u_i = u_f$), which is always meaningful. The non-zero elements of 12×12 Jacobian matrix are the following:

$A_1 = f(u_f) - \theta_{12}$ $\qquad$ $A_4 = \theta_{21}$

$B_2 = g(u_f) - \theta_{12}$ $\qquad$ $B_4 = \theta_{21}$

$C_3 = h(u_f) - \theta_{12}$ $\qquad$ $C_4 = \theta_{21}$

$D_1 = \beta\theta_{12}$ $\qquad$ $D_2 = f(u_f) - \beta(\theta_{21} + \theta_{23} + \theta_{20})$

$D_5 = \beta\theta_{42}$ $\qquad$ $E_1 = \beta\theta_{12}$

$E_3 = g(u_f) - \beta(\theta_{21} + \theta_{23} + \theta_{20})$ $\qquad$ $E_5 = \beta\theta_{42}$

$F_1 = \beta\theta_{12}$ $\qquad$ $F_4 = h(u_f) - \beta(\theta_{21} + \theta_{23} + \theta_{20})$

$F_5 = \beta\theta_{42}$ $\qquad$ $G_1 = \beta_1\theta_{43}$

$G_2 = f(u_f) - \beta_1\theta_{34}$ $\qquad$ $G_5 = \beta_1\theta_{43}$

$H_1 = \beta_1\theta_{23}$ $\qquad$ $H_3 = g(u_f) - \beta_1\theta_{34}$

$H_5 = \beta_1\theta_{43}$ $\qquad$ $I_1 = \beta_1\theta_{23}$

$I_4 = h(u_f) - \beta_1\theta_{34}$ $\qquad$ $I_5 = \beta_1\theta_{43}$

$J_1 = \beta_2\theta_{34}$ $\qquad$ $J_2 = f(u_f) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})$

$K_1 = \beta_2\theta_{34}$ $\qquad$ $K_3 = g(u_f) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})$

$L_1 = \beta_2\theta_{34}$ $\qquad$ $L_4 = h(u_f) - \beta_2(\theta_{42} + \theta_{43} + \theta_{40})$

It is easily seen that all elements of the Jacobian matrix which are off the main diagonal, are positive. Then by using *Sevastyanov's lemma* [21], one obtains the conditions for stability as follows:

$$A_1 < 0 \tag{4.49}$$

$$B_2 < 0 \tag{4.50}$$

$$C_3 < 0 \tag{4.51}$$

$$A_4D_1 - A_1D_2 < 0 \tag{4.52}$$

$$B_4E_1 - B_2E_3 < 0 \tag{4.53}$$

$$C_4F_1 - C_3F_4 < 0 \tag{4.54}$$

$$G_2 < 0 \tag{4.55}$$

$$H_3 < 0 \tag{4.56}$$

$$I_4 < 0 \tag{4.57}$$

$$G_5J_1 - G_2J_2 < 0 \tag{4.58}$$

$$H_5K_1 - H_3K_3 < 0 \tag{4.59}$$

$$I_5L_1 - I_4L_4 < 0 \tag{4.60}$$

4.3 Analysis of SS-X, SS-Y and, SS-Z

SS-X is the steady state in which only population A can survive. In this case, $y_i = z_i = 0$, $i = 1, ..., 4$. The values of x_i and u_i, $i = 1, ..., 4$ can be found by solving following equations:

$$[R_1(R_3+1)+1][f(u_1)-\alpha]x_1 + R_2[R_3(\gamma_1+1)+1]\alpha(x_2-x_1) = 0 \tag{4.61}$$

$$\begin{aligned}[R_1(R_3+1)+1]f(u_2)x_2 + \beta[R_1(R_3+1) + R_2R_3(\gamma_1+1) +\\ R_2+1]\alpha(x_1-x_2) + \beta R_3[\gamma_1(R_1+1)+1]\alpha(x_4-x_2) = 0\end{aligned} \tag{4.62}$$

$$\begin{aligned}[R_1(R_3+1)+1]f(u_3)x_3 + \beta_1R_4[\gamma_1(R_1+1)+1]\alpha(x_4-x_3) +\\ \beta_1[R_3(\gamma_1+1)+1]\alpha(x_2-x_3) - \beta_1\gamma_1[R_1(R_3+1)+1]\alpha x_3 = 0\end{aligned} \tag{4.63}$$

$$\begin{aligned}&[R_1(R_3+1)+1]f(u_4)x_4 - \beta_2(R_4+R_3+1)[\gamma_1(R_1+1)+1]\alpha(x_4-x_3)\\ &= 0\end{aligned} \tag{4.64}$$

$$x_1 + u_1 = u_f \tag{4.65}$$

$$x_2 + u_2 = u_f \tag{4.66}$$

$$x_3 + u_3 = u_f \tag{4.67}$$

$$x_4 + u_4 = u_f \tag{4.68}$$

From equation (4.64) it is evident that if SS-X is meaningful it must be that $x_4 > x_3$. From equation (4.61), one can find that $x_1 > x_2$ if $f(u_1) - \alpha > 0$. Then from equation (4.62), one can conclude that $x_2 > x_4$. Hence, if $f(u_1) > \alpha$ at a meaningful SS-X it is $x_1 > x_2 > x_4 > x_3$ and—from equations (4.65) through (4.68)— $u_3 > u_4 > u_2 > u_1$. If $f(u_1) - \alpha < 0$, one cannot directly sort x by increasing or decreasing order from the above equations. If one assumed that $x_1 = x_2 = x_3 = x_4$, it is easy to see that the steady state equations cannot be satisfied. Hence, when at SS-X, the entire system is spatially heterogeneous. Because of the complexity of equations (4.61) through (4.64), one cannot find analytically the conditions under which SS-X is meaningful and stable. The domain in the $\alpha - u_f$ plane where SS-X is meaningful and stable can only be found numerically. Results of numerical studies are presented in a later section of this thesis.

Analogous results and conclusions can be found for SS-Y (only population B can survive) and SS-Z (only population C can survive) since SS-X, SS-Y and, SS-Z are symmetric.

The complexity of the system is such that not even prelimenary analytical results can be obtained for the remaining steady states, i.e., SS-XY, SS-YZ, SS-XZ and SS-XYZ. These steady states have been studied only numerically.

4.4 Numerical Analysis, Computer Simulations and Operating Diagrams

The equations describing the system considered in this chapter, contain 15 parameters, namely, α, β, β_1, β_2, γ_1, η_1, u_f, φ_1, φ_2, ω_1, ω_2, R_1, R_2, R_3, and R_4. Baltzis and Kung [18] have divided these parameters into three categories: (1) system parameters, (2) design parameters and, (3) operating parameters. The system parameters depend on the type of rate-limiting substrate and the identity of the competing populations. For the problem studied here, the system parameters are φ_1, φ_2, ω_1, and ω_2, and they have been kept constant in all simulation studies. The design parameters (β, β_1, β_2) indicate the relative volumes of the vessels. For a system of three organisms, a given substrate, and a specified set of reactors (from the point of view of volume), one can vary during operation, the following parameters: α, γ, η_1, u_f, R_1, R_2, R_3, and R_4. These parameters (called operating parameters) have to do with flow rates of the various streams, and the composition of the externally fed media. These parameters were varied in a series of numerical studies, in order to study their effect on the system, and the outcome of competition.

Since the main objective of this study, was to explore the possibility of getting steady state coexistence of all three competitors (i.e., SS-XYZ), the system parameters were selected in a way which leads to the disposition of the specific growth rates shown in Figure 3.2–Case 6. Unless there is pairwise crossing of the specific growth rate curves, as shown in the aforementioned figure, steady state coexistence of all three species is impossible. In this work, the system parameter values used, are $\varphi_1 = 0.5$, $\varphi_2 = 0.4$, $\omega_1 = 0.25$, $\omega_2 = 0.125$. For this values, the crossing point of the f(u) and g(u) curves, is at $u_{c1} = 0.5$, at which, $f(u_{c1}) = g(u_{c1}) = a_{c1} = 0.333$; the crossing point of f(u) and h(u) curves, is at $u_{c2} = 0.458$, at which, $f(u_{c2}) = h(u_{c2}) =$

$a_{c2} = 0.314$; the crossing point of g(u) and h(u) curves, is at $u_{c3} = 0.375$, at which, $g(u_{c3}) = h(u_{c3}) = a_{c3} = 0.3$.

Except for the system parameters, there are 11 design and operating parameters in the system, as discussed previously. These parameters were varied in different simulation studies. From the numerical studies, answers to the following questions were sought: under what conditions is each possible steady state meaningful and stable? How many domains are there in the operating parameters space in which more than one steady state is meaningful and stable? Does a possible state (meaningful and stable) occur in a finite domain of the operating parameters space or does it occur just for some distinct values of the operating parameters?

Two main programs (given in the appendix) have been used in this study. One is a Newton-Raphson routine which is used to solve a system of equations at steady state. The other is the Michelsen method which is used to integrate the coupled ordinary differential equations which describe the system at all times. The subroutine EIG3 (IMSL Library) was used to find the eigenvalues of the Jacobian matrix and thus to determine the stability character of each steady state.

The procedure and methodology used in the numerical studies were the following: set the values of all parameters except α and u_f; fix u_f (usually, let $u_f = 5$ or $u_f = 10$); look for the boundary of the domain of SS-XYZ along the α direction by using the Michelsen method and Newton-Raphson method in turn; after finding the boundary of SS-XYZ, span the α-u_f plane for every other possible steady state. It was found that the Newton-Raphson method is very sensitive to the initial guess, for this reason, integrations were performed in many cases instead of the usual continuation. Results from integrations were used as initial guesses for the Newton-Raphson method. The steady state values from the Newton-Raphson method were used in order to calculate the eigenvalues of the Jacobian matrix.

A summary of the parameters used in the search for SS-XYZ but they have not yielded such a steady state, are given in Table 4.1. The parameters used for the Diagrams shown in Figures 4.2, 4.3 and, 4.4 are given in Tables 4.2, 4.3 and 4.4, respectively. Typical values for the state variables when the system is in an XYZ-coexistence domain shown in Figures 4.2, 4.3 and, 4.4, are presented in Tables 4.5, 4.6 and 4.7, respectively. The results of the numerical studies are presented in the form of operating diagrams [Jost *et al.*, (16)].

Looking at the diagrams shown in Figures 4.2 through 4.4 one can draw some conclusions. There is a domain on the α-u_f plane in which SS-XYZ is meaningful and stable. As was originally anticipated and discussed early in this thesis, this domain is always between boundaries of an XY, a YZ and, an XZ region. As the numerical results indicate, if the XYZ domain is between an XY and a YZ region, species Y grows faster than X and Z in two out of the four chemostats, for parameter values leading to XYZ coexistence. Apart from the SS-XYZ domain, there are 7 more domains (i.e., SS-0, SS-X, SS-Y, SS-Z, SS-XY, SS-YZ and, SS-XZ) .

From the numerical studies, it was found that the existence or not of SS-XYZ domain depends mainly on the values of γ_1, β, β_1, and β_2, and not so much on the values of R_1, R_2, R_3, and R_4 (which are recycle ratios, and thus, indicate the degree of interconnection of subenvironments). Comparing the diagrams shown in Figures 4.2 and 4.3, one can see that the SS-XYZ domain shifts to higher u_f values for decreasing γ_1 values.

The operating diagrams and computer simulations show that there is no domain in the operating parameters space where more than one steady state is meaningful and stable. In other words, the steady states are mutually exclusive. The results of the local stability analysis based on the character of eigenvalues of the Jacobian matrix, indicate that there are cases where damped oscillations will be observed during transients.

The main conclusion is that the special configuration of four interconnected chemostats considered here can lead to coexistence of three pure and simple competitors at steady state.

Table 4.1: Parameters used for Searching SS-XYZ domain[1]

$\gamma_1 = 1.0$	$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$
$\varphi_2 = 0.4$	$\beta = 1.8$	$\beta_1 = 1.6$	$\beta_2 = 1.2$	
$No.1$	$R_1 = 0.1$	$R_2 = 0.1$	$R_3 = 0.1$	$R_4 = 0.1$
$No.2$	$R_1 = 0.1$	$R_2 = 1.0$	$R_3 = 0.1$	$R_4 = 1.0$
$No.3$	$R_1 = 0.01$	$R_2 = 0.01$	$R_3 = 0.01$	$R_4 = 0.01$
$No.4$	$R_1 = 0.01$	$R_2 = 1.0$	$R_3 = 0.01$	$R_4 = 1.0$
$No.5$	$R_1 = 0.001$	$R_2 = 0.001$	$R_3 = 0.001$	$R_4 = 0.001$
$No.6$	$R_1 = 10.0$	$R_2 = 0.1$	$R_3 = 10.0$	$R_4 = 0.1$
$No.7$	$R_1 = 0.0001$	$R_2 = 0.0001$	$R_3 = 0.0001$	$R_4 = 0.0001$
$No.8$	$R_1 = 10.0$	$R_2 = 10.0$	$R_3 = 10.0$	$R_4 = 10.0$
$No.9$	$R_1 = 100.0$	$R_2 = 100.0$	$R_3 = 100.0$	$R_4 = 100.0$
$No.10$	$R_1 = 1000.0$	$R_2 = 1000.0$	$R_3 = 1000.0$	$R_4 = 1000.0$
$\gamma_1 = 1.0$	$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$
$\varphi_2 = 0.4$	$R_1 = 1.0$	$R_2 = 1.0$	$R_3 = 1.0$	$R_4 = 1.0$
$No.11$	$\beta = 0.2$	$\beta_1 = 0.6$	$\beta_2 = 0.8$	
$No.12$	$\beta = 0.2$	$\beta_1 = 1.0$	$\beta_2 = 0.2$	

[1]No SS-XYZ domains were found by using these parameters

$\gamma_1 = 1.27$	$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$
$\varphi_2 = 0.4$	$R_1 = 1.0$	$R_2 = 1.0$	$R_3 = 1.0$	$R_4 = 1.0$

$No.13$	$\beta = 0.2$	$\beta_1 = 0.6$	$\beta_2 = 0.8$
$No.14$	$\beta = 0.2$	$\beta_1 = 1.0$	$\beta_2 = 0.2$

$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$	$\varphi_2 = 0.4$
$\beta = 1.0$	$\beta_1 = 1.0$	$\beta_2 = 1.0$	$R_1 = 1.0$	$R_2 = 1.0$
$R_3 = 1.0$	$R_4 = 1.0$			

$No.15$	$\gamma_1 = 0.8$
$No.16$	$\gamma_1 = 0.5$
$N0.17$	$\gamma_1 = 0.2$
$No.18$	$\gamma_1 = 1.5$
$No.19$	$\gamma_1 = 2.0$
$No.20$	$\gamma_1 = 3.0$

$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$	$\varphi_2 = 0.4$
$\beta = 1.8$	$\beta_1 = 1.6$	$\beta_2 = 1.2$	$R_1 = 1.0$	$R_2 = 1.0$
$R_3 = 1.0$	$R_4 = 1.0$			

$No.21$	$\gamma_1 = 0.8$
$No.22$	$\gamma_1 = 0.5$

$No.23$	$\gamma_1 = 0.2$
$No.24$	$\gamma_1 = 1.5$
$No.25$	$\gamma_1 = 2.0$
$No.26$	$\gamma_1 = 3.0$

Table 4.2: Parameters used for The Diagram of Figure 4.2

$R_1 = 1.0$	$R_2 = 1.0$	$R_3 = 1.0$	$R_4 = 1.0$	$\gamma_1 = 1.0$
$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$	$\varphi_2 = 0.4$
$\beta = 1.8$	$\beta_1 = 1.6$	$\beta_2 = 1.2$		

Table 4.3: Parameters used for The Diagram of Figure 4.3

$R_1 = 1.0$	$R_2 = 1.0$	$R_3 = 1.0$	$R_4 = 1.0$	$\gamma_1 = 1.27$
$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$	$\varphi_2 = 0.4$
$\beta = 1.8$	$\beta_1 = 1.6$	$\beta_2 = 1.2$		

Table 4.4: Parameters used for The Diagram of Figure 4.4

$R_1 = 1.0$	$R_2 = 1.0$	$R_3 = 1.0$	$R_4 = 1.0$	$\gamma_1 = 1.0$
$\eta_1 = 1.0$	$\omega_1 = 0.25$	$\omega_2 = 0.125$	$\varphi_1 = 0.5$	$\varphi_2 = 0.4$
$\beta = 1.0$	$\beta_1 = 1.0$	$\beta_2 = 1.0$		

Table 4.5: Coexistence Concentration Values for Cases of Figure 4.2

	$\alpha = 0.3177$	$u_f = 9.5$	
$x_1 = 0.153476$	$y_1 = 1.563334$	$z_1 = 6.888419$	$u_1 = 0.394771$
$x_2 = 0.170221$	$y_2 = 1.620254$	$z_2 = 7.189718$	$u_2 = 0.019807$
$x_3 = 0.186985$	$y_3 = 6.233023$	$z_3 = 6.233023$	$u_3 = 6.233023$
$x_4 = 0.197931$	$y_4 = 7.104451$	$z_4 = 7.104451$	$u_4 = 0.067521$
	$\alpha = 0.3144$	$u_f = 10.0$	
$x_1 = 0.423697$	$y_1 = 2.856779$	$z_1 = 6.330318$	$u_1 = 0.389206$
$x_2 = 0.469834$	$y_2 = 2.947235$	$z_2 = 6.564629$	$u_2 = 0.018302$
$x_3 = 0.519122$	$y_3 = 2.692756$	$z_3 = 5.689020$	$u_3 = 1.099102$
$x_4 = 0.547187$	$y_4 = 2.950524$	$z_4 = 6.440660$	$u_4 = 0.061629$
	$\alpha = 0.3119$	$u_f = 13.0$	
$x_1 = 0.258189$	$y_1 = 12.315309$	$z_1 = 0.040920$	$u_1 = 0.385582$
$x_2 = 0.286018$	$y_2 = 12.653697$	$z_2 = 0.042209$	$u_2 = 0.018076$
$x_3 = 0.316980$	$y_3 = 11.549471$	$z_3 = 0.036483$	$u_3 = 1.097066$
$x_4 = 0.332631$	$y_4 = 12.570600$	$z_4 = 0.040988$	$u_4 = 0.055780$

Table 4.6: Coexistence Concentration Values for Cases of Figure 4.3

	$\alpha = 0.3195$	$u_f = 8.0$	
$x_1 = 0.966749$	$y_1 = 0.004227$	$z_1 = 6.558638$	$u_1 = 0.470387$
$x_2 = 1.017935$	$y_2 = 0.004376$	$z_2 = 6.974766$	$u_2 = 0.002923$
$x_3 = 1.036175$	$y_3 = 0.004044$	$z_3 = 6.223678$	$u_3 = 0.736102$
$x_4 = 1.071564$	$y_4 = 0.004323$	$z_4 = 6.916110$	$u_4 = 0.008002$
	$\alpha = 0.3126$	$u_f = 10.0$	
$x_1 = 4.147524$	$y_1 = 0.142330$	$z_1 = 5.219607$	$u_1 = 0.490539$
$x_2 = 4.297440$	$y_2 = 0.146673$	$z_2 = 5.552681$	$u_2 = 0.003205$
$x_3 = 4.246765$	$y_3 = 0.133587$	$z_3 = 4.905232$	$u_3 = 0.714416$
$x_4 = 4.393149$	$y_4 = 0.142884$	$z_4 = 5.455819$	$u_4 = 0.008148$
	$\alpha = 0.3060$	$u_f = 13.0$	
$x_1 = 7.119048$	$y_1 = 4.695833$	$z_1 = 0.782733$	$u_1 = 0.402386$
$x_2 = 7.526088$	$y_2 = 4.662106$	$z_2 = 0.784628$	$u_2 = 0.027179$
$x_3 = 7.350470$	$y_3 = 3.760823$	$z_3 = 0.602176$	$u_3 = 1.286531$
$x_4 = 7.940634$	$y_4 = 4.250685$	$z_4 = 0.701739$	$u_4 = 0.106942$

Table 4.7: Coexistence Concentration Values for Cases of Figure 4.4

	$\alpha = 0.4010$	$u_f = 6.0$	
$x_1 = 1.267590$	$y_1 = 1.862885$	$z_1 = 2.229594$	$u_1 = 0.639931$
$x_2 = 1.301673$	$y_2 = 2.055494$	$z_2 = 2.598591$	$u_2 = 0.044242$
$x_3 = 1.180402$	$y_3 = 1.905042$	$z_3 = 2.394410$	$u_3 = 0.520147$
$x_4 = 1.232309$	$y_4 = 2.055343$	$z_4 = 2.658971$	$u_4 = 0.053377$
	$\alpha = 0.4058$	$u_f = 8.0$	
$x_1 = 0.752746$	$y_1 = 5.092725$	$z_1 = 1.570612$	$u_1 = 0.583917$
$x_2 = 0.764150$	$y_2 = 5.446828$	$z_2 = 1.761265$	$u_2 = 0.027758$
$x_3 = 0.706135$	$y_3 = 5.141385$	$z_3 = 1.657143$	$u_3 = 0.495337$
$x_4 = 0.729084$	$y_4 = 5.437111$	$z_4 = 1.798579$	$u_4 = 0.035226$
	$\alpha = 0.4080$	$u_f = 10.0$	
$x_1 = 0.028425$	$y_1 = 1.555932$	$z_1 = 8.198089$	$u_1 = 0.217554$
$x_2 = 0.031691$	$y_2 = 1.618762$	$z_2 = 8.345777$	$u_2 = 0.003770$
$x_3 = 0.029639$	$y_3 = 1.566341$	$z_3 = 8.197147$	$u_3 = 0.206872$
$x_4 = 0.031842$	$y_4 = 1.615667$	$z_4 = 8.347118$	$u_4 = 0.005373$

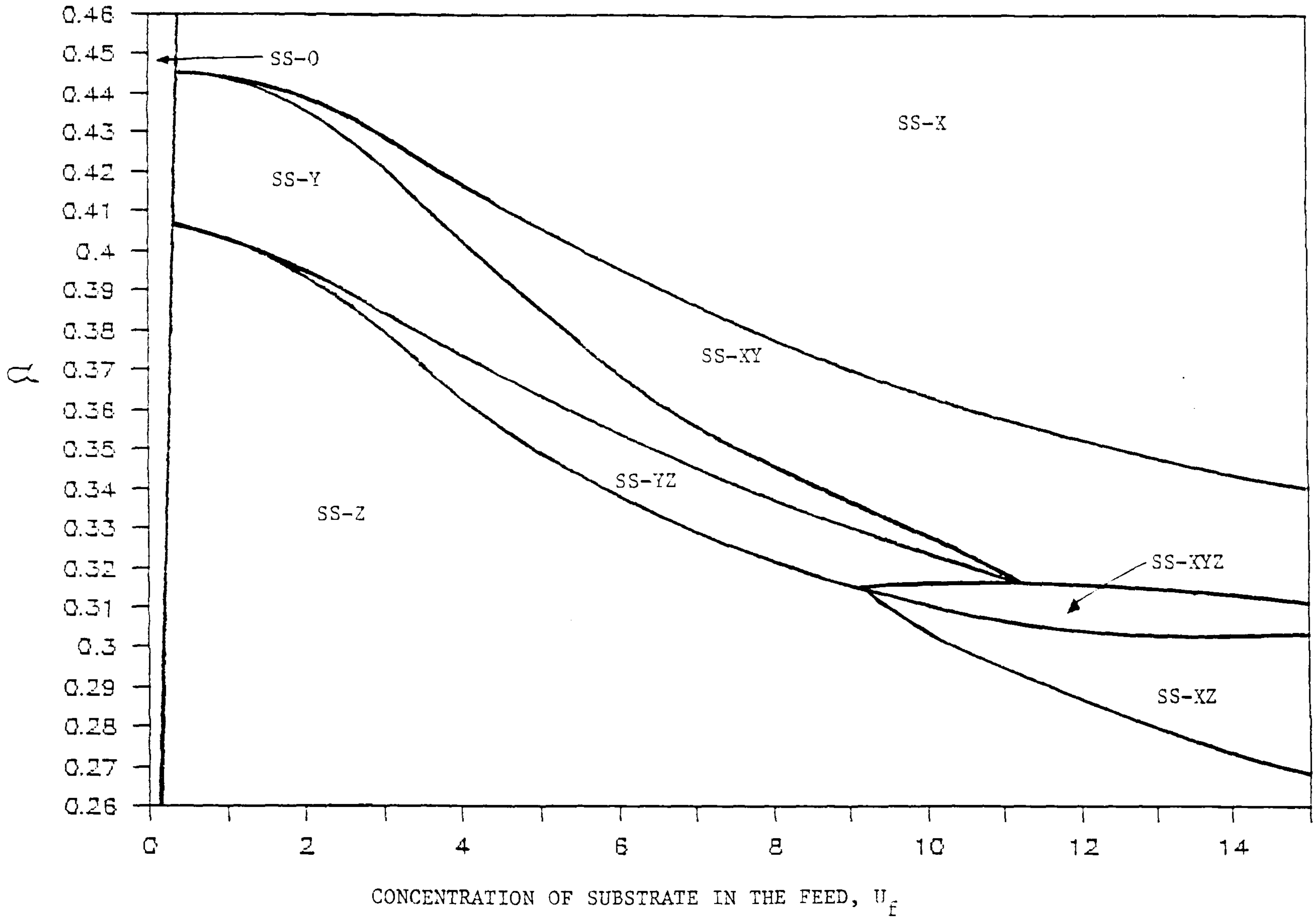


Figure 4.2: Operating Diagram I

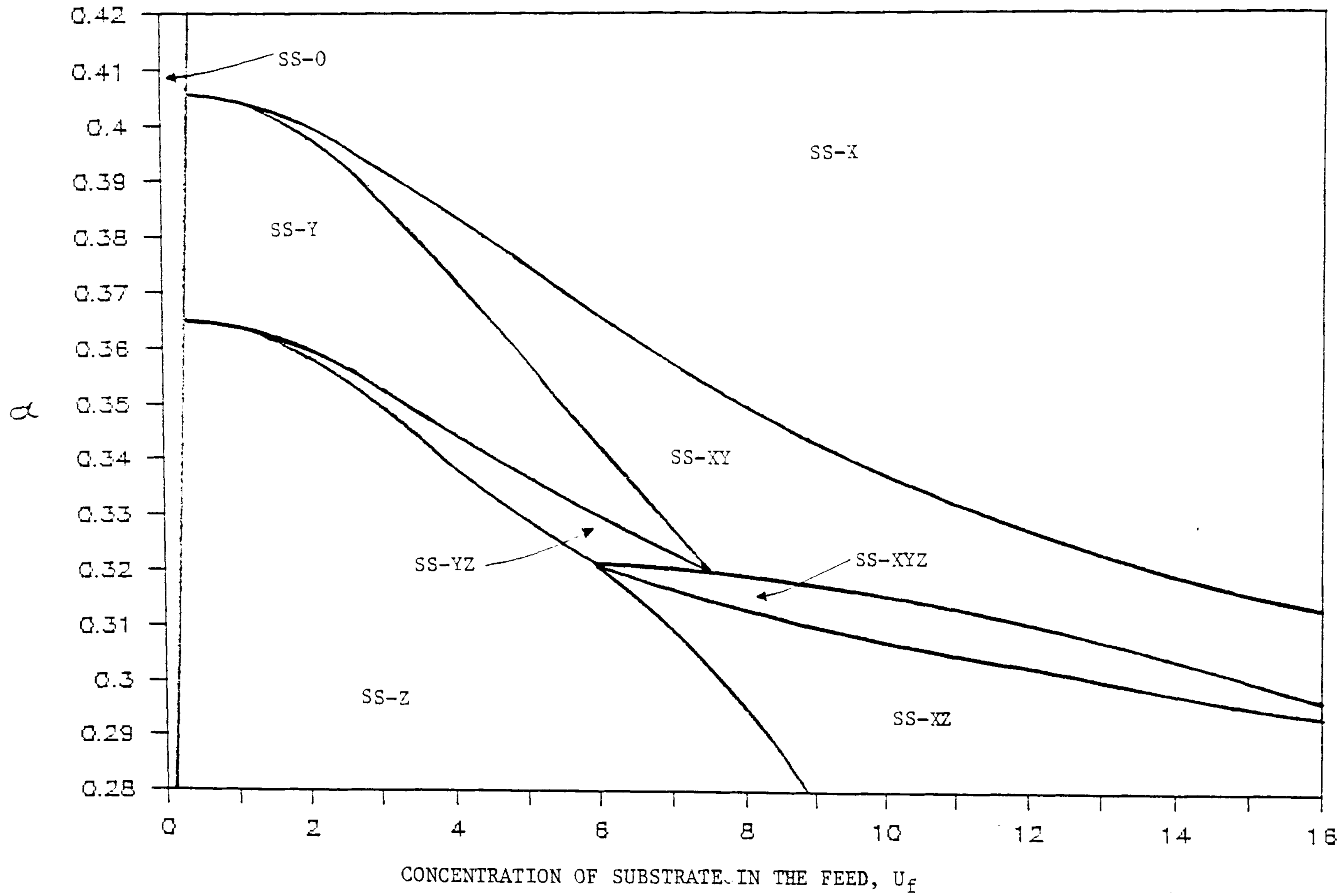


Figure 4.3: Operating Diagram II

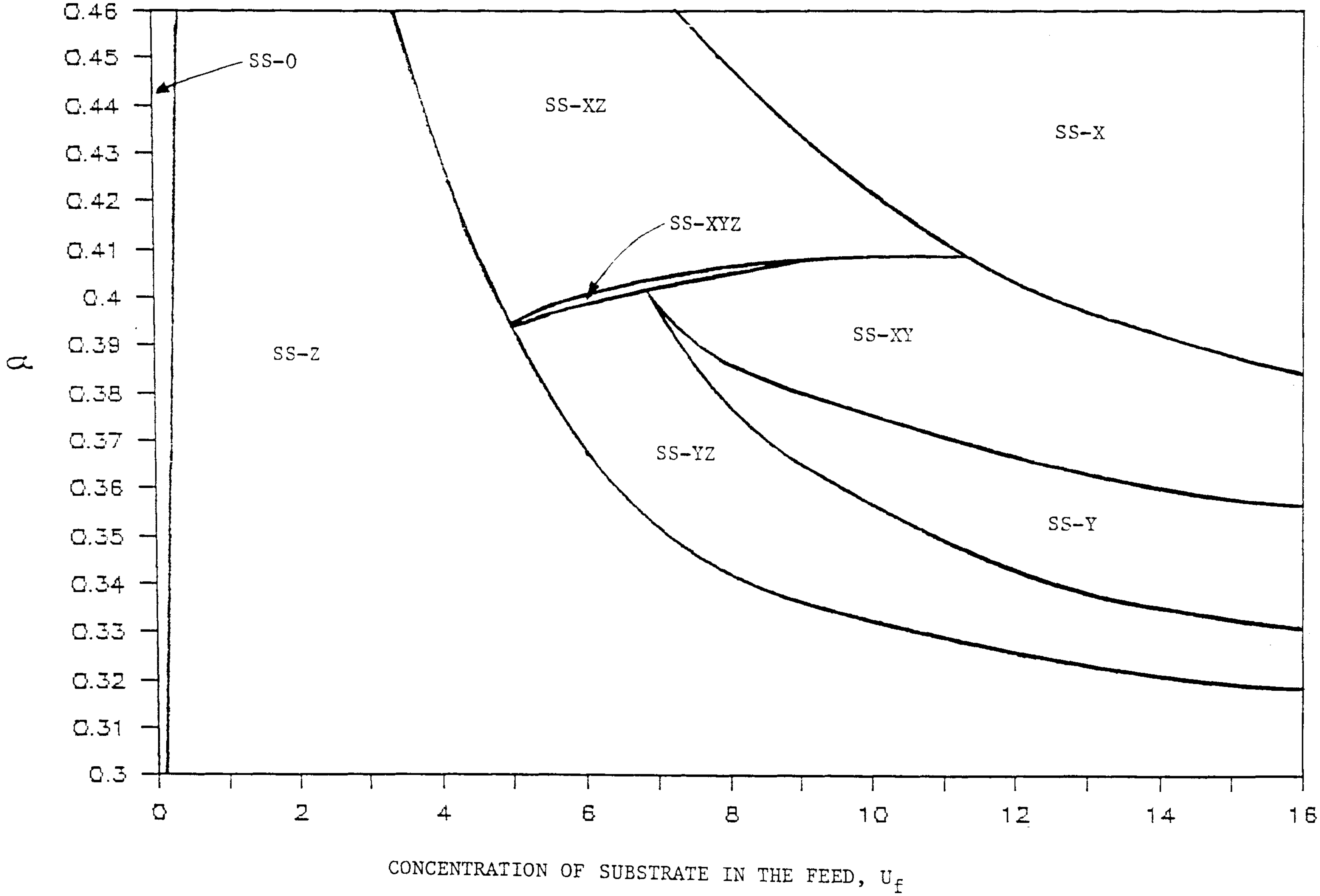


Figure 4.4: Operating Diagram III

Chapter 5

CONCLUSIONS

It was known that two pure and simple competitors can coexist in two interconnected reactors [Kung and Baltzis (18)], while three pure and simple competitors cannot coexist in three interconnected vessels [Chang and Baltzis (6)]. These facts lead to the basic question addressed in this thesis, namely, if three pure and simple competitors can coexist in four interconnected bioreactors. The answer is that coexistence of three populations competing purely and simply, is possible in such a bioreactors configuration.

Computer simulations have indicated that the domain of coexistence of three species (XYZ), if it exists, lies between domains of coexistence of two species.

Based on the results of this study, and what was already known about microbial competition one can conclude that N pure and simple competitors cannot coexist in N interconnected bioreactors, but coexistence seems to be possible in M vessels, where $M > N$. One can also argue that if there are N competitors, in order for them to coexist in an environment, this environment must be comprised of two subenvironments each one of which, should able to maintain N-1 species. In configurations of chemostats then, it seems that one needs 2^{N-1} vessels. This seems to be a necessary but not sufficient condition.

The disposition of the specific growth rate curves shown in Figure 3.2 (case 6) which allows one species to have the competitive advantage over the other two in at least one of the vessels is the only one which can allow coexistence of three species.

Computer simulations indicate that all eight types of steady states are mutually exclusive, in the sense that there is no domain in the operating parameters space where more than one steady state is meaningful and stable. Furthermore, none of the eight types of steady states exhibits multiplicity.

The results of this thesis further reenforce the argument that spatial heterogeneities can lead to a very diversified ecosystem, even under conditions of intense competition.

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APPENDIX

PROGRAM SOURCE FILE

The following source files are written in Fortran 77 and have been implemented on a VAX/VMS system.

```
C***********************************************************************
C
C
C     MONOD predicts the concentrations of biomass & substrate in four
C
C     interconnected chemostats by MONOD MODEL
C
C
C***********************************************************************

C              ------------------------------------------
C
C                 APPLIED NUMERICAL METHODS
C
C                 MICHELSEN'S METHOD
C              ------------------------------------------

      IMPLICIT REAL*16 (A-H,O-Z)
      PARAMETER (N=16)
      DIMENSION Y(N),YOLD(N),YOLD1(N),YA(N),F(N),FOLD(N)
      DIMENSION YK1(N),YK2(N),YK3(N),DF(N,N),DFOLD(N,N)
      DIMENSION W(N)
      COMMON/AB/ALFA,UF,R1,R2,R3,R4,FI1,FI2,W1,W2,
     *          BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
      COMMON/AB1/CTA12,CTA20,CTA21,CTA23,CTA34,CTA40,CTA42,CTA43
      EXTERNAL FUN,DFUN,OUT
      DATA NTAB/1/
      OPEN (5,FILE='MONOD.DAT',STATUS='OLD')
      OPEN (6,FILE='MONOD.OUT',STATUS='NEW')

C
      DO 10 J=1,N
        W(J)=1.0
   10 CONTINUE
C
      READ (5,*)ALFA,UF,acc
      READ (5,*)R1,R2,R3,R4
      READ (5,*)BETA,BETA1,BETA2,GA,GA1,GA2
      READ (5,*)ETA,ETA1,ETA2,FI1,FI2,W1,W2
      READ (5,*)H0,EPS,NPRINT,XEND
      READ (5,*)(Y(J),J=1,N)
C
      CTA=ALFA/(R1*(R3+1.0)+1.0)
      CTA12=CTA*(R1*(R3+1.0)+R2*R3*(GA1+1.0)+(R2+1.0))
      CTA23=CTA*(R3*(GA1+1.0)+1.0)
      CTA40=CTA*(GA1*(R1+1.0)+1.0)
      CTA34=(R4+R3+1.0)*CTA40
      CTA21=R2*CTA23
      CTA20=R1*CTA23
      CTA42=R3*CTA40
      CTA43=R4*CTA40
      XST=0.0
C
      WRITE(6,11)
   11 FORMAT(/17X,'****MICHELSEN METHOD FOR INTEGRATING****'/30X,
     *       '----MONOD----'/)
      WRITE(6,22)
   22 FORMAT(/21X,'****PARAMETER FOR INTEGRATING****')
```

```
      write (6,25) acc
 25   format(/6x,'ACCURACY=',G9.2)
      WRITE(6,33)H0,EPS,NPRINT,XEND,ALFA
 33   FORMAT(/3X,'H0=',F6.3,4X,'EPS=',G9.2,2X,'NPRINT=',I4,2X,'XEND='
     *       E14.6,3X,'ALFA=',F8.5)
      WRITE(6,44)UF,R1,R2,R3,R4
 44   FORMAT(/6X,'UF=',F6.3,4X,'R1=',F8.4,7X,'R2=',F8.5,3X,'R3=',F9.4
     *       7X,'R4=',F9.4)
      WRITE(6,66)GA,GA1,GA2,FI1,FI2
 66   FORMAT(/6X,'GA=',F5.2,5X,'GA1=',F5.2,6X,'GA2=',F5.2,2X,'FI1=',
     *       F5.2,6X,'FI2=',F5.2)
      WRITE(6,77)W1,W2,ETA,ETA1,ETA2
 77   FORMAT(/6X,'W1=',F6.3,4X,'W2=',F6.3,6X,'ETA=',F5.2,2X,'ETA1=',
     *       F5.2,5X,'ETA2=',F5.2)
      WRITE(6,88)BETA,BETA1,BETA2
 88   FORMAT(/6X,'BETA=',F5.2,3X,'BETA1=',F5.2,4X,'BETA2=',F5.2)
      WRITE(6,99)(Y(J),J=1,N)
 99   FORMAT(/1X,'INITIAL CONCENTRATIONS:'/5X,'Y=',8F9.6,/7X,8F9.6)

      TIME=(XEND-XST)/FLOAT(NTAB)

    ------MICHELSEN'S INTEGRATION BEGINS------

    X1=0.0
    DO 50 J=1,NTAB
    X2=J*TIME
    CALL STIFF3(N,N,NPRINT,FUN,DFUN,OUT,X1,
   *X2,H0,EPS,W,Y,YOLD,YOLD1,IP,YA,YK1,YK2,YK3,
   *DF,DFOLD,F,FOLD)
 50   X1=X2
      STOP
      END

    ------SUBROUTINE OUT FOR PRINTING DATA------

      SUBROUTINE OUT(T,Y,H)
      PARAMETER(N=16)
      IMPLICIT REAL*16 (A-H,O-Z)
      REAL*16 Y(N),x(n)

      do 145 i=1,n
      if (abs(y(i)-x(i)).le.acc) then
      stop
      endif
145    continue
      WRITE(6,1)T,H
  1   FORMAT(/6X,'TIME=',E14.6,5X,'H=',E14.6)
      WRITE(6,2)(Y(I),I=1,4)
  2   FORMAT(/1X,'X1=',f9.6,2x,'Y1=',f9.6,2X,'Z1=',f9.6,
     *       2X,'U1=',f9.6)
      WRITE(6,3)(Y(I),I=5,8)
  3   FORMAT(/1X,'X2=',f9.6,2X,'Y2=',f9.6,2X,'Z2=',f9.6,
     *       2X,'U2=',f9.6)
      WRITE(6,4)(Y(I),I=9,12)
  4   FORMAT(/1X,'X3=',f9.6,2X,'Y3=',f9.6,2X,'Z3=',f9.6,
     *       2X,'U3=',f9.6)
      WRITE(6,5)(Y(I),I=13,16)
  5   FORMAT(/1X,'X4=',f9.6,2X,'Y4=',f9.6,2X,'Z4=',f9.6,
     *       2X,'U4=',f9.6)
      do 123 i=1,16
```

```
      x(i)=y(i)
  123 continue
      RETURN
      END

C
C     ------SUBROUTINE FUN FOR EVALUTING THE VECTOR F-------
C
      SUBROUTINE FUN(X,Y,F)
      IMPLICIT REAL*16(A-H,O-Z)
      PARAMETER (N=16)
      DIMENSION Y(N),F(N)
      COMMON/AB/ALFA,UF,R1,R2,R3,R4,FI1,FI2,W1,W2,
     *          BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
      COMMON/AB1/CTA12,CTA20,CTA21,CTA23,CTA34,CTA40,CTA42,CTA43
C    ------CALCULATE RATE OF CHANGE OF COMPONENTS------

C
      B1=Y(4)/(Y(4)+1.0)
      B2=Y(8)/(Y(8)+1.0)
      B3=Y(12)/(Y(12)+1.0)
      B4=Y(16)/(Y(16)+1.0)
      C1=FI1*Y(4)/(W1+Y(4))
      C2=FI1*Y(8)/(W1+Y(8))
      C3=FI1*Y(12)/(W1+Y(12))
      C4=FI1*Y(16)/(W1+Y(16))
      D1=FI2*Y(4)/(W2+Y(4))
      D2=FI2*Y(8)/(W2+Y(8))
      D3=FI2*Y(12)/(W2+Y(12))
      D4=FI2*Y(16)/(W2+Y(16))
      E1=B1*Y(1)+C1*Y(2)+D1*Y(3)
      E2=B2*Y(5)+C2*Y(6)+D2*Y(7)
      E3=B3*Y(9)+C3*Y(10)+D3*Y(11)
      E4=B4*Y(13)+C4*Y(14)+D4*Y(15)
      F(1)=CTA21*Y(5)+(B1-CTA12)*Y(1)
      F(2)=CTA21*Y(6)+(C1-CTA12)*Y(2)
      F(3)=CTA21*Y(7)+(D1-CTA12)*Y(3)
      F(4)=ALFA*UF+CTA21*Y(8)-E1-CTA12*Y(4)
      F(5)=BETA*CTA12*Y(1)+BETA*CTA42*Y(13)+(B2-BETA*(CTA21+CTA23+CTA2(
     *     )*Y(5)
      F(6)=BETA*CTA12*Y(2)+BETA*CTA42*Y(14)+(C2-BETA*(CTA21+CTA23+CTA2(
     *     )*Y(6)
      F(7)=BETA*CTA12*Y(3)+BETA*CTA42*Y(15)+(D2-BETA*(CTA21+CTA23+CTA2(
     *     )*Y(7)
      F(8)=BETA*CTA12*Y(4)+BETA*CTA42*Y(16)-E2-BETA*(CTA21+CTA23+CTA20)
     *      *Y(8)
      F(9)=BETA1*CTA23*Y(5)+BETA1*CTA43*Y(13)+(B3-BETA1*CTA34)*Y(9)
      F(10)=BETA1*CTA23*Y(6)+BETA1*CTA43*Y(14)+(C3-BETA1*CTA34)*Y(10)
      F(11)=BETA1*CTA23*Y(7)+BETA1*CTA43*Y(15)+(D3-BETA1*CTA34)*Y(11)
      F(12)=ETA1*BETA1*GA1*ALFA*UF+BETA1*CTA23*Y(8)+BETA1*CTA43*Y(16)
     *      -E3-BETA1*CTA34*Y(12)
      F(13)=BETA2*CTA34*Y(9)+(B4-BETA2*(CTA42+CTA43+CTA40))*Y(13)
      F(14)=BETA2*CTA34*Y(10)+(C4-BETA2*(CTA42+CTA43+CTA40))*Y(14)
      F(15)=BETA2*CTA34*Y(11)+(D4-BETA2*(CTA42+CTA43+CTA40))*Y(15)
      F(16)=BETA2*CTA34*Y(12)-E4-BETA2*(CTA42+CTA43+CTA40)*Y(16)
      RETURN
      END
C
C
C     ----SUBROUTINE DFUN FOR EVALUTING THE JACOBINE MATRIX----
```

```
C
      SUBROUTINE DFUN(X,Y,DF)
      IMPLICIT REAL*16(A-H,O-Z)
      PARAMETER (N=16)
      DIMENSION Y(N),DF(N,N),F(4),G(4),H(4),FD(4),GD(4),HD(4)
      COMMON/AB/ALFA,UF,R1,R2,R3,R4,FI1,FI2,W1,W2,
     *          BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
      COMMON/AB1/CTA12,CTA20,CTA21,CTA23,CTA34,CTA40,CTA42,CTA43

C
      DO 100 I=1,4
      F(I)=Y(4*I)/(Y(4*I)+1.0)
      G(I)=FI1*Y(4*I)/(W1+Y(4*I))
      H(I)=FI2*Y(4*I)/(W2+Y(4*I))
  100 CONTINUE
      DO 150 I=1,4
      FD(I)=1.0/((1.0+Y(4*I))*(1.0+Y(4*I)))
      GD(I)=FI1*W1/((W1+Y(4*I))*(W1+Y(4*I)))
      HD(I)=FI2*W2/((W2+Y(4*I))*(W2+Y(4*I)))
  150 CONTINUE
      DO 200 I=1,16
      DO 200 J=1,16
      DF(I,J)=0.0
  200 CONTINUE
      DF(1,1)=F(1)-CTA12
      DF(1,4)=Y(1)*FD(1)
      DF(1,5)=CTA21
      DF(2,2)=G(1)-CTA12
      DF(2,4)=Y(2)*GD(1)
      DF(2,6)=CTA21
      DF(3,3)=H(1)-CTA12
      DF(3,4)=Y(3)*HD(1)
      DF(3,7)=CTA21
      DF(4,1)=-F(1)
      DF(4,2)=-G(1)
      DF(4,3)=-H(1)
      DF(4,4)=-CTA12-(Y(1)*FD(1)+Y(2)*GD(1)+Y(3)*HD(1))
      DF(4,8)=CTA21
      DF(5,1)=BETA*CTA12
      DF(5,5)=F(2)-BETA*(CTA21+CTA23+CTA20)
      DF(5,8)=Y(5)*FD(2)
      DF(5,13)=BETA*CTA42
      DF(6,2)=BETA*CTA12
      DF(6,6)=G(2)-BETA*(CTA21+CTA23+CTA20)
      DF(6,8)=Y(6)*GD(2)
      DF(6,14)=BETA*CTA42
      DF(7,3)=BETA*CTA12
      DF(7,7)=H(2)-BETA*(CTA21+CTA23+CTA20)
      DF(7,8)=Y(7)*HD(2)
      DF(7,15)=BETA*CTA42
      DF(8,4)=BETA*CTA12
      DF(8,5)=-F(2)
      DF(8,6)=-G(2)
      DF(8,7)=-H(2)
      DF(8,8)=-BETA*(CTA21+CTA23+cta20)-(Y(5)*FD(2)+Y(6)*GD(2)+Y(7)*
     *        HD(2))
      DF(8,16)=BETA*CTA42
      DF(9,5)=BETA1*CTA23
      DF(9,9)=F(3)-BETA1*CTA34
      DF(9,12)=Y(9)*FD(3)
```

```
      DF(9,13)=BETA1*CTA43
      DF(10,6)=BETA1*CTA23
      DF(10,10)=G(3)-BETA1*CTA34
      DF(10,12)=Y(10)*GD(3)
      DF(10,14)=BETA1*CTA43
      DF(11,7)=BETA1*CTA23
      DF(11,11)=H(3)-BETA1*CTA34
      DF(11,12)=Y(11)*HD(3)
      DF(11,15)=BETA1*CTA43
      DF(12,8)=BETA1*CTA23
      DF(12,9)=-F(3)
      DF(12,10)=-G(3)
      DF(12,11)=-H(3)
      DF(12,12)=-BETA1*CTA34-(Y(9)*FD(3)+Y(10)*
     *          GD(3)+Y(11)*HD(3))
      DF(12,16)=BETA1*CTA43
      DF(13,9)=BETA2*CTA34
      DF(13,13)=F(4)-BETA2*(CTA40+CTA42+CTA43)
      DF(13,16)=Y(13)*FD(4)
      DF(14,10)=BETA2*CTA34
      DF(14,14)=G(4)-BETA2*(CTA40+CTA42+CTA43)
      DF(14,16)=Y(14)*GD(4)
      DF(15,11)=BETA2*CTA34
      DF(15,15)=H(4)-BETA2*(CTA40+CTA42+CTA43)
      DF(15,16)=Y(15)*HD(4)
      DF(16,12)=BETA2*CTA34
      DF(16,13)=-F(4)
      DF(16,14)=-G(4)
      DF(16,15)=-H(4)
      DF(16,16)=-BETA2*(CTA40+CTA42+CTA43)-(Y(13)*FD(4)+Y(14)*GD(4)+
     *          Y(15)*HD(4))
      RETURN
      END
```

```
C     -----  SUBROUTINE STIFF3 :  MICHELSEN'S METHOD  -----
C
      SUBROUTINE STIFF3(N,ND,NPRINT,FUN,DFUN,OUT,X0,
     *X1,H0,EPS,W,Y,YOLD,YOLD1,IP,YA,YK1,YK2,YK3,
     *DF,DFOLD,F,FOLD)
        IMPLICIT real*16 (A-H,O-Z)
      DIMENSION IP(ND),Y(ND),YOLD(ND),YOLD1(ND),YA(ND),YK1(ND),YK2(ND)
      DIMENSION YK3(ND),W(ND),F(ND),FOLD(ND),DF(ND,ND),DFOLD(ND,ND)
      EXTERNAL FUN,DFUN,OUT
      ICON=0
      NOUT=0
      X=X0
      H=H0
      IF(X0+2.D0*H.LT.X1) GO TO 1
2     H=(X1-X)/2.D0
      ICON=1
1     IF(ICON.EQ.0.AND.X+4.D0*H.GT.X1) H=(X1-X)/4.D0
      CALL FUN(X,Y,F)
```

```
      CALL DFUN(X,Y,DF)
      IHA=-1
      DO 30 I=1,N
      YOLD(I)=Y(I)
      FOLD(I)=F(I)
      DO 30 J=1,N
30    DFOLD(I,J)=DF(I,J)
37    CALL SIRK3(X,N,ND,FUN,IP,F,Y,YK1,YK2,YK3,DF,2.D0*H)
      DO 35 I=1,N
      YA(I)=Y(I)
      Y(I)=YOLD(I)
      F(I)=FOLD(I)
      DO 35 J=1,N
35    DF(I,J)=DFOLD(I,J)
38    IHA=IHA+1
      CALL SIRK3(X,N,ND,FUN,IP,F,Y,YK1,YK2,YK3,DF,H)
      CALL FUN(X,Y,F)
      CALL DFUN(X,Y,DF)
      DO 40 I=1,N
40    YOLD1(I)=Y(I)
      CALL SIRK3(X,N,ND,FUN,IP,F,Y,YK1,YK2,YK3,DF,H)
      E=0.D0
      DO 41 I=1,N
      ES=W(I)*QABS(YA(I)-Y(I))/(1.D0+QABS(Y(I)))
      IF(ES.GT.E) E=ES
41    CONTINUE
      Q=E/EPS
      QA=(4.D0*Q)**.25D0
      IF(Q.LE.1.D0) GO TO 48
      DO 45 I=1,N
      YA(I)=YOLD1(I)
      F(I)=FOLD(I)
      Y(I)=YOLD(I)
      DO 45 J=1,N
45    DF(I,J)=DFOLD(I,J)
      H=H/2.D0
      ICON=0
      GO TO 38
48    DO 49 I=1,N
49    Y(I)=Y(I)+(Y(I)-YA(I))/7.D0
      X=X+2.D0*H
      QA=1.D0/(QA+1.D-10)
      IF(QA.GT.3.D0) QA=3.D0
      H=QA*H
      NOUT=NOUT+1
      HH=2.D0*H/QA
      IF((NOUT/NPRINT)*NPRINT.EQ.NOUT.OR.ICON.EQ.1) CALL OUT(X,Y,HH)
      IF(ICON.EQ.1) GO TO 187
      H0=H
      IF(X+2.D0*H.LT.X1) GO TO 1
      GO TO 2
187   RETURN
      END
C
C
C
C    -----  SUBROUTINE BACK :   BACK SUBSTITUTION ALGORITHM  -----
C
      SUBROUTINE BACK(ND,N,IPIV,A,V)
        IMPLICIT real*16 (A-H,O-Z)
```

```
      DIMENSION IPIV(ND),A(ND,ND),V(ND)
      N1=N-1
      DO 10 I=1,N1
      I1=I+1
      K=IPIV(I)
      IF(K.EQ.I) GO TO 11
      X=V(I)
      V(I)=V(K)
      V(K)=X
11    DO 10 J=I1,N
10    V(J)=V(J)+A(J,I)*V(I)
      V(N)=V(N)/A(N,N)
      DO 15 II=2,N
      I=N+1-II
      I1=I+1
      DO 16 J=I1,N
16    V(I)=V(I)-A(I,J)*V(J)
15    V(I)=V(I)/A(I,I)
      RETURN
      END
C
C
C
C   -----  SUBROUTINE LU :   FOR DECOMPOSING A MATRIX   A=LU  -----
C
      SUBROUTINE LU(ND,N,IPIV,A)
        IMPLICIT real*16 (A-H,O-Z)
      DIMENSION IPIV(ND),A(ND,ND)
      IPIV(N)=N
      N1=N-1
      DO 10 I=1,N1
      X=A(I,I)
      IF(X.LT.0.D0) X=-X
      IPIV(I)=I
      I1=I+1
      DO 11 J=I1,N
      Y=A(J,I)
      IF(Y.LT.0.D0) Y=-Y
      IF(Y.LE.X) GO TO 11
      X=Y
      IPIV(I)=J
11    CONTINUE
      IF(IPIV(I).EQ.I) GO TO 14
      K=IPIV(I)
      DO 12 J=I,N
      X=A(I,J)
      A(I,J)=A(K,J)
12    A(K,J)=X
14    DO 10 J=I1,N
      X=-A(J,I)/A(I,I)
      A(J,I)=X
      DO 10 K=I1,N
10    A(J,K)=A(J,K)+X*A(I,K)
      RETURN
      END
C
C
C
C   -----  SUBRROUTINE SIRK3 :
C                        SINGLE-STEP SEMI-IMPLICIT INTEGRATION  -----
```

```
C
      SUBROUTINE SIRK3(X,N,ND,FUN,IPIV,F,Y,YK1,YK2,YK3,DF,H)
        IMPLICIT real*16 (A-H,O-Z)
      DIMENSION F(ND),Y(ND),YK1(ND),YK2(ND),YK3(ND)
      DIMENSION IPIV(ND),DF(ND,ND),R(4)
      DATA A,R/.4358665215084589D0,1.037609496131859D0,
     *.8349304838526377D0,-.6302020887244523D0,-.2423378912600452D0/
      DO 5 I=1,N
      DO 6 J=1,N
      DF(I,J)=-H*A*DF(I,J)
      IF(QABS(DF(I,J)).LT.1.D-12) DF(I,J)=0.D0
6     CONTINUE
5     DF(I,I)=DF(I,I)+1.D0
      CALL LU(ND,N,IPIV,DF)
      CALL BACK(ND,N,IPIV,DF,F)
      DO 8 I=1,N
      YK1(I)=H*F(I)
8     YK2(I)=Y(I)+.75D0*YK1(I)
      CALL FUN(X,YK2,F)
      CALL BACK(ND,N,IPIV,DF,F)
      DO 9 I=1,N
      YK2(I)=H*F(I)
      Y(I)=Y(I)+R(1)*YK1(I)+R(2)*YK2(I)
9     YK2(I)=R(3)*YK1(I)+R(4)*YK2(I)
      CALL BACK(ND,N,IPIV,DF,YK2)
      DO 10 I=1,N
10    Y(I)=Y(I)+YK2(I)
      RETURN
      END
```

```
C*********************************************************************
C
C
C       MONOD MODEL predicts the concentrations of biomass & substrate
C
C       in four interconnected chemostats by Newton-Raphsen Method
C
C       NOTE:
C             LINK NR,CCI
C
C             SUBROUTINE  CALLED : EIG3, NEWTON, CALCN
C
C*********************************************************************
C
C
        PROGRAM NR
        IMPLICIT REAL*8(A-H,O-Z)
        PARAMETER (N=12)
        DIMENSION A(12,13),XOLD(12),XINC(12)
        DIMENSION EIG(N,1),V(5),u(4)
        COMMON/AB1/R1,R2,R3,R4,FI1,FI2,W1,W2,
     *            BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
        COMMON/AB2/ITMAX,EPS1,EPS2
C
        OPEN (5,FILE='MONOD.DAT',STATUS='OLD')
        OPEN (6,FILE='MONOD.OUT',STATUS='NEW')
C
        ITMAX=20
        EPS1=1.0e-08
        EPS2=1.0e-08
        READ (5,*)ALFA,UF
        READ (5,*)R1,R2,R3,R4
        READ (5,*)BETA,BETA1,BETA2,GA,GA1,GA2
        READ (5,*)ETA,ETA1,ETA2,FI1,FI2,W1,W2
        READ (5,*)(XOLD(I),I=1,N)
C
        WRITE(6,11)
   11   FORMAT(/16X,'**** Newton-Raphson Method for Iteration ****'//30X,
     *        '---- MONOD ----'/)
        WRITE(6,22)
   22   FORMAT(/21X,'**** PARAMETER FOR ITERATION ****')
        WRITE(6,33)ALFA
   33   FORMAT(/3X,'ALFA=',F8.5)
        WRITE(6,44)UF,R1,R2,R3,R4
   44   FORMAT(/3X,'UF=',F6.3,4X,'R1=',F6.3,8X,'R2=',F6.3,5X,'R3=',F6.3,
     *         6X,'R4=',F6.3)
        WRITE(6,66)GA,GA1,GA2,FI1,FI2
   66   FORMAT(/3X,'GA=',F5.2,5X,'GA1=',F5.2,8X,'GA2=',F5.2,5X,'FI1=',
     *         F5.2,6X,'FI2=',F5.2)
        WRITE(6,77)W1,W2,ETA,ETA1,ETA2
   77   FORMAT(/3X,'W1=',F6.3,4X,'W2=',F6.3,8X,'ETA=',F5.2,5X,'ETA1=',
     *         F5.2,5X,'ETA2=',F5.2)
        WRITE(6,88)BETA,BETA1,BETA2,EPS1,EPS2
   88   FORMAT(/3X,'BETA=',F5.2,3X,'BETA1=',F5.2,6X,'BETA2=',F5.2,
     *          3X,'EPS1=',E10.4,3X,'EPS2=',E10.4)
        WRITE(6,99)(XOLD(J),J=1,N)
   99   FORMAT(/3X,'INITIAL CONCENTRATIONS:'//
     *         5X,'Y=',6F13.6,//7X,6F13.6//)
C
C   ----CALL NEWTON-RAPHSON METHOD-----
```

```
C
  100    do 200 i=1,n
  200    xinc(i)=0.0
         CALL NTN (A,N,XOLD,XINC,ALFA,UF,ITER,u)
         stdy1=-1
         do 220 i=0,3
         if (xold(3*i+3).lt.eps2) stdy1=1
  220    continue
         if (stdy1.eq.-1) then
         alfa=alfa+1.0e-04
         goto 100
         end if
C
  850    FORMAT(/20x,'The number of iteration =',I2/)
         WRITE(6,900)ALFA,UF
  900    FORMAT(5X,'ALFA=',F10.4,5X,'UF=',F7.2/)
         WRITE(6,950)(XOLD(I),I=1,3),U(1)
  950    FORMAT(5X,'X1=',F13.6,5X,'Y1=',F13.6,5X,'Z1=',F13.6,5X,
     *          'U1=',F13.6/)
         WRITE(6,952)(XOLD(I),I=4,6),U(2)
  952    FORMAT(5X,'X2=',F13.6,5X,'Y2=',F13.6,5X,'Z2=',F13.6,5X,
     *          'U2=',F13.6/)
         WRITE(6,954)(XOLD(I),I=7,9),U(3)
  954    FORMAT(5X,'X3=',F13.6,5X,'Y3=',F13.6,5X,'Z3=',F13.6,5X,
     *          'U3=',F13.6/)
         WRITE(6,956)(XOLD(I),I=10,12),U(4)
  956    FORMAT(5X,'X4=',F13.6,5X,'Y4=',F13.6,5X,'Z4=',F13.6,5X,
     *          'U4=',F13.6/)
         WRITE(6,850) ITER
C
         CALL CALCN(A,N,XOLD,ALFA,UF,u)
C
C   ----CHECK STABILITY OF SOLUTION----
C
         CALL EIG3(A,N,EIG)
         WRITE(6,111)
   111   FORMAT (/25X,'Eigenvalues',//5X,'No. of Eigenvalues',10x,
     *            'Real Part',10x,'Imaginary Part'/)
         DO 75 J=1,N
         write(6,222) J,eig(j,1),eig(j,2)
  222    format(/10x,I2,19X,f12.8,11x,f10.8)
   75    CONTINUE
         STDY=-1.0
         DO 30 J=1,N
   30    IF (EIG(J,1).GT.0.0) STDY=1.0
         IF (STDY.EQ.1) THEN
         WRITE(6,32)
   32    FORMAT(//25X,'-----UNSTABLE POINT-----'/)
         ELSE
         WRITE(6,36)
   36    FORMAT(//25X,'-----STABLE POINT-----'/)
         END IF
         STOP
         END
C
C ---SUBROUTINE NEWTON:
C    SOLVE SIMULTANEOUS NON-LINEAR EQUATIONS BY NEWTON-RAPHSON ITERATION-
C
         SUBROUTINE NTN(A,N,XOLD,XINC,ALFA,UF,ITER,u)
         IMPLICIT REAL*8 (A-H,O-Z)
```

```
      DIMENSION A(12,13),xold(12),xinc(12),u(4)
      logical converge
      COMMON/AB1/R1,R2,R3,R4,FI1,FI2,W1,W2,
     *            BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
      COMMON/AB2/ITMAX,EPS1,EPS2
c
c    -----newton-raphson iteration
      do 30 ii=1,itmax
c    -----call on calcn to set up the matrix
      call calcn(a,n,xold,alfa,uf,u)
c    -----call simul to compute jacobian and correction in xinc
      indic=1
      deter=simul1(n,a,xinc,eps1,indic,n+1)
c    -----if deter isn't 0,the value of deter is set to 100 or -100 in th:
c    -----function call. if the determination is required you may call sir
      if (deter.ne.0) then
c    -----check for convergence and update xold value
      CONVERGE=.TRUE.
      do 5 i=1,n
         if(abs(xinc(i)).gt.eps2) converge=.false.
         xold(i)=xold(i)+xinc(i)
    5 CONTINUE
C     WRITE(6,900)ALFA,UF
C 900 FORMAT(5X,'ALFA=',F10.4,5X,'UF=',F7.2/)
C     WRITE(6,950)(XOLD(J),J=1,N)
C 950  FORMAT(5X,'X1=',F13.6,5X,'Y1=',F13.6,5X,'Z1=',F13.6
C    *       //5X,'X2=',F13.6,5X,'Y2=',F13.6,5X,'Z2=',F13.6
C    *       //5X,'X3=',F13.6,5X,'Y3=',F13.6,5X,'Z3=',F13.6
C    *       //5X,'X4=',F13.6,5X,'Y4=',F13.6,5X,'Z4=',F13.6/)
       if(CONVERGE.EQV..TRUE.)then
         iter=ii
         return
      endif
      else
         write(6,201)
         stop
      endif
 30   continue
      write(6,204) alfa,uf
      stop
c
c ----formats for input and output statements
 201  format(38h0matrix is ill-conditioned or singular)
 204  format(5x,'alfa=',f8.4,3x,'uf=',f8.4//)
      end

C
C ----SUBROUTINE CALCN FOR EVALUATION THE AUGUMENT JACOBIAN MATRIX----
C

      SUBROUTINE CALCN(A,N,X,ALFA,UF,u)
      IMPLICIT REAL*8 (A-H,O-Z)
      DIMENSION A(12,13),X(12),U(4),F(4),G(4),H(4),DF(4),DG(4),DH(4),V(5)
      COMMON/AB1/R1,R2,R3,R4,FI1,FI2,W1,W2,
     *            BETA,BETA1,BETA2,GA,GA1,GA2,ETA,ETA1,ETA2
C
      DO 10 I=1,12
      DO 10 J=1,13
      A(I,J)=0.0
   10 CONTINUE
```

```
C
      CTA=ALFA/(R1*(R3+1.0)+1.0)
      CTA12=CTA*(R1*(R3+1.0)+R2*R3*(GA1+1.0)+(R2+1.0))
      CTA23=CTA*(R3*(GA1+1.0)+1.0)
      CTA40=CTA*(GA1*(R1+1.0)+1.0)
      CTA34=(R4+R3+1.0)*CTA40
      CTA21=R2*CTA23
      CTA20=R1*CTA23
      CTA42=R3*CTA40
      CTA43=R4*CTA40
C
      V(5)=(UF*ALFA)/((CTA23+CTA20)*CTA40+CTA20*CTA42)
      V(1)=V(5)*(CTA21*CTA42*(GA1*ETA1+1.0)+CTA21*CTA40+(CTA23+CTA20)*
     *       CTA40+CTA20*CTA42)/CTA12
      V(2)=V(5)*(CTA42*(GA1*ETA1+1.0)+CTA40)
      V(3)=V(5)*(CTA43+CTA42+CTA40)*((CTA23+CTA20)*GA1*ETA1+CTA23)/CTA34
      V(4)=V(5)*((CTA23+CTA20)*GA1*ETA1+CTA23)
C
      U(1)=V(1)-X(1)-X(2)-X(3)
      U(2)=V(2)-X(4)-X(5)-X(6)
      U(3)=V(3)-X(7)-X(8)-X(9)
      U(4)=V(4)-X(10)-X(11)-X(12)
C
C
      DO 20 I=1,4
      F(I)=U(I)/(U(I)+1.0)
      G(I)=FI1*U(I)/(W1+U(I))
      H(I)=FI2*U(I)/(W2+U(I))
   20 CONTINUE
C
      DO 30 I=1,4
      DF(I)=1.0/((U(I)+1.0)*(U(I)+1.0))
      DG(I)=FI1*W1/((W1+U(I))*(W1+U(I)))
      DH(I)=FI2*W2/((W2+U(I))*(W2+U(I)))
   30 CONTINUE
C
      A(1,1)=F(1)-CTA12-X(1)*DF(1)
      A(1,2)=-DF(1)*X(1)
      A(1,3)=A(1,2)
      A(1,4)=CTA21
      A(2,1)=-DG(1)*X(2)
      A(2,2)=G(1)-CTA12-X(2)*DG(1)
      A(2,3)=A(2,1)
      A(2,5)=A(1,4)
      A(3,1)=-DH(1)*X(3)
      A(3,2)=A(3,1)
      A(3,3)=H(1)-CTA12-DH(1)*X(3)
      A(3,6)=A(1,4)
      A(4,1)=BETA*CTA12
      A(4,4)=F(2)-BETA*(CTA21+CTA23+CTA20)-DF(2)*X(4)
      A(4,5)=-DF(2)*X(4)
      A(4,6)=A(4,5)
      A(4,10)=BETA*CTA42
      A(5,2)=A(4,1)
      A(5,4)=-DG(2)*X(5)
      A(5,5)=G(2)-BETA*(CTA21+CTA23+CTA20)-DG(2)*X(5)
      A(5,6)=A(5,4)
      A(5,11)=A(4,10)
      A(6,3)=A(4,1)
      A(6,4)=-DH(2)*X(6)
```

```
      A(6,5)=A(6,4)
      A(6,6)=H(2)-BETA*(CTA21+CTA23+CTA20)-DH(2)*X(6)
      A(6,12)=A(4,10)
      A(7,4)=BETA1*CTA23
      A(7,7)=F(3)-BETA1*CTA34-DF(3)*X(7)
      A(7,8)=-DF(3)*X(7)
      A(7,9)=A(7,8)
      A(7,10)=BETA1*CTA43
      A(8,5)=A(7,4)
      A(8,7)=-DG(3)*X(8)
      A(8,8)=G(3)-BETA1*CTA34-DG(3)*X(8)
      A(8,9)=A(8,7)
      A(8,11)=A(7,10)
      A(9,6)=A(7,4)
      A(9,7)=-DH(3)*X(9)
      A(9,8)=A(9,7)
      A(9,9)=H(3)-BETA1*CTA34-DH(3)*X(9)
      A(9,12)=A(7,10)
      A(10,7)=BETA2*CTA34
      A(10,10)=F(4)-BETA2*(CTA40+CTA42+CTA43)-DF(4)*X(10)
      A(10,11)=-DF(4)*X(10)
      A(10,12)=A(10,11)
      A(11,8)=A(10,7)
      A(11,10)=-DG(4)*X(11)
      A(11,11)=G(4)-BETA2*(CTA40+CTA42+CTA43)-DG(4)*X(11)
      A(11,12)=A(11,10)
      A(12,9)=A(10,7)
      A(12,10)=-DH(4)*X(12)
      A(12,11)=A(12,10)
      A(12,12)=H(4)-BETA2*(CTA40+CTA42+CTA43)-X(12)*DH(4)
      A(1,13)=(CTA12-F(1))*X(1)-CTA21*X(4)
      A(2,13)=(CTA12-G(1))*X(2)-CTA21*X(5)
      A(3,13)=(CTA12-H(1))*X(3)-CTA21*X(6)
      A(4,13)=(BETA*(CTA21+CTA23+CTA20)-F(2))*X(4)-BETA*(CTA12*X(1)+
     *         CTA42*X(10))
      A(5,13)=(BETA*(CTA21+CTA23+CTA20)-G(2))*X(5)-BETA*(CTA12*X(2)+
     *         CTA42*X(11))
      A(6,13)=(BETA*(CTA21+CTA23+CTA20)-H(2))*X(6)-BETA*(CTA12*X(3)+
     *         CTA42*X(12))
      A(7,13)=(BETA1*CTA34-F(3))*X(7)-BETA1*(CTA23*X(4)+CTA43*X(10))
      A(8,13)=(BETA1*CTA34-G(3))*X(8)-BETA1*(CTA23*X(5)+CTA43*X(11))
      A(9,13)=(BETA1*CTA34-H(3))*X(9)-BETA1*(CTA23*X(6)+CTA43*X(12))
      A(10,13)=(BETA2*(CTA40+CTA42+CTA43)-F(4))*X(10)-BETA2*CTA34*X(7)
      A(11,13)=(BETA2*(CTA40+CTA42+CTA43)-G(4))*X(11)-BETA2*CTA34*X(8)
      A(12,13)=(BETA2*(CTA40+CTA42+CTA43)-H(4))*X(12)-BETA2*CTA34*X(9)
      RETURN
      END
```