Dynamical Modeling of Photosynthesis

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Abstract

Photosynthesis, the biochemical process responsible for our survival on earth, is still rife with unknowns more than half a century after its discovery. These unknowns include its modes of function and the role of the key processes taking place apart from its regenerative Calvin cycle. It seems that the knowledge of its chemical mechanism suffices plant physiologists, who usually assume that such a natural phenomenon must work in a steady state mode, where all concentrations of molecules are almost constant throughout time or if they change, they do so between definite concentrations depending on external influences like sunlight. This uncertainty prompted us to model this phenomenon in its key elements without implementing sudden changes in external factors. We were motivated to show that such a phenomenon might possess in its inherent nature a diversity in its mode of function. For instance, multiple steady states or periodic orbits might be provable for photosynthesis models.
First, we considered two already proposed models for photosynthesis and we studied the behavior of the different species thoroughly upon changing the parameters. Both models focus on unfolding the role of photorespiration, seen as a hindrance toward a better yield in crops and both models had shown maximally a single positive steady state and a single stable zero steady state signifying the collapse of the cycle.
In our new model, we incorporate, apart from photorespiration, the translocation of one of the Calvin cycle species beyond the chloroplast inner membrane compensated by the entry of a phosphate group into the chloroplast from the cytosol. This exchange sets a conservation quantity bounding all concentrations, something that abides with nature's order. Throughout the analysis, we use algebraic tools like the resultant and pure analytic ones like monotonicity of solutions starting from ordered initial data. The latter feature will guarantee that no stable oscillations will be present. Also we profit from the Singular Perturbation Theory to reduce our model from a four-dimensional model into a three-dimensional model with dynamics taking place over a two-dimensional manifold. We were able to discover a domain of parameters for which two positive stable steady states exist. This breaks with the tradition of many mathematical models' results, which conclude a single positive steady state and it anticipates then multiple inherent modes of photosynthesis functions.

To Ares

Erklärung

Sehr geehrte Damen und Herren,

hiermit erkläre ich, dass ich die beigefügte Dissertation selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel genutzt habe. Alle wörtlich oder inhaltlich übernommenen Stellen habe ich als solche gekennzeichnet.

Ich versichere außerdem, dass ich die beigefügte Dissertation nur in diesem und keinem anderen Promotionsverfahren eingereicht habe und, dass diesem Promotionsverfahren keine endgültig gescheiterten Promotionsverfahren vorausgegangen sind.

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Hussein Obeid

Acknowledgements

It is hard to write words that you know will certainly hurt the humbleness of those addressed by them. Therefore, I start with the ones who have passed to make it lighter for those living. Throughout my time in Mainz pursuing my Ph.D. studies, I've always been grateful to my father, who supported me with his money and morals while he was alive. I do wholeheartedly thank him, not only for his support but also for giving me the freedom to be what I am now. I also thank Mr. Alan Rendall, my graduate adviser, for being an excellent adviser. I highly appreciate his ability to listen, an art that we are slowly losing as people do their jobs faster than they ever have. My thanks also go to my wife, Julia, the mother of my son, Ares. She lightens up my life and the candle under my coffee pot.
During my four years in Mainz, I've thoroughly enjoyed getting to know the city and its lifeblood, the Rhine. I now feel like I am truly part of this amazing city and its history.

Contents

Note

i. Through this thesis, the reader will encounter words that refer to the same thing. Here, we list some of these words or notions:

   i.1. We use the word *steady state* and the following words as equivalent: *equilibrium* and *stationary solution*.

   i.2. We use the word *sustained oscillation* as equivalent to *periodic orbit*. Although, the term sustained oscillation is more general than the term periodic orbit. For example, it includes *relaxation oscillation* as well. However, it will be pointed out if this term is used more generally.

   i.3. We use the term *future time* as equivalent to *forward time* or *later in time*. They all mean that a property is satisfied, depending on the context, either for some or for all time sequences $\{t_n\}_n$ with $t_n \geq t_0$.

ii. The reader will encounter theorems, propositions and definitions that are labeled in blue inside the text, which is mainly written in black font. These correspond to theorems, propositions and definitions taken from literature and research papers. All other theorems, propositions and definitions are then the work of the author.

Chapter 1

Introduction

Photosynthesis is one of the essential biological processes for sustaining life throughout the history of geological time on earth. It is the usage of the energy captured from sunlight to synthesize organic compounds from inorganic ones, such as CO_2. Photosynthesis of plants and cyanobacteria[1] creates biomass[2] on earth. The latter is the source of energy for animals as well as humans. It includes the deposits of fossil fuels and atmospheric oxygen. Perhaps the best way to appreciate the importance of photosynthesis is to examine the crucial consequences of its absences. According to many serious research items, the catastrophic event called the *Cretaceous–Paleogene Extinction Event*, which caused the extinction of dinosaurs and most others species on earth, was caused by a huge amount of dust which covered sunlight for years and halted photosynthesis. Although in [83], the author argues about the contribution of dust which halted photosynthesis, he never denies that it was the main cause of extinction. Photosynthesis is divided by plant physiologists into two phases: light reactions and dark reactions. Light reactions start by capturing sunlight in a purely physical process to bring chlorophyll-typed pigments into a higher electronic excited state. The excited pigments are then used in two parallel ways: First, as a generator of a proton-motive force to drive ATP synthesis and second as a water oxidizer, leaving oxygen as waste and using the electron gained from water to reduce $NADP^+$ into NADPH. The ATP and NADPH produced are essential components of the dark reactions to reduce carbon dioxide into sugars. It is worth mentioning that the nomenclature dark and light reactions are misleading since both reactions are ultimately driven by light[3]. The conversion of solar energy into carbohydrates in dark reactions was identified in the middle of the last century by Melvin Calvin[4], Andrew Benson and James Bassham. Their discovery accounts mainly for the dark reactions, while light reactions were later discovered mainly by Louis Duysens[5] and his team upon the introduction of Photosystems I and II. Figure 1.1 shows a scheme of the key processes taking place in the dark reactions, namely: Carboxylation, Reduction, Regeneration and Photorespiration. RuBisCO, the enzyme catalyzing both the carboxylation

[1] Cyanobacteria are single-celled organisms (Prokaryotes). They live in colonies in water and manufacture their food through photosynthesis.

[2] Biomass, according to EIA (U.S. Energy Information Administration), is organic material that comes from plants and animals and it is a renewable source of energy. Examples include crops and waste materials burned as a fuel or converted to liquid biofuels.

[3] The interested reader may consult the book *Molecular Mechanisms of Photosynthesis by Robert Blankenship* or the standard reference *Plant Biochemistry by Hans-Walter Heldt.*

[4] It was the discovery of this mechanism which earned Melvin Calvin the 1961 Nobel Prize for chemistry: See "The Path of Carbon in Photosynthesis 1951" or the Nobel lecture 1961 holding the same title.

[5] See *Duysens et al. 1961, Two Photochemical Systems in Photosynthesis.*

reaction and photorespiration, is considered the most abundant enzyme to exist on earth. Plant physiologists describe photorespiration as an unwanted side reaction and they support this claim because it is an energy-consuming reaction. In reality, the overall cost of photorespiration is five ATP molecules and three NADPH molecules for each oxygenation event. If otherwise used by carboxylation, this energy could add up to 50 % of the actual carboxylation efficiency. We refer solely to the reactions forming the carboxylation, reduction and regeneration as the Calvin cycle, while we refer to the whole process, including photorespiration and export as photosynthesis. However, the claim does not provide an ultimate explanation of the purpose of photorespiration, which is supposed to have evolved during a time where carbon dioxide was much more concentrated in the atmosphere than oxygen. Plant physiologists solve this confusion by assuming that in ancient times RuBisCO had not yet evolved a mechanism to discriminate between the two similar substrates (O=C=O and O=O)[1]. Needless to say, the claim has yet to be scientifically proven. Mathematical models have been utilized to study population biology, epidemiology, economics, cell biology, immunology, plant physiology and ecology. Motivations for this were to conclude results, imagine possible scenarios, undergo experiments *in silico* and provide or confirm explanations for phenomena that experimenters could not confirm. The main tool for that has always been writing the system as a system of ordinary differential equations describing the change of concentrations, volumes, speed, or configuration of some unknowns $x \in \mathbb{R}^n$ as time changes. An ODE system depending on some parameters λ's reads:

$$\dot{x} = F(x, \lambda, t)$$

where t denotes time. It often happens that dynamics are described using *autonomous systems*, systems where the right-hand side of the above equation is written in terms of *phase space* variables, namely the independent concentrations denoted by 'x'. In other words, the velocities of such concentrations are dependent on time, yet not explicitly. A mathematician studying such systems for biology is essentially interested not in their time solutions for a special set of parameters, as much as he is interested in unfolding the changes which might be experienced by these solutions as some or all of the parameters enter or exit some domains. The qualitative change in the portrait (mathematically *phase portrait*) concerns him the most. It is not likely that a biologist hands a mathematician some parameter values to work on, but more likely, a mathematician asks a biologist if an interval of choice is meaningful [15]. The simplest types of bifurcations are those described by one equation of parameters. The equation is zero exactly at the boundary of bifurcation. Otherwise, it is signed when the bifurcation appears and disappears alternatively. If, in addition, some non-degeneracy conditions are satisfied, these bifurcations are called *codimension-one bifurcations*. For example, when one of the parameters approaches a bifurcation value, a stable equilibrium combines with an unstable equilibrium and they disappear together. Alternatively, stating it from the other direction, two equilibria are born out of the "blue sky". This is the *saddle-node bifurcation* (equivalently fold bifurcation), encountered often in bistable systems[2]. Another simple bifurcation occurs when a parameter value causes changes in the quality of equilibrium (i.e., from stable to unstable) and a periodic orbit is born hereupon. This is the *Hopf bifurcation*, suspected usually in systems that admit oscillations [79],[65],[5]. For instance, Hopf bifurcation often appears in autocatalytic systems,

1 See Koning, Ross E. 1994. "Photorespiration". Plant Physiology Information Website: http://plantphys.info/plant_physiology/photoresp.shtml.

2 Systems having two stable equilibria are referred to as bistable systems (exhibiting *bistability*).

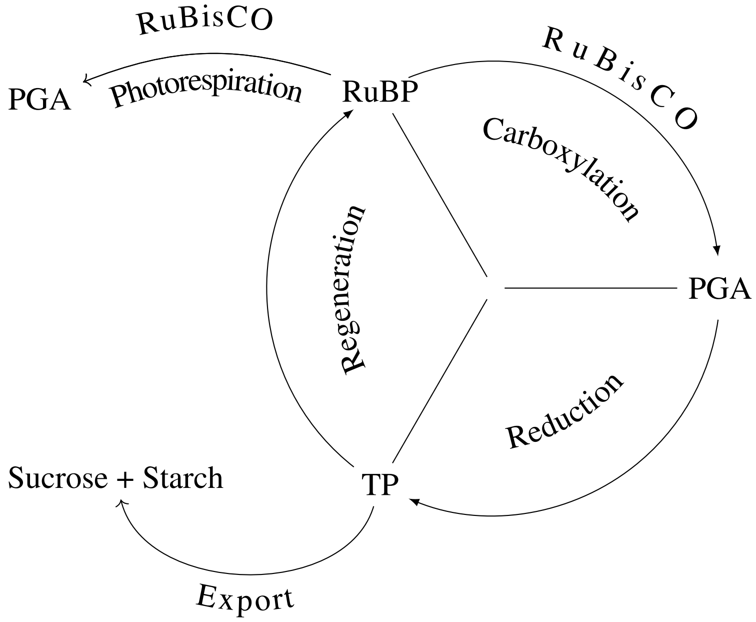


Figure 1.1: The main processes in the Calvin cycle

like the glycolytic oscillator or the calcium-induced calcium release models (see [21]). This type of bifurcation is expected usually in systems where a negative feedback mechanism is present but is neither necessary nor sufficient[1]. Interesting models that exhibit saddle-node bifurcation behavior include neural systems models [104] and cell cycles [81]. In analyzing the dynamics of a system of reactions, as it is evidently the case for photosynthesis, concentrations reach a steady state if they reach fixed values after some time from the start. Concentrations may also evolve in a simple rhythm represented by a waveform that repeats with time, or equivalently as a closed curve in the phase portrait. This rhythm is of the sustained oscillation type (in contrast to damped oscillations). It exists either as a limit cycle or as conservative oscillations, where the Lotka-Volterra model provides a good example ([70],[113],[42],[117]). In the limit cycle case, points near the periodic solution either converge to it or diverge from it. In talking about photosynthesis, it is not intended that the dynamics would demonstrate complex dynamical behavior (i.e., chaotic behavior). Chaotic behavior in chemical systems means: Concentrations would follow an infinite path, never passing through the same values twice and neither reaching a steady state nor behaving periodically. However, this avenue requires analytic exclusion rather than a predictive one since it has been proven already that chemical reaction systems are not refrained from demonstrating Chaos. In this sense, the famous Belousov–Zhabotinsky reaction was the first example of chemical systems behaving chaotically. Later on, other examples popped up ([23],[92]). The convergence into a steady state claim is supported by a biochemical model of photosynthetic CO_2 assimilation in C-3 leaves, which embraces such assumptions and which was successful in producing a good approximation of measured gas exchange rates in leaves and in predicting the CO_2 assimilation rate as a multiple of nitrogen density at different temperatures ([24], [25]). Nevertheless, it could not be claimed that photosynthesis does not regenerate periodically since experiments have not followed concentrations in leaf for a long duration. Thus the fairness of any conclusion made in favor or against oscillations is highly

[1] The model in [21] is a positive feedback model. Nevertheless, it admits oscillations in a parameter domain.

questionable [86]. Beyond this, simplified models have indeed shown the existence of damped oscillations ([87],[32],[90]). Moreover, in [32],[90] and [88], authors agree partially on the reactants responsible for oscillations being the kinases competing for ATP in the Calvin cycle. In [87], the author assumes a conformational change in RuBisCO to an inactive form, in which slow reverting activation leads to the observation of damped oscillations. However, this observation does not deviate from those obtained by exposing photosynthetic apparatus to the sudden transition from darkness to light in [66], or upon elevating CO_2 in [91] and [30].
Several hypotheses have been made to remedy the substrate-unspecific catalyzing of RuBisCO in the framework of Evolution [86]. In [106], the authors propose an interesting interpretation which fits the "Darwin's parlance", which states that natural selection has responded to reducing atmospheric CO_2:O_2 ratios by developing an advanced transition state for CO_2 in which CO_2 resembles a six-carbon Carboxyketone intermediate. CO_2 in this form awakes a more discriminatory RuBisCO but at the expense of tight binding, making cleavage to products like PGA slow down. This draws the attention toward genetic engineering attempts to enhance CO_2-fixation solely by introducing more specialized RuBisCO, rather than exploiting these complementary reactions [116].

General Settings

The following notations are adopted throughout the discussion: Square brackets denote concentrations, dots and primes above the variables denote the time derivative and the following abbreviations are used for the different species: RuBP, ribulose 1,5-bisphosphate; PGA, 3-phosphoglycerate; ADP, adenosine diphosphate; P_i, inorganic orthophosphates; ATP, adenosine triphosphate; TP, triose phosphate; CO_2, carbon dioxide; O_2, oxygen; GAP, glyceraldehyde 3-phosphate; DHAP, dihydroxyacetone phosphate; FBP, fructose 1,6-bispho sphate; F6P, fructose 6-phosphate; S7P, sedoheptulose 7-phosphate; SBP, sedoheptulose 1,7-bisphosphate; E4P, erythrose 4-phosphate; X5P, xylulose 5-phosphate; R5P, ribose 5-phosphate; Ru5P, ribulose 5-phosphate. Notice that triose phosphate is a notation for both GAP and DHAP since both species exist as a pool (the reaction is reversible). Starch and sucrose will not be written in their chemical names.
We will investigate in Chapters 3 and 4 successively two variants of a model of photosynthesis according to Hahn [44]. The first is two-dimensional and the second is three-dimensional. The chemical reactions of Hahn's model are written under the Law of Mass Action (see [16]). The model is mechanistic because the qualitative behaviors of solutions are tracked and not only the final result. The results will not be compared with real measurements since no extensive measurements and coherent data are known. Substrates in the leaf are optimally known to exist within a range of concentrations. Moreover, no complete database for a specific leaf exists to our knowledge. The Calvin cycle is a network of thirteen reactions involving a large number of species. The reactions are shown in Figure 1.3. We notice the consumption of ATP and NADPH, the energy components formed during the light phase of photosystems II and I in sequence. A plant cannot be sustained depending on these energy carriers enzymes in the dark. This necessitated the evolution of a sophisticated mechanism to save this energy in storage compartments where it can be used later again using a mechanism that releases this energy at night, so the plant stays alive. This physio-chemical energy formed by the interaction with light is mainly consumed in the second step follo-

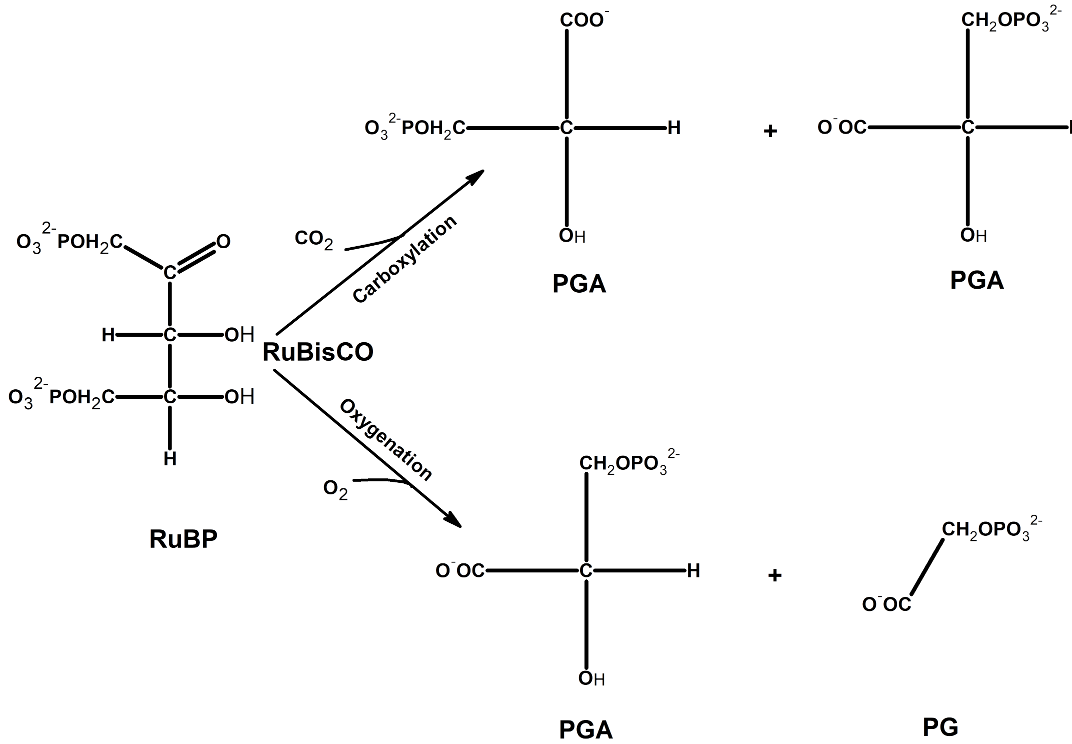


Figure 1.2: RuBisCO is involved in both carboxylation and oxygenation reactions

wing carboxylation, namely during the reduction phase in the form of ATP and NADPH. Another ATP is later (not chronologically but chemically) consumed in the regeneration phase. However, the main loss of this energy takes place in the reduction phase. Five out of six carbons assimilated in the carboxylation phase are recovered to generate RuBP and thus driving the cycle, while one of the carbons is lost in the breakage at the triose phosphate, where it is used to manufacture starch in the chloroplast and sucrose in the cytoplasm. Another breakage happens at RuBP itself, undergoing oxygenation and utilizing the same enzyme utilized for carboxylation, namely RuBisCO. Oxygenation is also called photorespiration and it is significantly perplexing to adhere to the evolutionary scheme of nature. This is because it competes with carboxylation for RuBisCO and follows its first yield PGA and phosphoglycolate PG with a series of reactions, taking place in no one compartment of the leaf and costing energy. The question of why such a reaction evolved in the past where the air was full of CO_2 is partially remedied if we hypothesize that RuBisCO had never been a smart enzyme, as it could not discriminate between both species oxygen and carbon dioxide. However, it is not clear that such a hypothesis is provable at all. This opened the door for other more concrete hypotheses. The authors in [106] proposed an interesting explanation that RuBisCO has already responded to this inefficiency by forming a special RuBP, a six-carbon compound which is more affinity specific. Other authors suppose that photorespiration is necessary to transform phosphoglycolate PG, a deadly compound for the plant. Another hypothesis suggests that photorespiration evolved to shrink water loss in C_3 plants. C_3 plants, in contrast to C_4 plants, do not store water efficiently [17]. C_4 plants, growing mainly in water-stressed environments, have a better affinity for water than C_3

plants, whose channels for passing water are tighter although their stomata open for a shorter period. C_3 plants have their channels more relaxed and lose water easier than C_4 plants [22]. This loss could have been greater if H_2O had not been utilized in the same manner as photorespiration. Hahn's model explicitly considers the role of photorespiration, starch and sucrose synthesis, but it is still incomplete regarding two missing important processes. The first is the translocation of TP from the chloroplast to the cytoplasm substituted by the entry of the inorganic phosphate P_i and vice versa. This translocation is recommended to be modeled explicitly in any model for photosynthesis. The other process is the lack of conservation law. Conservation law is a natural, realistic feature of the leaf on a big scale and it is believed that such a law exists [50]. However, when talking about the chloroplast, it is unclear whether such a law exists or not and it is unclear concerning which compound it is: is it concerning the carbons or the phosphates? For instance, the author in [90] was able to establish this law but in an extended chloroplast. Moreover, Hahn's model does not study the variations of CO_2, O_2 pressures or ATP, NADPH concentrations as the authors in [66],[33] and [68] do and as it is typical to test the photosynthetic response to a presumed favorable or unfavorable variation. The motivation of studying a model lacking the natural bound set manifested by a conservation law is testing the limitations set by the breakages to starch and sucrose synthesis and by photorespiration on the photosynthetic rate of photosynthesis if an abundant uptake of phosphate is guaranteed. It is shown that photorespiration is a huge obstacle limiting any improvement in the crops' biomass. The model considers photosynthesis in its working mode when light is present. Any shut down during the night was not studied. However, this restriction is satisfactory since photosynthesis itself during its working period is a quite sophisticated phenomenon so that any extra sophistication risks groping in a very tolerant erroneous field where any detail is exposed to model-disqualifying errors. Check [49] for a comparison between over-simplified and over-sophisticated models in science and technology.

Main Results

In Chapter 3, we consider a two-dimensional model according to Hahn [44] capturing the main events in photosynthesis. In the absence of any conservative law, we investigate the role of photorespiration. Many plant physiologists aim to increase crop yield and devise tools to reach this goal and one of the approaches utilized for this purpose was increasing the efficiency of photosynthesis over photorespiration. Not all results were promising, although research is still in an early stage (see [99]). The model is studied for an open set of parameters, which has the advantage of not getting stuck in inaccurate kinetic data (e.g., the *a priori* fixing of the range of the reaction rates). It is well-known that determining reaction rates is a challenging task backed by inaccurate technologies.
At this point, we are interested in studying the model in two variants, once with photorespiration and again without photorespiration. In the former case, no stable positive steady states were found. Moreover, it was shown that some solutions diverged toward infinity. While nature did not implement a mechanism in plants that allows them to produce an indefinite amount of sugar and starch, two conclusions can be drawn hereupon. It is either that the modeler overlooked some limiting process in the Calvin cycle (e.g., a conservation law), or it is photorespiration which halts overproduction in the cycle. However, the last expression stands on shaky ground since it is not known whether halting photorespiration without killing the cycle is possible at all. Contrary to this belief, some hypotheses [8] claim that

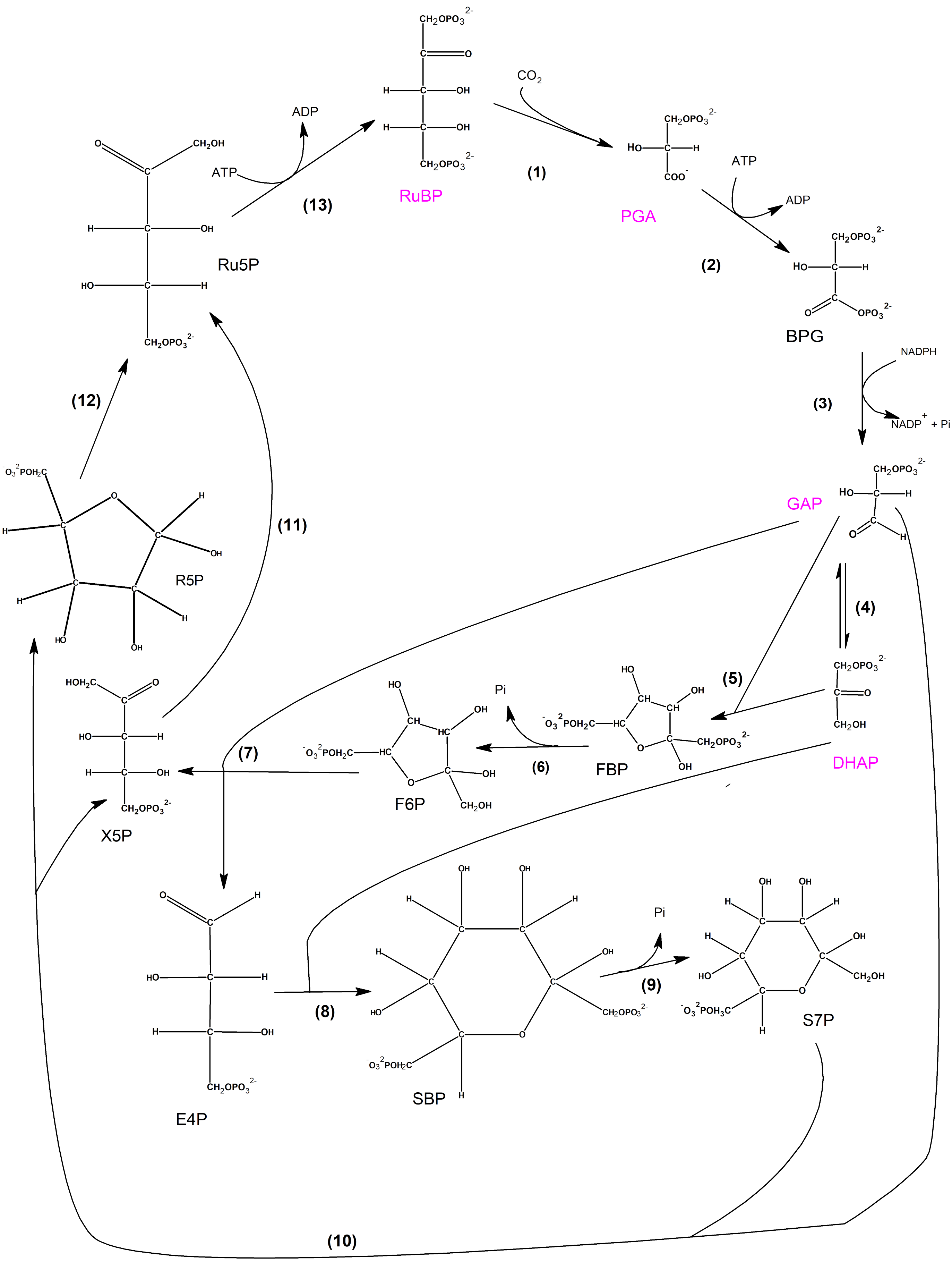


Figure 1.3: The reactions of Calvin cycle. In red are the species that will be utilized in Hahn's model

photorespiration is essential for the cycle itself to get rid of poisonous phosphoglycerate PG, which otherwise might break the cycle.
The case with photorespiration shows a stable positive solution in an open set of parameters, together with an unstable steady state and a trivial stable one corresponding to the origin. The latter is when concentrations of all species are exhausted at a later time. The existence of an unstable equilibrium simultaneously with the other stable ones might be interpreted as though the cycle is indeed shifted from its stable routine for a while, probably due to a kind of "weak" feedback, which then loses its control later, allowing the cycle to return to its natural behavior. The boundedness of solutions under photorespiration is also one reason to believe that conclusions are plausible. While some solutions diverge to infinity in the absence of photorespiration, it was interesting to determine their rates of accumulation. It was convenient to know the rates of accumulation of the different species, which could be significant for specialists to know once they have an opportunity to increase the main players' concentrations up to a higher limit. At the end of the chapter, it will be explained how the three-dimensional model of Hahn was reduced to the already studied two-dimensional one, thus easing the burden of having considered a simple two-dimensional model. This was done by making use of Singular Perturbation Theory in an obvious yet plausible way. It is worth mentioning that big models are not generally a sign of rigor. Being aware of the large number of reactions taking place in the leaf compartments, research is left to flounder in a gray area since many of these reactions are not known for certain to operate for a long time or whether they shortly reach their balance between the forth and back reactions.

A two-dimensional model for photosynthesis limits the possible modes of functioning to steady states. Species in photosynthesis do not compete in general. Thus a rise in one of the concentrations does not cause the decline of other concentrations. This feature is crucial for the existence of periodic solutions. Especially in two-dimensional models, the lack of this property prohibits sustained rhythms (periodic orbits). For that reason, it was interesting to study the three-dimensional variant of Hahn's model for photosynthesis in Chapter 4. The model was investigated when photorespiration was shut down. However, interesting behavior arises when photorespiration is present. It was shown that only in that case and with two positive steady states can sustained oscillations occur, although at the cost of being unstable. The instability of sustained oscillations is the direct outcome of the monotonicity that prevails in partially ordered sets. The union of these sets is dense in the domain of interest, namely the non-negative orthant. It is only near the basin of attraction of the unstable equilibrium that such "rebellious" oscillations may be born. Everywhere else, solutions tend infinitely to a rest point (steady state). It is shown that solutions approaching a stable equilibrium form a dense set, whose complement admits a zero measure. It was shown that "rebellious" periodic orbits exist singularly. That is, they do not form a disk in $\mathbb{R}^3_{\geq 0}$.
Despite this limitation, once they exist, they exist evenly (i.e., only an even number of periodic orbits is plausible). Just like in Tango, it seems it takes two periodic orbits at least to rebel against the monotone "well-behaved" dynamics converging to equilibrium. Although it is concluded that no periodic orbits exist for the model, it is, however, a model-specific feature and it does not infer anything about models sharing the same qualitative properties with the three-dimensional model of Hahn. Periodic orbits have never been found in photosynthesis models and no conformity is ever assumed between the nomenclature 'cycle' and periodic orbits seen as cycles in the phase portrait. In reality, the Calvin cycle is said to properly operate infinitely reproducing itself if solutions converge to a stable equilibrium. It is

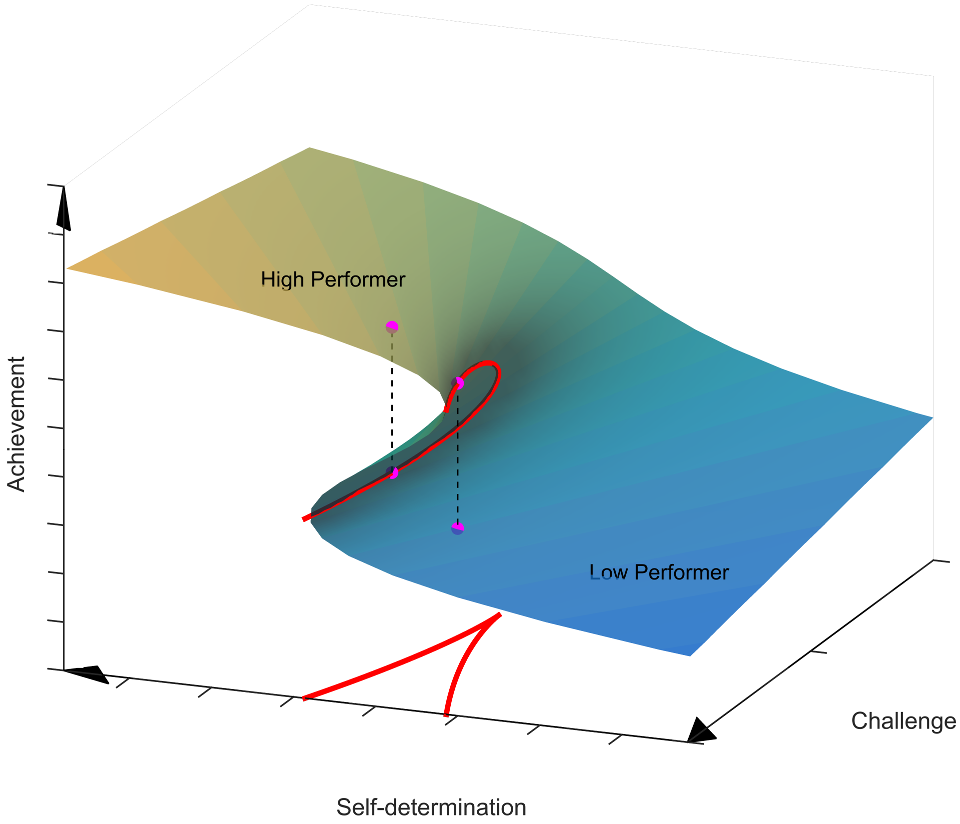


Figure 1.4: Cusp bifurcation happens at the meeting point of the two branches of the red curve. Simple fold bifurcation happens anywhere else once the parameters are on one of the branches

believed that two essential processes should be explicitly modeled in addition to the closed cycle processes. These are the translocated phosphate from and to the cytosol and photorespiration and the latter isn't disguised by being modeled indirectly through the increase of the former's rate.
In the absence of a clear-cut conservation law, it is recommended to assume that the translocated phosphate entering and leaving the stroma exercise a regulatory influence on the Calvin cycle reactions and photorespiration. Adopting this perspective is expected to deliver more complex dynamics, including periodic orbits backed by the cycle's seemingly intrinsic functioning, namely working with constant concentrations for all species.

Our new model for photosynthesis, introduced in Chapter 5, focuses on the main events taking place beside the Calvin cycle. These are photorespiration and the translocation of triose phosphate/inorganic phosphate. The model is then a four-dimensional model satisfying a conservation law. Hence, in reality, dynamics take place on a three-dimensional manifold and thus the degree of complexity of possible dynamics is that of a three-dimensional model. Writing the model in the Singular Perturbation Theory setting legitimizes the considering of the dynamics on a two-dimensional manifold. Similar behavior as that witnessed in Hahn's three-dimensional model was detected in the new model for certain domains of parameters, namely, fold bifurcation. In fold bifurcation, a non-hyperbolic equilibrium (i.e., Jacobian

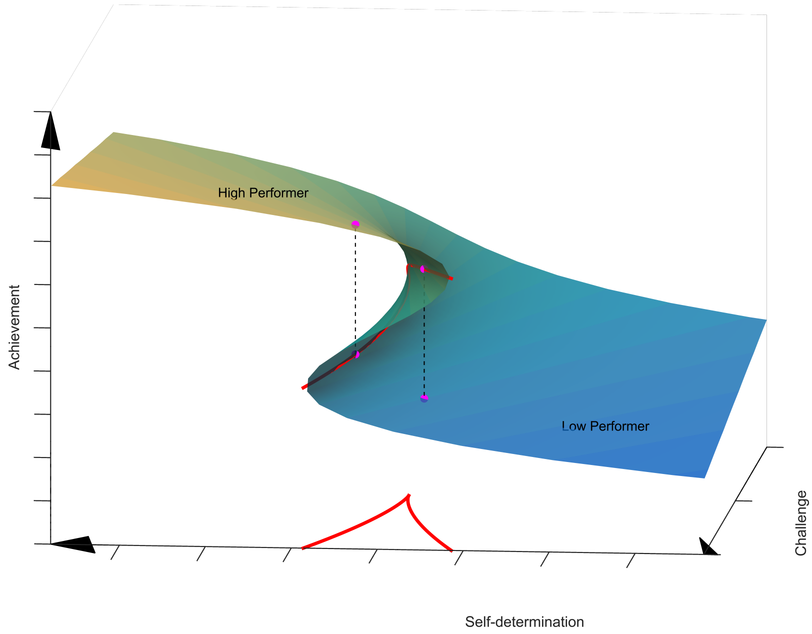


Figure 1.5: Hysteresis is when a stable equilibrium is lost via fold bifurcation. There remains then a single stable equilibrium either on the upper layer (projection of dotted lines) or over the lower layer

matrix admits a zero eigenvalue at this equilibrium) is born when changing a single parameter. A further slight change pushes this equilibrium to bifurcate into two hyperbolic equilibria, one of them is stable and the other is unstable. We might call this bifurcation simple fold bifurcation whenever the reduction to the one-dimensional centre manifold maintains a non-zero second-order term. Simple fold bifurcation is a codim-1 bifurcation because it depends on what is equivalent to the bias of a single parameter. We refer to the general fold bifurcation by fold-type bifurcation. Another interesting behavior is encountered in the new model; this is the cusp bifurcation. Again we are dealing with fold-type bifurcation, yet this time the second-order term in the equation governing the centre manifold vanishes at the bifurcation moment. Cusp bifurcation is a codim-2 bifurcation since it requires two degrees of freedom (i.e., two parameters must vary independently). Cusp bifurcation is always accompanied by a phenomenon called hysteresis. Hysteresis is when two stable equilibria and another unstable one coexist. In reality, a cusp bifurcation is on the extremity of hysteresis. Upon varying two parameters called control parameters, a simple fold bifurcation occurs in an alternative fashion whenever the control parameters touch one of two different branches of the bifurcation curve, meeting exactly where the cusp point is located. Thus a cusp point is eventually the meeting of the three equilibria at one single equilibrium.

To make things concrete, we provide an example that shows how cusp bifurcation can possess a relevant interpretation of real-life phenomena.

Authors in [89] approach self-determination in social life and job by referring to what they call three basic intrinsic needs: The need for autonomy, competency and relatedness. According to them, self-determination depends on the degree these needs are fostered or thwarted by the leader in the job, society, culture, or group to which the individual belongs. The fulfillment of these needs enhances performance and consistency in functioning. We adopt this perspective in our example for an employer and we assume he is autonomous in the sense that his job represents an authentic interest and a volitional act from his side. Also he is well-connected and feels socially involved in his work environment. Normally, he feels able to operate effectively and contribute to his work-team in the majority of situations they encounter. This last feature is called competency. In our real-life example, competency will serve as the main characteristic that influences the employer's self-determination, yet implicitly, either positively or negatively. Thus, only the sum total of fulfillment of these three needs will be considered in the model as a variable under self-determination. Competency and then self-determination are easily threatened, for example, by increasing challenges, by negative feedback from the boss, or by exaggerated self-criticism. Nevertheless, we exclude challenges from this list of factors and we let it be the other variable. A criterion dependent on these two variables, self-determination and challenges, is what we call achievement function. It must increase if both variables increase.

In short, our example will utilize: i) challenges and self-determination[1] acting as the variables (or control parameters), ii) achievement as an evaluation function, whose plot is depicted in Figure 1.4. Additionally, we coarsely dissect the plot of the achievement function into two descriptive areas. The lower area corresponds to a low performer at work and the higher one to a high performer. A low performer might put to good use stressful challenges in the job if he succeeds at being better self-determined. If he continues to do well, facing escalating challenges with a greater ability to concentrate on main issues and to make good decisions, he might become a high performer at some point. This could be interpreted as a jump from one category to another and mathematically, is interpreted as a jump from a lower layer position in achievement function to a higher layer position (see Figures 1.4 and 1.5). Such sudden change in achievement when this jump takes place is justified by the fact that a low performer might have the same mental readiness that a high performer has, yet achievement is not directly influenced by mental abilities as much as it is influenced by the psychological strength of overcoming stress and utilizing these abilities. Once partly attained, this psychological strength, named self-determination, requires no time to influence achievements. We consider now the other way round, having initially a high performer who usually faces the career challenges which get more stressful as he climbs the ladder and aspires to reach a higher post. Suppose that he at some point loses his self-determination, for example, due to some incident when one of his direct reports proves to have better decision-making abilities than him in a crucial job situation. If this experience recurs, he starts then to ponder losing the trust of his direct boss and colleagues, especially if he was reprimanded. In this situation, he either tends to recover a good level of self-determination or, worse, lose it more. Assuming the second scenario, our high performer turns into a low performer at some point in his career, unable to handle difficulties and prove his superior decision-making abilities. He does not feel competent anymore and so he is less motivated, less self-determined, thus making a jump into a lower position and mathematically into a lower layer of his career achievements. This is exactly what is meant by hysteresis. It means a sudden switch from a stable equilibrium into another stable equilibrium. In our example, both individuals resemble stable equilibria. This is because a failure of remaining a high performer and the success of becoming one are changes that both do not happen overnight.

Concretely, there coexist initially two stable equilibria and another unstable one. When the control parameters touch one of the red curve branches, seen in Figures 1.4 and 1.5, one of

[1] Not to be confused with self-determination, the highly debated principle in modern international law.

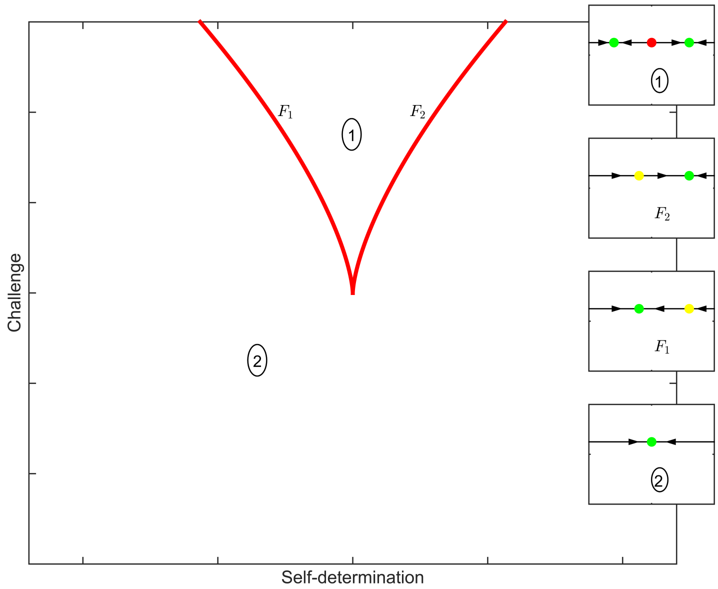


Figure 1.6: Record of the dynamics taking place on every region of the control parameters in cusp bifurcation' space

the stable equilibria coincide with the unstable equilibrium and a fold equilibrium is born. If control parameters keep changing in a certain direction, crossing the branch, the fold equilibrium withers away and we are left with a single stable equilibrium. Which of the stable equilibria undergoes the fold bifurcation with the unstable equilibrium depends on which branch of the red curve is approached from the control parameters. The projection of the red curve on the control parameters space gives a better recognition of these branches. It is exactly at the meeting point of these two branches that all equilibria join together, forming a single fold equilibrium, yet with second-order degeneracy. This point is called the cusp. Figure 1.6 shows a detailed record of dynamics taking place upon crossing from a region to another in the control space. F_1 and F_2 designate the bifurcation curves on which fold bifurcation happens. They split the control space into two connected regions, where either one stable equilibrium or two stable equilibria are present. This interesting behavior is proven to hold in our new model, signifying photosynthesis working in two different stable modes and the switch between them depending on exactly two parameters of the system.

Chapter 2

Introduction to Monotone Dynamical Systems

Monotone dynamical systems are the systems that preserve partial order upon starting from partially ordered initial data. This property guarantees that almost all solutions converge to steady states in future time. Monotonicity has been fruitful in proving general results. For instance, the most complex behavior possible for a model is the complement of a convergent residual set. This universality of essential behavior has led to devising several criteria that help check for monotonicity in a model, regardless of the significance of the parameters involved or their values. For example, it is solely important to check the non-diagonal entries of the Jacobian matrix for positivity. Alternatively, the authors in [1] and [64] derived graph-theoretic approaches, which require knowing only the signs of the chosen parameters and the sets of substrates and products.
This chapter provides the basic definitions and some chosen ramifications, which build the necessary material required for further analysis in the following chapters.

Definition 2.0.1 *A flow ϕ_t generated by*

$$\begin{aligned} &\dot{x} = f(x) \\ &x \in \Omega\,,\ \Omega \subset \mathbb{R}^n\,, \Omega\ \textit{open} \end{aligned}$$

is a strongly monotone flow if $u_0 \leq v_0$ and $u_0 \neq v_0 \implies \phi_t(u_0) \ll \phi_t(v_0),$ for $t \geq 0$.

We write $u_0 \leq v_0$ if $u_i \leq v_i,$ for all i and write $u_0 \ll v_0$ if $u_i < v_i,$ for all i.
A general monotonicity is then whenever $u_0 \leq v_0 \implies \phi_t(u_0) \leq \phi_t(v_0)$, which is obviously weaker. We notice that the above definition works nicely with orthants in $\mathbb{R}^n$. For instance, a monotone flow starting in the positive orthant of $\mathbb{R}^n$, namely $\mathbb{R}^n_+$, would never leave it in future time if the solution starting at the origin O does not leave it in future time. This property is called positive invariance[1] and is especially relevant in systems where the variables represent a quantity which is supposed to be non-negative, like concentrations. Then the violation of this property disqualifies a proposed model from being representative of such quantities. A generalized version of monotonicity is defined on a pointed[2] cone K if the forward flow satisfies $v_0 - u_0 \in K \setminus \{0\} \implies \phi_t(v_0) - \phi_t(u_0) \in K \setminus \{0\}$. The same system is said to be *strongly monotone* if $v_0 - u_0 \in K \setminus \{0\} \implies \phi_t(v_0) - \phi_t(u_0) \in \operatorname{int} K$ instead. The latter condition is according to Hirsch [51] and it requires non-emptiness of $\operatorname{int} K$. Before that, Matano [71] introduced a weaker hypothesis compared to strong monotonicity. It is based on a neighborhood-strong order preserve notion, assumingly allowing

[1] a set A is positively invariant under the application of the flow ϕ_t if $\phi_t A \subset A,\;$ for $t \geq 0$.
[2] a pointed cone is a cone K that satisfies $K \cap \{-K\} = \{0\}$.

more flexibility in choosing the state space [96]. From now on, these symbolic equivalences will be adopted $u_0 \leq_K v_0 \Leftrightarrow v_0 - u_0 \in K$, $u_0 <_K v_0 \Leftrightarrow v_0 - u_0 \in K \setminus \{0\}$ and $u_0 \ll_K v_0 \Leftrightarrow v_0 - u_0 \in \operatorname{int} K$.

Definition 2.0.2 *A flow ϕ_t generated by*

$$\dot{x} = f(x)$$
$$x \in X \supset K \text{ } (K \textit{ pointed cone})$$

is strongly order preserving over the Banach space X if it is monotone with respect to K and whenever $u_0 \leq_K v_0$ implies the existence of $t_0 \geq 0$ and $\delta > 0$ such that $\phi_{t_0}(u) \leq_K \phi_{t_0}(v)$ for all u and v that satisfy: $\|u - u_0\| < \delta$, $\|v - v_0\| < \delta$.

A continuous-time system admits a well-known fundamental dynamics if its forward flow ϕ_t satisfies the following properties: First, ϕ_t is strongly monotone (or strongly order preserving) over X. Second, ϕ_t of any compact subset $C \subset X$ has a compact closure. Such systems do not have a chaotic attractor. Even if a monotone system demonstrates chaos, these dynamics would not be noticed since they are extremely unstable.
A fundamental property of continuous monotone systems is the *Order Interval Trichotomy*. This property enables the direct recognition of dynamics in intervals bounded by equilibria. The dynamics will be so confined that one of the equilibria is reached from any point inside the interval. If both equilibria are stable, then a third equilibrium in between both is implied, thus being the origin of stability. This geometric characterization of monotone systems facilitates the next-to-be-done Search for more complex behavior upon locating the equilibria. The importance of trichotomy is accentuated because omega limits sets of comparable initial starting points x and y are consequently comparable. In other words, equilibria of monotone systems are ordered (*dichotomy*) if reached from ordered points. The latter generally fails to hold for continuous monotone systems that satisfy a milder monotonicity condition, namely just monotone (non-strongly monotone) [98].
Recall that the orbit of $x \in X$ under the forward flow is defined as $O(x) := \{\phi_t(x) : t \geq 0\}$ and the omega limit set is then $\omega(x) := \cap_{t\geq 0}\overline{\cup_{s\geq t}\phi_s(x)}$ well defined for orbits with compact closure. In an analogous way, we define $\alpha(x) := \cap_{t\leq 0}\overline{\cup_{s\leq t}\phi_s(x)}$. An equilibrium is a point $x \in X$ for which $O(x) = \{x\}$. The set of equilibria is then : $E = \{x \in X \mid O(x) = \{x\}\}$. The set of convergent points C in X is defined by $C := \{x \in X \mid \omega(x) = \{e\}\,,\ e \in E\}$ and the set of quasiconvergent points is defined by $Q := \{x \in X \mid \omega(x) \subset E\}$. Clearly $C \subset Q$. It is assumed throughout the following discussion, that the orbit $O(U)$ of any compact set $U \subset X$ has a compact closure and we use the following notation for $<, \leq, \ll, >, \geq, \gg$ in $\mathbb{R}^n$

$x \leq y$ denotes that $x_i \leq y_i,\ \forall i,\ 1 \leq i \leq n.$
$x < y$ denotes that $x_i \leq y_i,\ \forall i,\ 1 \leq i \leq n$ and $\exists j,\ 1 \leq j \leq n$ such that $x_j < y_j$.
$x \ll y$ denotes that $x_i < y_i,\ \forall i,\ 1 \leq i \leq n.$

By analogy, this definition is generalized for any order with respect to a pointed cone $K = K_1 \times K_2 \times \cdots \times K_n$. This means that:

$x \leq_K y$ denotes that $x_i \leq_{K_i} y_i,\ \forall i,\ 1 \leq i \leq n,$ meaning $y - x \in K$.
$x <_K y$ denotes that $x_i \leq_{K_i} y_i,\ \forall i,\ 1 \leq i \leq n$ and $\exists j,\ 1 \leq j \leq n$ such that $x_j <_{K_j} y_j,$
meaning $y_i - x_i \in K, \forall i \neq j$ und $y_j - x_j \in K \setminus \{0\}$.
$x \ll_K y$ denotes that $y_i - x_i \in \operatorname{int} K_i,\ \forall i$

However, checking for monotonicity as it is stated in Definitions 2.0.1 and 2.0.2 requires solving the system of differential equations, which is mostly not in reach. This prompts characterizing this property with its generalization for ordered cones K by using the right-hand side of the system of differential equations. A famous condition was earlier introduced by Kamke and Müller in [62] and [73], which requires, however, a kind of weak convexity for the Banach space (or a subset of Banach space) X. Usually, it suffices that this criterion is valid for the interior of X. Here we consider p-convexity for X.

Definition 2.0.3 *A set $\Omega \subset \mathbb{R}^n$ is said to be p-convex if it contains the entire line segment between any two points x and y such that $x \leq y \quad x, y \in \Omega$.*

Remark 1 Kamke-Müller Condition *Let Ω be a p-convex domain. If for each choice i, let $x, y \in \Omega$ such that $x_i = y_i$, and $x \leq y$ then it follows that $f_i(x) \leq f_i(y)$.*

This condition follows from the realization that for x and y in p-convex domain Ω, the difference $f_i(y) - f_i(x)$ can be otherwise characterized by The Fundamental Theorem of Calculus: whenever $x_i = y_i$, then

$$f_i(y) - f_i(x) = \int_0^1 \sum_{i \neq j} \frac{\partial f_i}{\partial x_j} \left(x + t(y - x)\right)(y_j - x_j) dt$$

Then the connection between the Kamke-Müller condition and monotonicity is demonstrated by the following result [56]

Proposition 1 *Let f be satisfying the Kamke-Müller condition on an open subset $D \subset \mathbb{R}^n$. Let $<_r$ denotes one of the relations $\leq, <$ or $\ll$. If $x <_r y$, $t > 0$ and if $\phi_t x$ and $\phi_t y$ are defined then $\phi_t x <_r \phi_t y$.*

It is a direct implication that Kamke-Müller condition is satisfied with respect to the non-negative orthant $\mathbb{R}_{\geq 0}$ (i.e., the usual $\leq$) whenever $\frac{\partial f_i}{\partial x_j} \geq 0\, \forall i\, \forall j, i \neq j$. The system is then called *cooperative* in the sense that an increase in any of the concentrations has a positive impact on all the other concentrations' growth rates. Cooperativity generates, in general, a monotone flow, derived from the above formula and Propostion 1. However, most of the monotone systems framework's advanced results require more than just monotonicity, namely either strong order preserving SOP or strong monotonicity.
In order to elaborate at the point of monotonicity with respect to general pointed cone K (see [115]), we consider the following toy system of differential equations in $\mathbb{R}^2$ borrowed (with modifications) from [2]:

$$\dot{x} = -\theta_1(x) + \theta_2(1 - x - y)$$
$$\dot{y} = \theta_3(1 - x - y) - \theta_4(y)$$

with θ_i's continuous increasing functions. If we denote the right-hand sides by f_1 and f_2 respectively and check for the following inequalities with $\leq$ and $\geq$ to mean the usual partial order in $\mathbb{R}$: Let $(x^1, y^1), (x^2, y^2) \in \mathbb{R}^2$ with $x^1 \leq x^2$ and $y^1 \geq y^2$. It is obvious that this conclusion cannot imply monotonicity in the sense of Definition 2.0.1 since it does not suit the formulation there. However, it could be possible to establish monotonicity with respect to a generalized pointed cone in $\mathbb{R}^2$ which suits then the formulation. This cone is $K = \mathbb{R}_{\geq 0} \times \mathbb{R}_{\leq 0}$. We notice

$$x^1 \leq x^2 \Leftrightarrow x^2 - x^1 \geq 0 \Leftrightarrow x^2 - x^1 \in \mathbb{R}_{\geq 0} \Leftrightarrow x^1 \leq_{\mathbb{R}_{\geq 0}} x^2$$
$$y^1 \geq y^2 \Leftrightarrow y^2 - y^1 \leq 0 \Leftrightarrow y^2 - y^1 \in \mathbb{R}_{\leq 0} \Leftrightarrow y^1 \leq_{\mathbb{R}_{\leq 0}} y^2$$

If we check now the Kamke-Müller condition, it follows that $f_1(x, y^1) \leq f_2(x, y^2)$ and $f_2(x^1, y) \geq f_2(x^2, y)$. This could be formulated with the partial order in K

$$f_1(x, y^1) \leq f_1(x, y^2) \Leftrightarrow f_1(x, y^2) - f_1(x, y^1) \geq 0 \Leftrightarrow f_1(x, y^2) - f_1(x, y^1) \in \mathbb{R}_{\geq 0}$$
$$\Leftrightarrow f_1(x, y^1) \leq_{\mathbb{R}_{\geq 0}} f_1(x, y^2)$$
$$f_2(x^1, y) \geq f_2(x^2, y) \Leftrightarrow f_2(x^2, y) - f_2(x^1, y) \leq 0 \Leftrightarrow f_2(x^2, y) - f_2(x^1, y) \in \mathbb{R}_{\leq 0}$$
$$\Leftrightarrow f_2(x^1, y) \leq_{\mathbb{R}_{\leq 0}} f_2(x^2, y)$$

Hence $(x^1, y^1) \leq_K (x^2, y^2) \Rightarrow \phi_t(x^1, y^1) \leq_K \phi_t(x^2, y^2)$ and the system is monotone with respect to the pointed cone $K = \mathbb{R}_{\geq 0} \times \mathbb{R}_{\leq 0}$.

Ordering Properties of Monotone Flows

Theorem 1 Non-ordering of Limit sets and Dichotomy
Let ϕ_t be strongly order preserving on X. It follows

i) If $O(x)$ contains two ordered points then u converges to an equilibrium $e \in E$. We write $\omega(u) = e$.

ii) Non-ordering of Limit sets: no two points of $\omega(u)$ for any $u \in X$ are related by $<$.

iii) Limit set dichotomy: if $u < v$ then either $\omega(u) < \omega(v)$ or $\omega(u) = \omega(v) \subset E$.

The non-ordering of limit sets serves as a geometric constraint on the existence of periodic orbits or non-steady state limit sets in general. It guarantees that no such behaviors would exist over manifolds where points are generally partially ordered. For instance, it prohibits the existence of periodic orbits for plane monotone systems. This idea is illustrated in Figure 2.1, showing a periodic orbit on the plane in $\mathbb{R}^2$, which upon a suitable choice of fixed x_0, the projection of two points of the periodic orbit on the x-axis shows that their ordinates do not escape order. This order between the two points leads to a strict order of their future solution,

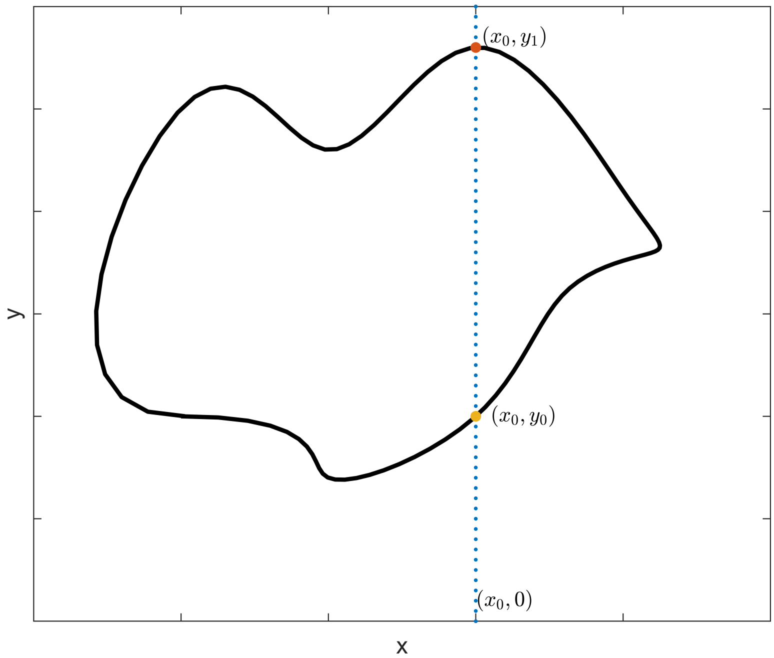


Figure 2.1: Periodic orbit on plane has ordered points

which, however, contradicts the fact that each of them is met by the solution starting at the other at some future time.
There is ground reasoning for why systems in biology are likely to behave monotonically. This feature guarantees under easy-to-be-checked conditions the generic[1] convergence to equilibria. These results are manifested in the sequential papers of Hirsch ([52],[53],[54],[55],[56],[57]) and the works of Kamke and Hadeler [43]. For example, it is quite a traditional result to talk about global asymptotic stability when only one steady state (equilibrium) exists. This is illustrated in the next theorem.

Theorem 2 Global Asymptotic Stability *Let ϕ_t be strongly order preserving on X and suppose that X contains exactly one equilibrium e and that every point of $X \setminus e$ can be approximated from above and from below in X. Then $\omega(x) = e \; \forall x \in X$.*

A point $x \in X$ is approximated from below (respectively from above) in X if there is a sequence $\{x_n\}_n \in X$ such that $x_n < x_{n+1} < x$ (resp. $x < x_{n+1} < x_n$) for $n \geq 1$ and $x_n \to x$ as $n \to \infty$. This property is natural for the non-negative orthant $\mathbb{R}_{\geq 0}$, which is the domain of interest for many biochemical systems. It is also impossible for such systems to exhibit stable oscillations in the other cases. This is due to the fact that convergent and quasiconvergent points are dense in X.

Theorem 3 *Let ϕ_t be strongly order preserving on X and suppose that every point $x \in X$ can be approximated from below or from above. Then $X = \operatorname{int} Q \cup \overline{\operatorname{int} C}$. In particular, $\operatorname{int} Q$ is dense in X.*

This reinforces the chemists' orthodox view of stable oscillations in chemical systems as a perpetual motion, which contradicts the Second Law of Thermodynamics, stating that

[1] Generic in the sense of almost everywhere in state space.

processes in nature are irreversible (see [23]). Although this view is surpassed by many examples and measurements, which confirm that many natural processes are eventually oscillatory (see [35]), stable equilibrium remains the intrinsic component of systems in biology or chemistry. The intuition that many non-monotone systems in biology contain a monotone structure has led to huge theory advancements. It is suggested that biological systems are at least decomposable into small monotone systems [2] and the interaction between these systems is then studied in the light of control theory in the next section.
We state now an essential trichotomy, which proves to be useful in the later discussions. This trichotomy tells that a flow is either uni-directed in an interval $[u, v]$ (with respect to a partial order cone K) whenever u and v are equilibria or there exists a third equilibrium somewhere in between u and v. The latter implies stability for generic u and v in finite-dimensional spaces since if each of u and v admits one dimensional stable manifold. They admit then an $n-1$ unstable manifold, which is approximated from above and from below by points that converge to u or v, which is impossible by strongly order preserving property.

Theorem 4 Trichotomy
Let ϕ_t be strongly order preserving on $X = [u, v]$ where u and v belong to the set of equilibria. If $\overline{\phi_t([u, v])}$ is compact for each $t > 0$, then one of the following holds:

i) $\exists w \in [u, v]$, *w is an equilibrium and* $w \neq u, v$.

ii) $\phi_t(x) \to u$ *as* $t \to \infty$, $\forall x \in [u, v] \setminus \{v\}$.

iii) $\phi_t(x) \to v$ *as* $t \to \infty$, $\forall x \in [u, v] \setminus \{u\}$.

To conclude the section, we state an important result due to Hirsch, which resembles Poincaré-Bendixson Theorem for planar vector fields.

Theorem 5 *Let g be a cooperative vector field with respect to the partial order induced by the non-empty cone $K \subset \mathbb{R}^3$ in a p-convex domain $D \subset \mathbb{R}^3$. Then a compact limit set of g that contains no equilibrium points is a periodic orbit.*

This theorem, combined with the fact that no periodic orbit of a cooperative system can be attracting (i.e., then $\omega-$limit set of it's neighborhood), conserves its meaning for compact $\omega-$limit sets of competitive systems and equivalently compact $\alpha-$limit sets of cooperative ones. Notice that cooperative systems are competitive systems in reverse times and vice versa. Therefore, an $\omega-$limit set of one is an $\alpha-$limit set of the other. Thus the theorem might suit the models discussed in the next chapters, generators of cooperative dynamics if we will come across a compact limit set, which is not an equilibrium. It will also be easier to track repelling limit sets of a cooperative system. Equivalently the model can be studied in negative time by multiplying the differential equations with a minus. Then the search turns out to attracting sets in the new forward time, which is easier to simulate. We hope this theorem could be an efficient tool for discovering periodic orbits for photosynthesis models. Although interesting by itself, finding an $\omega-$ limit set for a competitive system away from equilibria is a kind of severe demand, to the point that more counterexamples exist for models in biology resembling periodic orbits, which are not compact $\omega-$limits sets. However, the authors in [119] do succeed in setting the ground hypothetically for a competitive system that does have an attracting periodic orbit.

Monotone Dynamics in Control Theory

Two small monotone systems with one of them considered as negative feedback for the first would exhibit monotone system's behaviors' traits, like global convergence, if the negative feedback does not dominate the positive feedback exercised by the first system on the second. Figure 2.2 shows two systems Σ_1 and Σ_2 connected by a loop of feedback. A system Σ has an input u where u is a Lebesgue-measurable function $u(\cdot) : \mathbb{R}_{\geq 0} \to \mathcal{U}$ that takes values in a compact subset of $\mathcal{U}$ for bounded intervals. Similarly, Σ has an output function y taking values in some compact subset in $\mathcal{Y}$ for bounded real non-negative intervals. Under the assumption that the input of Σ_2 is the output of Σ_1 and vice versa, the loop could be written as:

$$\dot{x} = f(x, w), \qquad y = h_1(x) \tag{2.1}$$

$$\dot{z} = g(z, y), \qquad w = h_2(z) \tag{2.2}$$

where y and w are now the outputs of x and z respectively. In order to utilize a *Small Gain Theorem* [2] which generalizes monotone system's generic convergence to systems with negative feedbacks, we need first to introduce some natural definitions.

Definition 2.2.1 *A controlled dynamical system, as in (2.1-2.2), is endowed with the static Input/State characteristic*

$$k_x(\cdot) : \mathcal{U} \to X$$

if for each constant input $u(t) \equiv \overline{u}$ there exists a unique globally asymptotically stable equilibrium $k_x(\overline{u})$. For systems with an output map $y = h(x)$, we also define the static Input/Output characteristic as $k_y(\overline{u}) := h(k_x(\overline{u}))$, provided that an Input/State characteristics exists and that h is continuous.

In this section, we demonstrate the strength of monotone systems in control theory by providing two examples. The first is a well understood dynamical system with global asymptotic stability, while the second is a generalization of the main result for which multi-stability is allowed. We consider now the following system to illustrate the strong implications of *Theorem 2* in [2]:

$$\begin{aligned} \dot{x}_1 &= \frac{1}{1 + x_3^m} - \alpha x_1 \qquad m \in \mathbb{N}, m \geq 1 \\ \dot{x}_2 &= x_1 - \beta x_2 \\ \dot{x}_3 &= x_2 - \gamma x_3 \end{aligned} \tag{2.3}$$

Although the system itself is not monotone shown by the signs of the partial derivatives $\frac{\partial \dot{x}_i}{\partial x_j},\ i \neq j$, however if we consider x_1 as a parameter in the subsystem defined by $\dot{x}_2$ and $\dot{x}_3$, we obtain the following partial derivatives signs:

$$\frac{\partial \dot{x}_2}{\partial x_3} = 0, \ \frac{\partial \dot{x}_3}{\partial x_2} = 1 > 0$$

We remark that non-negative partial derivatives $\frac{\partial \dot{x}_i}{\partial x_j} \geq 0,\ i \neq j$ for a system $\dot{X}$ over a p-convex domain (p-convexity is convexity satisfied for partially ordered points in a set)

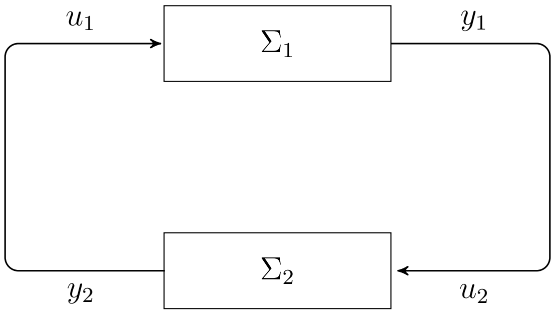


Figure 2.2: Feedback loop of two systems Σ_1 and Σ_2

define *cooperative systems* in the non-negative orthant $\mathbb{R}^n_{\geq 0}$. This cooperativity generates a monotone dynamical system but not a strongly monotone one (we will see later that irreducibility of Jacobian matrix is needed for cooperative systems to generate a strongly monotone dynamics). Therefore, the subsystem of (2.3) defined by $\Sigma_2 = \{\dot{x}_2, \dot{x}_3\}$ over the non-negative orthant $\mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0}$ is monotone (the non-negative orthant is convex). Moreover, the three-dimensional non-negative orthant $\mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0}$ is positively invariant under the flow of (2.3) for positive choice of parameters. We will break (2.3) down into two systems connected with a feedback loop.

$$\Sigma_1 : \ \dot{x}_1 = \frac{1}{1 + x_3^m} - \alpha x_1, \ \ u_1 = x_3, \ \ y_1 = x_1 \tag{2.4}$$

$$\Sigma_2 : \ \begin{cases} \dot{x}_2 = x_1 - \beta x_2, \\ \dot{x}_3 = x_2 - \gamma x_3 \end{cases}, \ \ u_2 = x_1, \ \ y_2 = x_3 \tag{2.5}$$

Due to continuity of the right-hand side of (2.3) and the positive invariance of the non-negative orthant $\mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0} \times \mathbb{R}_{\geq 0}$, both $u_1(\cdot) : \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ and $u_2(\cdot) : \mathbb{R}_{\geq 0} \to \mathbb{R}_{\geq 0}$ are continuous and hence Lebesgue-measurable functions and essentially compacts as required. We call $\mathcal{U}_1$ and $\mathcal{U}_2$ the input spaces of Σ_1 and Σ_2 respectively. Similarly, $\mathcal{Y}_1$ and $\mathcal{Y}_2$ are their output spaces. Moreover, it is assumed by definition that $\mathcal{U}_1 = \mathcal{Y}_2$ and $\mathcal{U}_2 = \mathcal{Y}_1$. For the sake of simplification, we choose $m = 1$.
The characteristics are well-defined as:

$$k_{x_1}(u_1) = \frac{1}{\alpha(1 + u_1)}, \quad k_{y_1}(u_1) = \frac{1}{\alpha(1 + u_1)} \tag{2.6}$$

$$k_{x_2}(u_2) = \frac{u_2}{\beta}, \quad k_{y_2}(u_2) = \frac{u_2}{\gamma\beta} \tag{2.7}$$

Solutions of Σ_1 are bounded. Consider: $\dot{x}_1 < 0 \Leftrightarrow \frac{1}{1+x_3} - \alpha x_1 < 0 \Rightarrow x_1 > \frac{1}{\alpha(1+x_3)}$. Hence, all solutions approach $x_1 \leq \frac{1}{\alpha(1+x_3)}$ at a later time and thus boundedness follows. Similarly consider: $\frac{d(x_2+\beta x_3)}{dt} = x_1 - \beta\gamma x_3 < 0 \Rightarrow x_3 > \frac{x_1}{\beta\gamma}$ and then all trajectories approach $x_3 \leq \frac{x_1}{\beta\gamma}$ at a later time. Therefore, solutions of the closed loop are all bounded. Actually, the boundedness of trajectories and the uniqueness of equilibrium for each system

implies then the global asymptotic stability of their equilibria and hence, the characteristics are well-defined according to Definition 2.2.1.
Σ_1 is monotone (see [2]) because $\frac{\partial \dot{x}_1}{\partial u_1} = -\frac{1}{(1+u_1)^2} < 0$ and simultaneously $\frac{\partial k_{y_1}}{\partial u_1} < 0$. A generalized Kamke-Müller condition in Theorem 1 in [2] tells that Σ_1 is monotone whenever the input u_1 of Σ_1 is ordered with respect to the non-positive cone $\mathbb{R}_{\leq 0}$ and its output y_1 with respect to the usual cone $\mathbb{R}_{\geq 0}$ i.e. $u_1^1 \geq u_1^2,\ x_1^1 = x_1^2 \Rightarrow \phi_{\Sigma_1}(t, x_1^1, u_1^1) \leq \phi_{\Sigma_1}(t, x_1^2, u_1^2),\ k_{y_1}(u_1^1) \leq k_{y_1}(u_1^2)$.
Σ_2 is monotone with respect to its input and initial values because $\frac{\partial \dot{x}_2}{\partial x_3} = 0,\ \frac{\partial \dot{x}_3}{\partial x_2} = 1 > 0$ and $\frac{\partial \dot{x}_2}{\partial u_2} = 1 > 0,\ \frac{\partial \dot{x}_3}{\partial u_2} = 0$ and then it is anti-monotone with respect to its output (i.e., the input u_1 of Σ_1) since the order was reversed by the output of y_1 of Σ_1. It follows then by Theorem 2 in [2] (later called *Small Gain Theorem SGT for monotone systems*) that (2.3) admits a globally attracting equilibrium if the following discrete dynamical system evolving in $\mathcal{U}_1$ the input space of Σ_1 admits a globally attractive equilibrium:

$$u_{k+1} = k_{y_2} \circ k_{y_1}(u_k)$$

Knowing that the mapping $u_{k+1} = k_{y_2} \circ k_{y_1}(u_k) = \frac{1}{\alpha\beta\gamma(1+u_k)}$ has the following first derivative shown by using the chain rule $u'_{k+1} = k'_{y_2}\left(k_{y_2} \circ k_{y_1}(u_k)\right) k'_{y_1}(u_k) = \frac{1}{\gamma\beta}\frac{-1}{\alpha(1+u_k)^2}$. Then for $u_k > \frac{1}{\sqrt{\alpha\beta\gamma}} - 1$, it follows that $\left|u'_{k+1}\right| < 1$ and the mapping is a contraction in the relevant interval. Moreover, the mapping is single-valued and decreasing, which, besides the fact that limit cycles[1] are ruled out for (2.3) when $m = 1$, implies that existence of a unique equilibrium u^0, which is globally attracting. We now perturb 2.3 by adding the terms $\zeta x_2^2 - \varepsilon x_2^3$ to $\dot{x}_2$ and choosing $m = 1$.

$$\begin{aligned} \dot{x}_1 &= \frac{1}{1+x_3} - \alpha x_1 \\ \dot{x}_2 &= x_1 - \beta x_2 + \zeta x_2^2 - \varepsilon x_2^3 \\ \dot{x}_3 &= x_2 - \gamma x_3 \end{aligned} \tag{2.8}$$

We can again break (2.8) down into two systems just as we did for (2.3) and the subsystems will look like:

$$\tilde{\Sigma}_1 :\ \ \dot{x}_1 = \frac{1}{1+x_3} - \alpha x_1,\ \ u_1 = x_3,\ \ y_1 = x_1 \tag{2.9}$$

$$\tilde{\Sigma}_2 :\ \begin{cases} \dot{x}_2 = x_1 - \beta x_2 + \zeta x_2^2 - \varepsilon x_2^3 \\ \dot{x}_3 = x_2 - \gamma x_3 \end{cases},\ \ u_2 = x_1,\ \ y_2 = x_3 \tag{2.10}$$

The decomposition is still that of Single-Input-Single-Output type and flow of the closed loop is bounded. $-\varepsilon x_2^3$ is a term which is added to keep trajectories bounded. $\tilde{\Sigma}_1$ and its output function y_1 are monotone for initial data and input u_1 with respect to the non-positive cone $K = \mathbb{R}_{\leq 0}$. Characteristics are now:

$$k_{x_1}(u_1) = \frac{1}{\alpha(1+u_1)},\ \ k_{y_1} = \frac{1}{\alpha(1+u_1)} \tag{2.11}$$

[1] In fact, (2.3) does not admit periodic solutions for $m < 8$. This is a well-known feature of such models which was proven first in [39] and appears later in [74].

$k_{x_2}(u_2),\ k_{y_2}(u_2) = \frac{k_{x_2}(u_2)}{\gamma}$ are not in general single-valued since $\dot{x}_2$ has a third order polynomial on its right-hand side and consequently are only defined implicitly. $\frac{\partial \dot{x}_2}{\partial x_3} = 0$ and $\frac{\partial \dot{x}_3}{\partial x_2} = 1 > 0$, hence $\tilde{\Sigma}_2$ is monotone for partially ordered initial data.
We choose now $\varepsilon = 0.01, \alpha = 1, \zeta = 1, \gamma = 1$ and $\beta = 3$ to guarantee that $\dot{x}_2$ admits three real positive roots for all values of input u_2. The choice is motivated by the search for a model where the discrete system $u_{k+1} = k_{y_2} \circ k_{y_1}(u_k)$ converges to more than one equilibrium and still implies the convergence of the original system to more than one equilibrium as proven in [18]. ε is small enough to be considered just as a small perturbation of the second-order truncation of $\dot{x}_2$, hence not destroying its existing roots for suitable parameters. Moreover, the roots exist in this case for all valid inputs u_2 where inputs u_2 are all bounded from above by $\frac{1}{\alpha}$. Due to the fact that $\dot{x}_2 = x_1 - \beta x_2 + \zeta x_2^2 - \varepsilon x_2^3$ has a finite number of solutions and no cycles for each choice of x_1, it follows that every solution of both subsystems is an equilibrium. It could then be easily checked that the set of equilibria of characteristics of each subsystem contain no chain and hence all sequence solutions $\{u_k\}$ of $k_{y_2} \circ k_{y_1}$ converge. Hence, the model differs from that discussed in [18] that inputs u_2 here does not approach a single invariant interval where the characteristic k_{x_2} is single-valued and then a unique equilibrium is concluded. Rather, there are two invariant intervals for inputs u_2. Substituting $k_{x_2} = \gamma k_{y_2}$ in the right-hand side of $\dot{x}_2$ and setting it to zero and then differentiating with respect to u_2, we obtain:

$$-3\varepsilon\gamma^3 k_{y_2}(u_2)^2 k'_{y_2}(u_2) + 2\zeta k_{y_2}(u_2) k'_{y_2}(u_2) - \beta k'_{y_2}(u_2) + 1 = 0$$

Then $k'_{y_2}(u_2) = \frac{-1}{-3\varepsilon\gamma^3 k_{y_2}(u_2)^2 + 2\zeta k_{y_2}(u_2) - \beta}$ and consequently:

$$\left|k'_{y_2}\left(k_{y_2} \circ k_{y_1}(u_k)\right) k'_{y_1}(u_k)\right| = \left|\frac{-1}{\alpha(1+u_k)^2\left(-3\varepsilon\gamma^3 u_k^2 + 2\zeta u_k - \beta\right)}\right|$$

$-3\varepsilon\gamma^3 u_k^2 + 2\zeta u_k - \beta$ is strictly increasing and negative in the interval $[0, \frac{2}{5}]$, hence it attains its minimum exactly at $u_k = 0.4$, then for all $u_k \in [0, \frac{2}{5}]$:

$$\left|k'_{y_2}\left(k_{y_2} \circ k_{y_1}(u_k)\right) k'_{y_1}(u_k)\right| < \frac{1}{2}$$

Then $u_{k+1} = k_{y_2} \circ k_{y_1}$ is a contraction over the invariant interval $[0, \frac{2}{5}]$ and single-valued (because it is strictly decreasing), hence it admits there a unique attracting equilibrium. Similarly, for $u_k > 80$, the polynomial $-3\varepsilon\gamma^3 u_k^2 + 2\zeta u_k - \beta$ is strictly decreasing and negative, thus it attains its minimum at $u_k = 80$. Consequently, $\left|k'_{y_2}\left(k_{y_2} \circ k_{y_1}(u_k)\right) k'_{y_1}(u_k)\right| < \frac{1}{35}$ and the mapping is again a contraction over the invariant interval $[80, \infty[$ and strictly decreasing and then single-valued. Hence, it admits there a unique attracting equilibrium. Therefore, multistability of (2.8) is implied by the multistability of the discrete system $u_{k+1} = k_{y_2} \circ k_{y_1}$, which shows the dominance of monotone systems behavior illustrated in generic convergence over the influence of the negative feedback connection.
The goal of this example is to demonstrate an efficient method (SGT) of treating systems with a negative feedback term $\frac{1}{1+x_n^m}$, a term which can be incorporated in models of photosynthesis if we assume that one of the three essential metabolites RuBP, PGA or TP listed in Figure 1.1 exerts negative feedback on the cycle. This is the case in many cellular metabolic processes (e.g., mRNA transcription models (see [111])). In the given example, the mRNA M encoding for a protein E is repressed by a metabolite produced by the protein itself. We

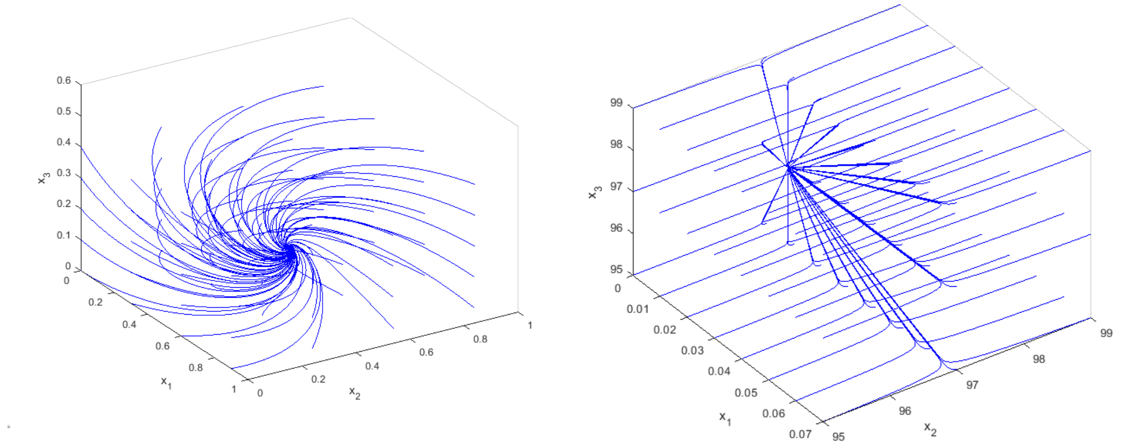


Figure 2.3: The two attracting equilibria of system (8)

might believe that this is the case in photosynthesis for a finite interval of time. Knowing that once TP accumulates in the chloroplast, the chloroplast's membrane obligates its exit in correspondence with inorganic phosphate P_i entry. The latter is known to reduce the carbon reduction cycle's efficiency by inhibiting key enzymes like fructose 1,6-bisphosphate, sedoheptulose 1,7-bisphosphate and erythrose-4-phosphate. Although this interpretation assumes an efficient TP/P_i translocation between the sides of the membrane, it resembles the only scenario-to our knowledge-where negative feedback mechanism is witnessed in photosynthesis (see [31]). If we replace $\frac{1}{1+x_n^m}$ by $\frac{x_n^m}{1+x_n^m}$ (see [94], [39], [40]), we will be back in the positive feedback scenario, which holds for all models discussed later. Hence photosynthesis modeling lies between these two "standard" modelings, which resemble convergence to steady states as key feature. Griffith in [39] and Tyson in [110] had shown already that negative feedback models with the term $\frac{1}{1+x_n^m}$ can resemble sustained oscillations (i.e., periodic orbits) provided that $m > 8$. However, this is far from being satisfied in photosynthesis models due to the fact that only one of six TPs will be translocated out of the chloroplast each time the cycle runs. Accumulated TP in the chloroplast is known for enhancing starch production but is not known as inhibiting the cycle.

Singularly Perturbed Monotone Systems

It is well-known that Quasi-Steady State Assumption was always one of the major tools for chemists to simplify the settings in search of useful approximate measurements. This method was utilized by chemists Michaelis and Menten to write the velocities of Enzyme/Substrate reaction. Let's consider the famous Michaelis-Menten Kinetics (see [10]):

$$\underset{\text{Substrate}}{\mathrm{S}} + \underset{\text{Enzyme}}{\mathrm{E}} \underset{k_{-1}}{\overset{k_1}{\rightleftharpoons}} \underset{\text{Complex}}{\mathrm{SE}} \xrightarrow{k_2} \underset{\text{Product}}{\mathrm{P}} + \underset{\text{Enzyme}}{\mathrm{E}}$$

This reaction mechanism generates the following system of differential equations written in Mass-Action kinetics:

$$\begin{aligned}\frac{ds}{dt} &= -k_1 e_0 + (k_1 s + k_{-1})c \\ \frac{dc}{dt} &= k_1 e_0 s - (k_1 s + k_{-1} + k_2)c\end{aligned} \tag{2.12}$$

where e_0 is the initial enzyme concentration. There are many Quasi-Steady State assumptions which all lead to setting one of the equations in (2.12) to zero and thus reducing the dimension of the system. The general assumption tells that catalyzing enzyme quantity stands in no relation to the substrate concentration, to the extent that after a short time interval, the entire amount of enzyme would be saturated by the substrate. Due to the low initial concentration of enzyme, it is assumed that substrate almost does not change during the first phase (Pre-Steady State phase) while the complex c is assumed to be reaching an equilibrium $\frac{dc}{dt} \approx 0$, where it stays for a considerable interval of time in a Quasi-Steady State of the system in the second phase. In fact, the relatively slow change in substrate s in the transient phase together with the product reaction k_2 once a recognized quantity of complex is formed leads us to consider the complex c as keeping up with the substrate. Hence, $\dot{c}$ is the outcome of the dynamics of s on the manifold $\frac{dc}{dt} \approx 0$. Experimenters usually like then to reduce the system to a single differential equation of the substrate

$$\frac{ds}{dt} = -\frac{k_2 e_0 s}{s + K_m}, \tag{2.13}$$

where $K_m = \frac{k_{-1}+k_2}{k_1}$ is the Michaelis Menten constant. (2.13) could be reestablished in the light of Singular Perturbation Theory if there is good reasoning to consider some ratios of parameters as too small. The works of Fenichel [27], [28], Tikhonov [108] and Gradshtein [36] provided the rigorous foundation of Singular Perturbation Theory with the basic idea that species -after a suitable non-dimensionalization- work on different time scales. For example, some reactions might yield much faster than the others, which requires that the reaction kinetics resemble a huge discrepancy. In this sense, a parameter ε is defined to be, in the simplest case, the ratio of two reactions' rates (e.g., $\varepsilon = \frac{k_1}{k_{-1}}$) and is required to be small enough $\varepsilon \ll 1$. A non-dimensionalization of the concentrations is then utilized so that a system like:

$$\begin{aligned}\dot{X} &= f(X, Y) \\ \dot{Y} &= g(X, Y)\end{aligned} \tag{2.14}$$

where $(X, Y) \in \mathbb{R}^n \times \mathbb{R}^m,\ m, n \in \mathbb{N}$ is rescaled upon the non-dimensionalization[1] into:

$$\begin{aligned}\dot{x} &= f(x, y) \\ \varepsilon\dot{y} &= g(x, y)\end{aligned} \tag{2.15}$$

[1] For notational ease, the same naming f and g is kept after non-dimensionalization. f and g in 2.15 is just a rescaled version of those in 2.14.

(2.15) is the slow-time system formulation of (2.14) in $\mathcal{O}(t)$ in contrast to the fast-time system[1] formulation done by scaling $t = \varepsilon\tau$:

$$\begin{aligned} x' &= \varepsilon f(x,y) \\ y' &= g(x,y) \end{aligned} \tag{2.16}$$

where x' instead of $\dot{x}$ is the usual notation of velocity for $x(\tau), y(\tau)$. Writing the solutions of (2.15) as a regular Taylor Expansion with respect to ε, $x(\varepsilon;t) := \sum_{n\geq 0} \varepsilon^n x_n(t)$, $y(\varepsilon;t) := \sum_{n\geq 0} \varepsilon^n y_n(t)$ will not satisfy arbitrary initial conditions $x(0)$ and $y(0)$ (see [74]). This motivates considering the system in fast-settings as in (2.16) and comparing the terms of the ansatz $x(\varepsilon;\tau) := \sum_{n\geq 0} \varepsilon^n x_n(\tau)$, $y(\varepsilon;\tau) := \sum_{n\geq 0} \varepsilon^n y_n(\tau)$ for which the system admits two degrees of freedom for each coefficient (not reduced) and leads to consistent calculations up to higher degrees as long as the right-hand sides are smooth enough. (2.16) serves to describe the dynamics in the fast-transient phase $0 < t \ll 1$ (a layer of time), while for the larger interval during the slow-phase, approximations based on (2.15) are used. Solutions of both systems are then unified by matching the first coefficients according to the following identity:

$$\lim_{\tau\to\infty} [x_0(\tau); y_0(\tau)] = \lim_{t\to 0} [x_0(t); y_0(t)] \tag{2.17}$$

under the implicit condition that both t and ε approach zero and the latter is faster as noticed from $\tau \to \infty$. This matching establishes the solution for t for all $t > 0$, regardless of how tiny it could be. However, it is ε dependent, which does not reflect the relative freedom of choosing initial values for x, y. Hence, another matching is needed for the exact moment $t = 0$ and where ε does not come into play. We may suppose $\varepsilon > 0$, it is then straightforward to check that for $t = \tau = 0$, the solutions $x(\varepsilon;\tau)$ and $y(\varepsilon;\tau)$ satisfy:

$$x(\varepsilon;0) = x(0), \quad y(\varepsilon;0) = y(0)$$

$[x(\varepsilon,\tau); y(\varepsilon,\tau)]$ is then used for the time scale $0 < \varepsilon < t \ll 1$ and for late time, the solution $[x(\varepsilon,\tau); y(\varepsilon,\tau)]$ provides already a good approximation, which usually suffices the chemists. Quasi-Steady State Assumption does not imply necessarily the existence of time scales as presented by the Singular Perturbation Theory. Actually, QSS remains heuristic, whereas SPT is based on rigorous mathematical foundations and interpreting QSS in the light of singular perturbation was not always a success. For instance, if we consider k_2 as our small parameter ε in (2.12) (or $\frac{k_2}{k_1} = \varepsilon$ at least), applying the QSS Assumption for the complex $\frac{dc}{dt} \approx 0$ leads to $\frac{ds}{dt} \approx 0$ since velocities' ratio is a constant in case $k_2 = 0$. Hence, both variables are of the same quality (i.e., both are slow variables), which is essentially an oversimplification not intended by the Singular Perturbation motive (see [34]). Nevertheless, successful efforts have been devoted to regenerate QSS from the Singular Perturbation Theory (see [93]) upon choosing a suitable scaling[2] and which resembled a significant correspondence between the dynamics of (2.12), for example and the physical assumption, on

[1] The naming is justified by the fact that ε multiplied with $f(x,y)$ for $\varepsilon \ll 1$ significantly slows down the velocity of x.

[2] There is no prescribed way of how scaling should be chosen. General insights as well as 'unmature' methods are listed in [93].

which the QSS is based. Authors in [93] were able to broaden the typical assumption of small parameter, namely $\frac{e_0}{s_0} = \varepsilon \ll 1$ into $\frac{e_0}{K_m + s_0} = \varepsilon \ll 1$, where same results hold. As mentioned before, Singular Perturbation Theory is based on Fenichel's fundamental work, among others. Their work has shown the ability to reduce the study of a dynamical system into investigating the dynamics of an invariant manifold of lower dimension. This manifold is called the *critical manifold* and is defined as

$$C_0 := \{(x, y) \in \mathbb{R}^n \times \mathbb{R}^m \mid 0 = f(x, y, 0)\} \tag{2.18}$$

if we switch to the prevalent notation of systems, namely the fast system being described by:

$$\begin{aligned} x' &= f(x, y, \varepsilon) \\ y' &= \varepsilon g(x, y, \varepsilon) \end{aligned} \tag{2.19}$$

and the slow system by the following

$$\begin{aligned} \varepsilon \dot{x} &= f(x, y, \varepsilon) \\ \dot{y} &= g(x, y, \varepsilon) \end{aligned} \tag{2.20}$$

and where ε adjoined the variables x, y on the right-hand sides to emphasize that this formulation is equally valid to that in (2.15) and (2.16). (2.19) and (2.20) are called *the layer problem* and *the reduced problem* whenever $\varepsilon = 0$. Then C_0 is the manifold where dynamics of the reduced problem are taking place. Stability analysis of C_0 is then studied with respect to the layer problem. For instance, if the Jacobian of the layer problem admits exactly n_s eigenvalues of negative real part at C_0 then C_0 admits locally a stable invariant manifold of dimension $n_s + m$ because m stable dimensions are guaranteed from C_0 itself being invariant for the reduced flow. The Critical Manifold C_0 does not disappear if $1 \gg \varepsilon > 0$ provided that it is *normally hyperbolic* in addition to smoothness. C_0 is *normally hyperbolic* whenever the Jacobian $\frac{\partial f}{\partial x}|_{C_0, \varepsilon=0}$ has all eigenvalues bounded away from the imaginary axis. Here is an accurate definition of normal hyperbolicity:

Definition 2.3.1 *A subset $S \subset C_0$ is called normally hyperbolic if the $n \times n$ matrix $(D_x f)(p, 0)$ of first partial derivatives with respect to the fast variables has no eigenvalues with zero real part for all $p \in S$.*

Violation of normal hyperbolicity by the invariant manifold C_0 is independent of the dynamics taking place on it or by those dynamics which are considered as parallel to them in a close neighborhood. In other words, an invariant manifold of some equilibrium lying on C_0 shifting nearby trajectories in a direction tangent to C_0 does not contribute to the violation of the property. $f(x, y, 0) = 0$ is solved by $x = h_0(y)$ by the Implicit Function Theorem if $\frac{\partial f}{\partial x}|_{(x_0, y_0)} \neq 0$ leading to the reduced system over the critical manifold C_0

$$\dot{y} = g(h_0(y), y, 0) \tag{2.21}$$

The existence of such $h_0 : \mathbb{R}^m \to \mathbb{R}^n$ is essential by itself for checking for *normal hyperbolicity*, although it is not surprising that such locality arises in the discussion. This locality

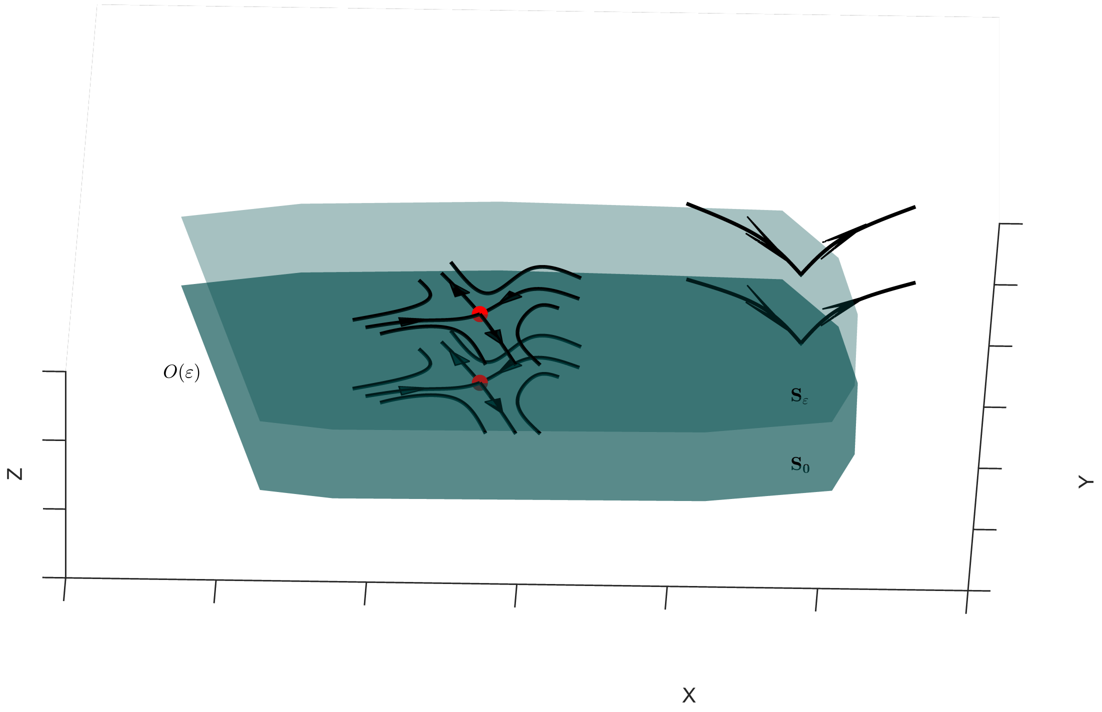


Figure 2.4: S_0 perturbs to S_ε within a Hausdorff distance $\mathcal{O}(\varepsilon)$. Moreover, both $W^u(S_0)$ and $W^s(S_0)$ perturb

is inherited from the Centre Manifold Theory, on which the singular perturbation scheme is based. Hence, in reality normal hyperbolicity will be locally checked at some compact subset S_0 of C_0. Urged by the propensity for completion, we state the two following main theorems of Fenichel's work.

Theorem 6 *For f, g C^k in (x, y, ε) and S_0 a normally hyperbolic compact subset of the critical manifold C_0 given by $S_0 = \{(h_0(y), y) \mid y \in U\}$, there exists $\varepsilon_0 > 0$ such that for $\varepsilon \in (0, \varepsilon_0]$ there exists a locally invariant n-dimensional C^k manifold S_ε given as a graph $S_\varepsilon = \{(h(y, \varepsilon), y)\}$, where h is C^k in x and ε and $h(y, 0) = h_0(y)$.*

The theorem states that S_0 perturbs locally into an invariant manifold S_ε for $\varepsilon > 0$. The next question is: How far is S_ε from S_0? Does the (n_s+m)-dimensional stable manifold $W^u(S_0)$ of S_0 and consequently, its $(n_u + m)$-dimensional unstable manifold $W^s(S_0)$ continuously perturb into stable and unstable manifolds of S_ε. The next theorem confirms this assumption.

Theorem 7 Fenichel's Theorem *Suppose $S = S_0$ is a compact normally hyperbolic submanifold (probably with boundary) of the critical manifold C_0 of System (2.20) and that $f, g \in C^k(k < +\infty)$. Then for $\varepsilon > 0$ sufficiently small, the following hold:*

(F1): *There exists a locally invariant manifold S_ε diffeomorphic to S_0. Local invariance means that trajectories can enter or leave S_ε only through its boundaries.*

(F2): *S_ε has Hausdorff distance $\mathcal{O}(\varepsilon)$ (as $\varepsilon \to 0$) from S_0.*

(F3): *The flow on S_ε converges to the slow flow as $\varepsilon \to 0$.*

(F4): *S_ε is C^k smooth.*

(F5): *S_ε is normally hyperbolic and has the same stability properties with respect to the fast variables as S_0 (attracting, repelling or of saddle type).*

(F6): *S_ε is usually not unique. In regions that remain at a fixed distance from ∂S_ε, all manifolds satisfying $(F1)-(F5)$ lie at a Hausdorff distance $\mathcal{O}(e^{-\frac{K}{\varepsilon}})$ from each other for some $K > 0, K = \mathcal{O}(1)$.*

Note that all asymptotic notation refers to $\varepsilon \to 0$. The same conclusions as for S_0 hold locally for its stable and unstable manifolds

$$W^s_{loc}(S_0) = \bigcup_{p \in S_0} W^s_{loc}(p) \quad W^u_{loc}(S_0) = \bigcup_{p \in S_0} W^u_{loc}(p)$$

where we view points $p \in S_0$ as equilibria for the fast system. These manifolds also persist for $\varepsilon > 0$ sufficiently small: There exists local stable and unstable manifolds $W^s_{loc}(S_\varepsilon), W^u_{loc}(S_\varepsilon)$, respectively, for which conclusions $(F1) - (F6)$ hold if we replace S_0 and S_ε by $W^s_{loc}(S_\varepsilon)$ and $W^s_{loc}(S_0)$ (or similarly by $W^u_{loc}(S_\varepsilon)$ and $W^u_{loc}(S_0)$).

To make things better understandable, we provide the following example. We consider the following simple linear system of differential equations written in fast-slow settings:

$$\begin{aligned} \varepsilon \dot{x}_1 &= -x_1 - 3x_2 \\ \dot{x}_2 &= 2x_2 \end{aligned} \tag{2.22}$$

with $\varepsilon > 0$ sufficiently small. If we substitute by $\varepsilon = 0$, we obtain the reduced problem:

$$\begin{aligned} 0 &= -x_1 - 3x_2 \\ \dot{x}_2 &= 2x_2 \end{aligned} \tag{2.23}$$

The slow flow generated by System (2.23) is restricted over the critical manifold given by:

$$C_0 = \left\{(x_1, x_2) \in \mathbb{R}^2 \mid -x_1 - 3x_2 = 0\right\} \tag{2.24}$$

Notice that x_1 represents the fast variable in the above notation and $D_{x_1} f(x_1, x_2, \varepsilon)|_{\varepsilon=0}$ represents the Jacobian matrix of the fast variable equation at $\varepsilon = 0$. We conclude that C_0 is normally hyperbolic manifold with respect to the fast flow since $D_{x_1} f(x_1, x_2, \varepsilon)|_{\varepsilon=0} = -1$. It remains then to study the slow flow on C_0, which is a one-dimensional invariant manifold and geometrically a line in $\mathbb{R}^2$. Clearly, any solution starting on C_0 near $O(0, 0)$, the unique equilibrium, diverges eventually from it as $t \to \infty$. It suffices to consider the differential equation $\dot{x}_2 = 2x_2$, whose solutions is $x_2(t) = c_2 e^{2t}$ with c_2 being the initial point. Hence, O is a repelling equilibrium on C_0. To see how C_0 perturbs, let us consider System (2.22) and solve it explicitly. The solutions are given by:

$$x_1(t) = c_1 e^{-\frac{t}{\varepsilon}} - \frac{3c_2}{2\varepsilon + 1} e^{2t} + \frac{3c_2}{2\varepsilon + 1} e^{-\frac{t}{\varepsilon}} \tag{2.25}$$

$$x_2(t) = c_2 e^{2t} \tag{2.26}$$

A direct candidate for C_ε the perturbed invariant manifold is $x_1(t) + 3x_2(t) + R(t, \varepsilon)$ with $R(t,\varepsilon) \underset{\varepsilon\to 0}{\to} 0$. It is given by the following implicit equation:

$$x_1(t) + 3x_2(t) - 3c_2 \left(\frac{2\varepsilon}{2\varepsilon + 1}\right) e^{2t} - \left(\frac{2\varepsilon c_1 + c_1 - 3c_2}{2\varepsilon + 1}\right) e^{-\frac{t}{\varepsilon}} = 0 \tag{2.27}$$

This equation can be written in terms of x_1, x_2 and ε solely by:

$$x_1(t) + 3x_2(t) - 3c_2 \left(\frac{2\varepsilon}{2\varepsilon + 1}\right) \log \left(\frac{x_2(t)}{c_2}\right)^2 - \left(\frac{2\varepsilon c_1 + c_1 - 3c_2}{2\varepsilon + 1}\right) \log \left(\frac{x_2(t)}{c_2}\right)^{-\frac{1}{\varepsilon}} = 0 \tag{2.28}$$

Both terms $\log \left(\frac{x_2(t)}{c_2}\right)^2$ and $\log \left(\frac{x_2(t)}{c_2}\right)^{-\frac{1}{\varepsilon}}$ are bounded as $\varepsilon \to 0$ since $\frac{x_2(t)}{c_2} \geq 1, \forall t \geq 0$. Eventually, the Hausdorff distance between C_0 and C_ε, $d_H(C_0, C_\varepsilon) = \mathcal{O}\left(\left|3c_2 \left(\frac{2\varepsilon}{2\varepsilon+1}\right) \log \left(\frac{x_2(t)}{c_2}\right)^2\right|\right)$ $= \mathcal{O}(\varepsilon)$. Notice that in this example $W^s(C_0) = C_0$ and it perturbs then into $W^s(C_\varepsilon) = C_\varepsilon$ by the same given perturbation equation.

Chapter 3

Hahn's Two-Dimensional Model

The Calvin cycle is a part of photosynthesis. There are many mathematical models for this biochemical system in the literature. Reviews of these can be found in [3], [4] and [59]. This is an interesting example in which the relations between different mathematical models for the same biological situation can be investigated. Mathematical comparison of a number of these models was carried out in [84]. There it was pointed out that it would be desirable to look more closely at the minimal model of the Calvin cycle introduced by Hahn [44]. Hahn's paper contains several related systems of ordinary differential equations of dimensions two and three and the present chapter aims to obtain an understanding of the dynamics of the two-dimensional models of Hahn, which is as complete as possible. There is also a brief discussion of the relation of the two-dimensional models to the three-dimensional one. The latter will be thoroughly discussed in the next chapter.

The function of the Calvin cycle is to use carbon dioxide to produce sugars. This process is fuelled by ATP and NADPH produced in the light reactions of photosynthesis, where the energy contained in light is captured as chemical energy. A comprehensive introduction to the biochemistry of photosynthesis can be found in [50]. The Calvin cycle's primary step, resulting in the production of PGA (phosphoglycerate), is catalyzed by the enzyme RuBisCO. Interestingly, this enzyme has dual functionality. It can catalyze the reaction of carboxylation, which is the primary way carbon dioxide is fixed in the Calvin cycle and an oxidation reaction. This second reaction competes with the first and reduces the efficiency with which the Calvin cycle produces sugar. The reason for the existence of this seemingly wasteful alternative reaction is not clear. One possible explanation, for which the Hahn model is relevant, is that photorespiration stabilizes the system - it creates the possibility of the existence of a stable positive steady state. Moreover, it has been recently argued [8] that such a seemingly wasteful process is, in reality, an essential evolution process to get rid of the intermediate 2-phosphoglycolate (2PG), which, if not converted into phosphoglycerate, practices inhibition [29] on necessary enzymes and would obstruct RuBP ribulose 1,5-bisphosphate regeneration.

This chapter is organized as follows: In Section 3.1, the two-dimensional system of Hahn is introduced. In dimensionless form, the equations depend on two non-negative parameters α and β. The case $\beta > 0$ corresponds to including photorespiration in the model. The dynamics of the model are first analyzed in the case without photorespiration ($\beta = 0$). The main result is Proposition 5, which describes the global asymptotic behavior of general solutions in detail. There exists a unique positive steady state S_1, which is unstable. For an open set of initial data, which will be described in detail, all concentrations tend to zero as $t \to \infty$. For another open set of initial data, all concentrations tend to infinity as $t \to \infty$. The com-

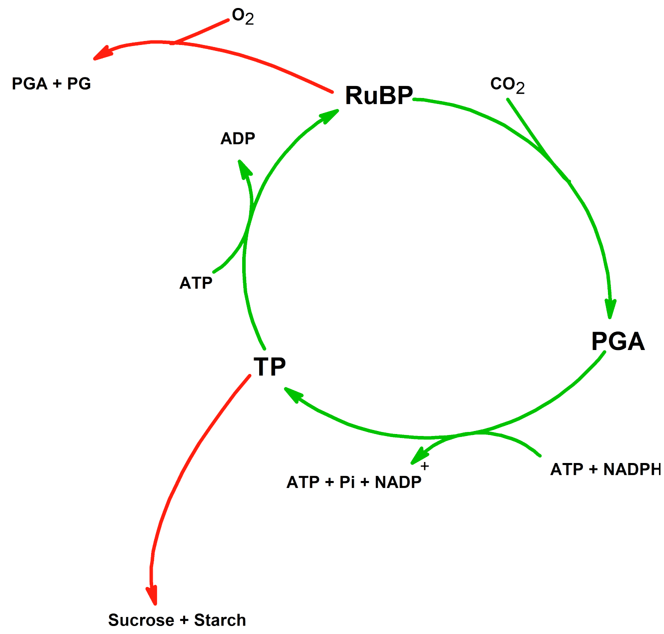


Figure 3.1: The main reactions in photosynthesis considered by Hahn

plement of these two sets' union is the stable manifold of the steady state S_1. A formula is derived for the leading order asymptotics of the solutions, which tend to infinity. In Section 3.2, the case $\beta > 0$ will be addressed. The main result is Proposition 8. In one open set of parameter space, for which an explicit formula is given, all solutions' concentrations tend to zero as $t \to \infty$. In the interior of the complement of that set, more interesting behavior is observed. There are two positive steady states, one stable and one unstable. For an open set of initial data, all concentrations tend to zero as $t \to \infty$. For another open set of initial data, the solutions tend to the stable positive steady state as $t \to \infty$. Many models of the Calvin cycle contain the fifth power of the concentration of the substance GAP (glyceraldehyde phosphate). This is because in the usual coarse-grained descriptions of the Calvin cycle, where many elementary reactions are combined, there is an effective reaction where five GAP molecules with three carbon atoms each go in and three molecules of a five-carbon sugar come out. Applying mass-action kinetics to this leads to the fifth power. In deriving the model studied in Sections 3.1 and 3.2, Hahn replaces the fifth power with the second power. His motivation is to make the model analytically more tractable. He implicitly assumes that this change makes no essential difference to the solutions' qualitative behavior but gives no justification for this assumption. In Section 3.3, we will show that the solutions of the model with the fifth power do indeed behave in a way which is very similar to the behavior of the model with the second power. The main difference in the analysis is that no explicit formula is obtained for the boundary between the two generic behaviors in parameter space for the fifth power. The results are summarized in Propositions 10 and 11. In [44], the two-dimensional systems are obtained from a three-dimensional one by informal arguments. In Section 3.4, it will be shown how the relationship between the three-dimensional system and the two-dimensional system with the fifth power can be formalized in a rigorous way using the theory of fast-slow systems (for an introduction to this theory, we refer to [63]). This also gives some limited information about the dynamics of solutions of the three-dimensional system. In Section 3.5, we provide a theoretical basis for some propositions and conclusions demonstrated in the previous sections. This will be pointed out every time the results from Section 3.5 are used. The main content of this chapter was treated and published in [76].

The System of Hahn

It is beneficial at this point to reconsider the set of reactions which highlight the significance of the model.

$$\underset{\text{Carbon dioxide}}{\mathrm{CO_2}} + \underset{\text{Ribulose 1,5-bisphosphate}}{\text{RuBP}} \xrightarrow{k_1} \underset{\text{Phosphoglycerate}}{\text{2 PGA}}$$

$$\underset{\text{Oxygen}}{2\,\mathrm{O_2}} + \underset{\text{Ribulose 1,5-bisphosphate}}{\text{2 RuBP}} \xrightarrow{k_2} \underset{\text{Phosphoglycerate}}{\text{3 PGA}} + \underset{\text{Carbon dioxide}}{\mathrm{CO_2}}$$

$$\underset{\text{Phosphoglycerate}}{\text{PGA}} \xrightarrow{k_3} \underset{\text{Triose phosphate}}{\text{TP}}$$

$$\underset{\text{Triose phosphate}}{\text{5 TP}} \xrightarrow{k_4} \underset{\text{Ribulose 1,5-bisphosphate}}{\text{3 RuBP}}$$

$$\underset{\text{Triose phosphate}}{\text{TP}} \xrightarrow{k_5} \underset{\text{Carbon dioxide}}{3\,\mathrm{CO_2}}$$

$$\underset{\text{Triose phosphate}}{\text{TP}} \xrightarrow{k_6} \text{Sucrose} + \text{Starch}$$

These reactions generate the following system of differential equations if the law of mass action kinetics is used.

$$\begin{aligned}
\frac{d[\text{RuBP}]}{dt} &= -k_1[\text{RuBP}] - 2k_2[\text{RuBP}]^2 + 3k_4[\text{TP}]^5 \\
\frac{d[\text{PGA}]}{dt} &= 2k_1[\text{RuBP}] + 3k_2[\text{RuBP}]^2 - k_3[\text{PGA}] \\
\frac{d[\text{TP}]}{dt} &= k_3[\text{PGA}] - 5k_4[\text{TP}]^5 - (k_5 + k_6)[\text{TP}]
\end{aligned} \tag{3.1}$$

Hahn has first simplified the system by setting the second of the differential equations to zero and reducing TP's power to two instead of five. This simplified system is what will be examined in what follows and consists of the equations (41)-(42) in [44]:

$$\frac{dx}{dt} = -\alpha x - 2\beta x^2 + 3y^2, \tag{3.2}$$

$$\frac{dy}{dt} = 2\alpha x + 3\beta x^2 - 5y^2 - y. \tag{3.3}$$

Due to the biological interpretation of the solutions, we are interested in solutions which lie in the positive quadrant, which is forward invariant. In addition to the system with $\alpha > 0$ and $\beta > 0$, which we will call the full system, we also address the cases where $\alpha = 0$

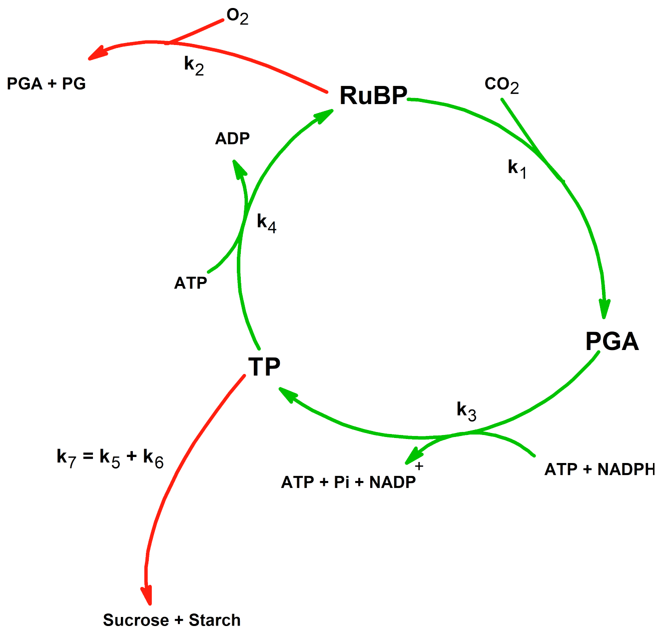


Figure 3.2: The main reactions in photosynthesis considered by Hahn shown with their kinetic rates

(no photosynthesis), $\beta = 0$ (no photorespiration) or both. Note for future reference that the derivative of the right-hand side of this system at the point (x, y) is

$$\begin{bmatrix} -\alpha - 4\beta x & 6y \\ 2\alpha + 6\beta x & -10y - 1 \end{bmatrix} \tag{3.4}$$

with determinant $\alpha + 4\beta x - 2\alpha y + 4\beta xy$. Consider first the case $\alpha = \beta = 0$. There, any solution satisfies the inequality $\frac{dy}{dt} \leq -y$ and thus y decays exponentially at late times. In particular, there are no positive steady states. The non-negative steady states are precisely the points on the x-axis. Apart from the zero eigenvalue, due to the continuum of steady states, the other eigenvalue of the linearization at any of these points is -1 and this manifold is normally hyperbolic [63]. It follows that given any $x_0 > 0$, there exists a positive solution with $\lim_{t\to\infty} x(t) = x_0$.

Consider next the case $\alpha = 0$, $\beta > 0$. Any positive steady state satisfies $y = \sqrt{\frac{2\beta}{3}x}$ by (3.2). Substituting this into (3.3) gives $y(-\frac{1}{2}y - 1) = 0$. Thus, there is no positive steady state. The only non-negative steady state is at the origin. In fact, $\frac{d}{dt}(3x + 2y) = -y^2 - 2y$. Thus, $3x + 2y$ is a strict Lyapunov function on the positive quadrant and it follows that all solutions converge to the origin as $t \to \infty$.

In the case $\alpha > 0$, $\beta = 0$, we have the inequality $\frac{d}{dt}(5x + 3y) \leq \frac{1}{5}\alpha(5x + 3y)$ so that all solutions exist globally in the future. Equation (3.2) shows that for a steady state $x = \frac{3}{\alpha}y^2$. Substituting this into (3.3) gives $y^2 - y = 0$. Thus the steady states are $S_0 = (0, 0)$ and $S_1 = \left(\frac{3}{\alpha}, 1\right)$.

Now we carry out a nullcline analysis, as described in Section 3.5. The nullclines are given by $x = \frac{3}{\alpha}y^2$ and $x = \frac{1}{2\alpha}(5y^2 + y)$. These are the graphs of functions of y and it is clear that the complement of the union of the nullclines has four connected components (cf. Figure 3.3).

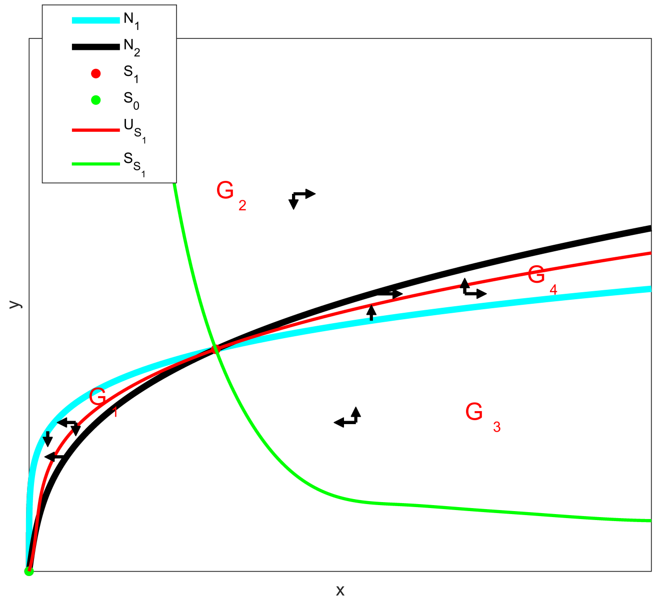


Figure 3.3: Nullclines (solid lines) and direction field (arrows) in the absence of photorespiration

These are:

$$G_1 = (-,-) = \{(x,y) \mid x > \frac{3}{\alpha}y^2, x < \frac{1}{2\alpha}(5y^2+y)\}, \tag{3.5}$$

$$G_2 = (+,-) = \{(x,y) \mid x < \frac{3}{\alpha}y^2, x < \frac{1}{2\alpha}(5y^2+y)\}, \tag{3.6}$$

$$G_3 = (-,+) = \{(x,y) \mid x > \frac{3}{\alpha}y^2, x > \frac{1}{2\alpha}(5y^2+y)\}, \tag{3.7}$$

$$G_4 = (+,+) = \{(x,y) \mid x < \frac{3}{\alpha}y^2, x > \frac{1}{2\alpha}(5y^2+y)\}. \tag{3.8}$$

The complement of S_1 in one of the nullclines has two connected components, which can be distinguished by the sign of the time derivative, which does not vanish. We write:

$$N_1 = S_0 \cup (0,-) \cup S_1 \cup (0,+), \tag{3.9}$$

$$N_2 = S_0 \cup (-,0) \cup S_1 \cup (+,0). \tag{3.10}$$

Note that (for general α and β) if $\dot{x} = 0$ at some point in time then $\ddot{x} = 6y\dot{y}$ and that if $\dot{y} = 0$ at some point then $\ddot{y} = (2\alpha + 6\beta x)\dot{x}$.

Proposition 2 *A solution of (3.2)-(3.3) belongs to one of the following three cases.*

i) It converges to S_0 as $t \to \infty$.

ii) It converges to S_1 as $t \to \infty$.

iii) There is a time t_1 such that it belongs to G_4 for $t \geq t_1$.

Proof: Consider a solution which starts at a point on the boundary of G_1 rather than S_0 or S_1. If it is on N_1, then $\dot{y} < 0$ and using the equation for $\ddot{x}$ shows that $\dot{x}$ immediately becomes negative. If a solution starts on N_2 then $\dot{x} < 0$ and $\dot{y}$ immediately becomes negative. It follows that any solution which starts in G_1 remains in G_1 and any solution that starts at a point on the boundary of G_1 other than a steady state immediately enters G_1. Since y is decreasing for solutions in G_1, any solution which is ever in G_1 converges to the origin as $t \to \infty$. Consider next a solution which starts in G_2. Since y is decreasing on G_2, this solution is bounded. By Proposition 12 of Section 3.5, it either converges to S_0 or S_1 as $t \to \infty$, or it reaches another point of the boundary of G_2 after a finite time. In the latter case, it reaches a point of the boundary of G_1 or G_4 after a finite time. By an analogous argument, we can reach a similar conclusion about a solution which starts in G_3: Either it converges to S_0 or S_1 or it reaches another point of the boundary of G_1 or G_4 after a finite time. An analysis similar to that done for G_1 can be carried out for G_4: A solution that starts in G_4 must remain there and a solution that starts on the boundary of G_4 must immediately enter G_4. Thus any solution which does not belong to case (i) or case (ii) must enter G_4 after a finite time and then it stays there. □

Proposition 3 *The stable manifold of S_1 intersects both axes. If a solution starts below the stable manifold of S_1, it converges to S_0 as $t \to \infty$. If it starts above the stable manifold, it eventually lies in G_4.*

Proof: Consider the derivative of the right-hand side of the system at S_1. This matrix has trace $-\alpha - 11 < 0$ and determinant $-\alpha < 0$. Thus, it has one positive and one negative eigenvalue. Its stable manifold V_s is one-dimensional and lies in $G_2 \cup G_3$. Along this manifold $\frac{\dot{y}}{\dot{x}}$ is negative. It follows that V_s is the graph of a function of x. As x decreases along the part of V_s to the left of S_1 the derivative of this function remains bounded. We have $\frac{dy}{dx} = \frac{2\alpha x + 3\beta x^2 - 5y^2 - y}{-\alpha x - \beta x^2 + 3y^2}$. In the given situation, x is bounded. Hence, at a point where y is sufficiently large, $|-\alpha x - \beta x^2| \leq y^2$ and the modulus of the denominator is bounded below by $2y^2$. This implies that $\frac{dy}{dx}$ is bounded. It follows that V_s intersects the y-axis. As x increases along the part of V_s to the right of S_1, the derivative of the function of which it is, the graph remains bounded away from zero. The proof is analogous to that just given for the other part of V_s. It follows that V_s intersects the x-axis. It can be concluded that the complement of V_s in the positive quadrant has two connected components: H_1 and H_2, where H_1 has compact closure. A point is said to lie below the stable manifold if it belongs to H_1 and above the stable manifold if it belongs to H_2. A solution that starts in one of these two components remains in it. A solution which starts in H_1 cannot reach G_4 and one which starts in H_2 cannot reach G_1. Thus Proposition 3 follows from Proposition 2. □

Proposition 4 *A solution of (3.2)-(3.3) which is eventually contained in G_4 has, after a suitable translation of t, the asymptotics $x = \frac{\alpha}{5} e^{\frac{\alpha t}{5}} + \cdots$, $y = \frac{\sqrt{2}\alpha}{5} e^{\frac{\alpha t}{10}} + \cdots$ for $t \to \infty$.*

Proof: If a solution is eventually contained in G_4 then $r = \sqrt{x^2 + y^2}$ must tend to infinity as $t \to \infty$. For r is an increasing function of t and if it were bounded, the solution would have to converge to a steady state. However, there are no steady states in G_4. It then follows from the defining equations for G_4 that both x and y tend to infinity as $t \to \infty$. We now consider the Poincaré compactification of the system [79]. This compactification is usually constructed using two charts, covering neighborhoods of the x- and y-axes, respectively. For a solution which is in G_4 for $t \geq t_1$, we have seen that y tends to infinity for $t \to \infty$ and hence $\frac{x}{y}$ tends to infinity. This means that the solution eventually leaves a neighborhood of the origin in the chart covering a neighborhood of the y-axis and lies in the chart covering a neighborhood of the x-axis. Moreover, it tends to the origin in the latter chart as $t \to \infty$. The chart we are talking about is defined by the coordinates $X = \frac{1}{x}$ and $Z = \frac{y}{x}$. We define a new time coordinate τ which satisfies $\frac{d\tau}{dt} = x$. The transformed system is

$$\frac{dX}{d\tau} = \alpha X^2 - 3XZ^2, \tag{3.11}$$

$$\frac{dZ}{d\tau} = 2\alpha X + (\alpha - 1)XZ - 5Z^2 - 3Z^3. \tag{3.12}$$

Both eigenvalues of the linearization at the origin are zero and so we must blow up the origin to get more information. This will be done employing a quasihomogeneous blow-up following [19]. In the notation used there, the exponents calculated using the Newton polygon are $(2, 1)$. There are two transformations to be done, corresponding to the two coordinates. The first of these is given by the correspondence $(X, Z) = (u^2, uv)$. We have

$$\frac{dX}{d\tau} = 2u\frac{du}{d\tau} = \alpha u^4 - 3u^4v^2 \tag{3.13}$$

and hence,

$$\frac{du}{d\tau} = \frac{1}{2}(\alpha u^3 - 3u^3v^2). \tag{3.14}$$

Furthermore,

$$\frac{dZ}{d\tau} = u\frac{dv}{d\tau} + v\frac{du}{d\tau} = 2\alpha u^2 - 5u^2v^2 + (\alpha - 1)u^3v - 3u^3v^3 \tag{3.15}$$

and hence,

$$\frac{dv}{d\tau} = 2\alpha u - 5uv^2 - (\alpha - 1)u^2v + 3u^2v^3 - \frac{1}{2}(\alpha u^3v - 3u^3v^3). \tag{3.16}$$

If we now introduce a new time coordinate s satisfying $\frac{ds}{d\tau} = u$ then the system becomes

$$\frac{du}{ds} = \frac{1}{2}(\alpha u^2 - 3u^2v^2), \tag{3.17}$$

$$\frac{dv}{ds} = 2\alpha - 5v^2 + (\alpha - 1)uv - 3uv^3 - \frac{1}{2}(\alpha u^2v - 3u^2v^3). \tag{3.18}$$

When $v = 0$, the derivative of v is positive. Thus, no solution can have an ω-limit point on the u-axis. Hence the solution must eventually be contained in the chart defined by the second transformation, which is given by $(X, Z) = (uv^2, v)$. In this case,

$$\frac{dZ}{d\tau} = \frac{dv}{d\tau} = 2\alpha uv^2 - 5v^2 + (\alpha - 1)uv^3 - 3v^3. \tag{3.19}$$

Furthermore,

$$\frac{dX}{d\tau} = v^2\frac{du}{d\tau} + 2uv\frac{dv}{d\tau} = \alpha u^2v^4 - 3uv^4 \tag{3.20}$$

and hence,

$$\frac{du}{d\tau} = \alpha u^2v^2 - 3uv^2 - 4\alpha u^2v + 10uv - 2(\alpha - 1)u^2v^2 + 6uv^2. \tag{3.21}$$

If we now introduce a new time coordinate s satisfying $\frac{ds}{d\tau} = v$ then the system becomes

$$\frac{du}{ds} = 10u + 3uv - 4\alpha u^2 - (\alpha - 2)u^2 v, \tag{3.22}$$
$$\frac{dv}{ds} = -5v + 2\alpha uv + (\alpha - 1)uv^2 - 3v^2. \tag{3.23}$$

The u- and v-axes are invariant. The origin is a steady state, which is a hyperbolic saddle and there is an additional steady state $(\frac{5}{2\alpha}, 0)$. The latter steady state has one negative and one zero eigenvalues. If we transform any positive solution then in the blown-up Poincaré compactification, it must tend to that point. To get more details, we translate the steady state to the origin using a coordinate transformation. Let $w = u - \frac{5}{2\alpha}$ be a new coordinate. Then the equations become

$$\frac{dw}{ds} = -10w - 4\alpha w^2 + 3wv + \frac{15}{2\alpha}v - (\alpha - 2)\left(w + \frac{5}{2\alpha}\right)^2 v, \tag{3.24}$$
$$\frac{dv}{ds} = 2\alpha wv + (\alpha - 1)\left(w + \frac{5}{2\alpha}\right)v^2 - 3v^2. \tag{3.25}$$

The first can be rewritten as:

$$\frac{dw}{ds} = -10w + \frac{5(\alpha + 10)}{4\alpha^2}v - 4\alpha w^2 - \frac{2(\alpha - 5)}{\alpha}wv - (\alpha - 2)w^2 v. \tag{3.26}$$

We now apply Centre Manifold Theory (cf. [79], Section 2.7). The centre manifold can be written in the form $w = \frac{\alpha+10}{8\alpha^2}v + r(v)$ with a remainder term r which is at least quadratic. Consider the contributions to the right-hand side of the evolution equation for v which are quadratic in v. We get

$$\begin{aligned}\frac{dv}{ds} &= \left[\frac{\alpha + 10}{4\alpha} + \frac{5\alpha - 5}{2\alpha} - 3\right]v^2 + \cdots \\ &= -\frac{1}{4}v^2 + \cdots \end{aligned}\tag{3.27}$$

After translating s, if necessary, we get $v = \frac{4}{s} + \cdots$. Since all solutions on the centre manifold starting near the steady state converge to it and the non-zero eigenvalue is negative, all solutions starting near the steady state converge to it. Moreover, by Theorem 2 on p. 4 of [14], any such solution is exponentially close to a solution on the centre manifold. Thus, it has the same leading order asymptotics for v as a solution on the centre manifold and the leading order asymptotics for u is obtained by substituting this into the equation of the centre manifold. Substituting the asymptotic expression for v into the defining equation for s gives $\tau = \frac{1}{8}s^2$ and $v = \sqrt{\frac{2}{\tau}} + \cdots$. It follows that $X = \frac{5}{\alpha\tau} + \cdots$ and $Z = \sqrt{\frac{2}{\tau}} + \cdots$. Next we compute the transformation from τ to t. We have $\frac{dt}{d\tau} = \frac{5}{\alpha\tau} + \cdots$ and hence, up to a translation of the time coordinate, $t = \frac{5}{\alpha}\log\tau + \cdots$ and $\tau = e^{\frac{\alpha t}{5}} + \cdots$. When written in the original variables, these relations give $x = \frac{\alpha}{5}e^{\frac{\alpha t}{5}} + \cdots$, $y = \frac{\sqrt{2}\alpha}{5}e^{\frac{\alpha t}{10}} + \cdots$. □

Proposition 5 *A positive solution of (3.2)-(3.3) with $\alpha > 0$ and $\beta = 0$ belongs to one of the following three classes.*

i) It starts below the stable manifold of S_1 and x and y converge to zero as $t \to \infty$.

ii) It starts on the stable manifold of S_1 and converges to S_1 as $t \to \infty$.

iii) It starts above the stable manifold of S_1 and x and y tend to infinity as $t \to \infty$, with the asymptotics given in Proposition 4.

In particular, every bounded solution converges to a steady state as $t \to \infty$.

Proof: This is obtained by combining Proposition 2 - Proposition 4. □
Note that because after transformation to the Poincaré compactification, each solution converges to a steady state, there exist no periodic solutions. In other words, the system does not exhibit sustained oscillations. The eigenvalues of the system's linearization about S_0 are real because the axes are invariant manifolds. The steady state S_1 has been shown to be hyperbolic with the linearization's eigenvalues about that point being real. Thus, damped oscillations decaying to one of the steady states are also ruled out.

The Case with Photorespiration

In this section, we will consider the full system where α and β are both positive.

Proposition 6 *Corresponding to positive initial data for (3.2)-(3.3) with $\alpha > 0$ and $\beta > 0$ given at $t = t_0$, there exists a solution on the interval (t_0, ∞) and it is bounded.*

Proof: Taking a suitable linear combination of the equations gives $\frac{d}{dt}(5x+3y) = -\beta x^2 + \alpha x - 3y$. If $x \geq \alpha/\beta$, then the right-hand side is negative. If $x \leq \alpha/\beta$, then $\alpha x \leq \alpha^2/\beta$. Thus if also $y \geq \alpha^2/3\beta$ the right hand side is negative. If a solution satisfies $5x + 3y > \beta^{-1}(5\alpha + \alpha^2)$ at some point in time then it must be in one of the regions where the time derivative of $5x + 3y$ is negative. Thus, the value of $5x + 3y$ is bounded by the maximum of its initial value and $\beta^{-1}(5\alpha+\alpha^2)$. It follows that all solutions of this system can be extended to exist globally in the future and are bounded. □
Consider now steady states of (3.2)-(3.3):

Proposition 7 *i) For $\alpha^2/\beta < 32$, the only non-negative steady state is the origin, which we once again denote by S_0.*

ii) For $\alpha^2/\beta = 32$, there is precisely one positive steady state, which we call S_1.

iii) For $\alpha^2/\beta > 32$, there are precisely two positive steady states. For one of these, which we call S_1, both coordinates are smaller than the corresponding coordinates of the other steady state, which we call S_2.

Proof: Any steady state satisfies $\alpha x = y^2 + 2y$ so that its y-coordinate determines its x-coordinate. In fact, the y-coordinate is a monotone function of the x-coordinate. At the same time, $\beta x^2 = y^2 - y$. Squaring the first of these equations and substituting it into the second gives

$$\beta(y^2 + 2y)^2 = \alpha^2(y^2 - y) \tag{3.28}$$

and hence,

$$y[\beta y^3 + 4\beta y^2 + (4\beta - \alpha^2)y + \alpha^2] = yp(y) = 0. \tag{3.29}$$

The positive steady states are in one to one correspondence with the positive roots of the cubic $p(y)$. Since $p(0) > 0$, there is at least one negative root and there are at most two positive roots. If $4\beta - \alpha^2 \geq 0$, then there are no positive roots. Further information about the number of positive roots can be obtained by looking at the discriminant of the polynomial p. It is given by

$$\Delta = \alpha^2 \beta [96\beta^2 - 131\alpha^2\beta + 4\alpha^4]. \tag{3.30}$$

There are two positive values of α^2/β for which Δ vanishes, namely $\zeta_\pm = \frac{131 \pm 125}{8}$. We have $\zeta_- = \frac{3}{4}$ and $\zeta_+ = 32$. When $\Delta < 0$, the polynomial p has only one real root and it must be negative. When $\Delta \geq 0$, all roots are real. Only in this case can there be more than one positive root. For $\alpha^2/\beta = 32$, there is a root that is at least double. If this root was negative, then it would follow that $4\beta - \alpha^2 > 0$, a contradiction. Thus, the double root is positive. For $\alpha^2/\beta > 32$, there are two positive roots. □

Both of the nullclines of this system are of the form $f(x) = g(y)$ for monotone increasing functions f and g. Thus, we can write them as graphs of functions of x or functions of y. Due to Proposition 7, we know that the two nullclines intersect at the origin and at no, one or two points in the positive region, depending on the parameters. It can then be concluded that when there are no, one and two positive steady states, the complement of the nullclines' union has three, four and five connected components, respectively. As in the previous section, these components can be labeled with the signs of $\dot{x}$ and $\dot{y}$. In case (i) of Proposition 7, there is one component with each of the labels $(-,-)$, $(-,+)$ and $(+,-)$. In case (ii), there are two components with the label $(-,-)$ and one component with each of the labels $(-,+)$ and $(+,-)$. In case (iii) (cf. Figure 3.4), there are two components with the label

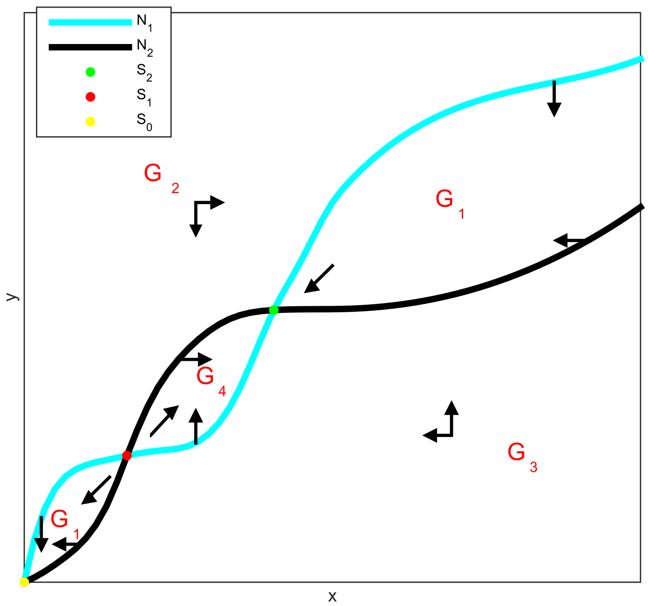


Figure 3.4: Nullclines (solid lines) and direction field (arrows) in the presence of photorespiration

$(-,-)$ and one component with each of the labels $(-,+)$, $(+,-)$ $(+,+)$. The components of the complements of the set of steady states in the nullclines can be labeled as $(-,0)$, $(0,-)$, $(+,0)$ and $(0,+)$. At a point where the nullclines cross, they are tangent if and only if the linearization at the point has a zero eigenvalue. This happens precisely when the determinant of the linearization at that point is zero. This is the only way a steady state can fail to be hyperbolic since the trace is negative rules out the possibility of a pair of complex conjugate imaginary eigenvalues. With the information we already have about steady states, it can be concluded that the determinant is zero precisely when:

$$q(y) = 4\beta y^3 + 12\beta y^2 + (8\beta - 2\alpha^2)y + \alpha^2 = 0. \tag{3.31}$$

Now we take linear combinations of the equations $p(y) = 0$ and $q(y) = 0$ in order to obtain simpler equations. The equation $q(y) - 4p(y) = 0$ is a quadratic equation for y. On the other hand, $q(y) - p(y) = yr(y)$ for a quadratic polynomial r so that non-zero solutions y satisfy the quadratic equation $r(y) = 0$. The two quadratic equations can be combined to give a linear equation for y and substituting this back into the equation $r(y) = 0$ leads to the equation

$$9\gamma(-4\gamma^2 + 131\gamma - 96) = 0 \tag{3.32}$$

where $\gamma = \frac{\alpha^2}{\beta}$. It follows that all steady states are hyperbolic when $\gamma > 32$. It can be concluded that except in case (ii), the steady states are hyperbolic. In case (ii), the linearization at S_1 has one zero and one negative eigenvalue. In case (iii), it has one positive and one negative eigenvalue.

Proposition 8 *Any positive solution of (3.2)-(3.3) with $\alpha > 0$ and $\beta > 0$ converges a steady state as $t \to \infty$ according to the following scheme.*

i) If $\frac{\alpha^2}{\beta} < 32$, there are no points S_1 and S_2 and all solutions converge to S_0.

ii) If $\frac{\alpha^2}{\beta} = 32$, there is no point S_2 and points above or on and below the unique centre manifold of S_1 converge to S_1 and S_0 respectively.

iii) If $\frac{\alpha^2}{\beta} > 32$, then points above, on or below the stable manifold of S_1 converge to S_2, S_1 and S_0 respectively.

Proof: Note that the stable manifold of S_1 is always one-dimensional. By the same arguments as in the case of $\beta = 0$, it can be shown that this manifold is the graph of a function of x and that it intersects both axes and that its complement is the union of two components H_1 and H_2. Components with the sign combination $(-,-)$ have boundaries with the sign combinations $(-,0)$ and $(0,-)$. Using the information on the signs of $\ddot{x}$ and $\ddot{y}$ shows that these components are invariant. For instance, a solution which satisfies $\dot{x} = 0$ and $\dot{y} < 0$ at some point satisfies $\ddot{x} < 0$. Similarly, components with the sign combination $(+,+)$ are invariant. It can be shown as in the case of $\beta = 0$ that any solution which starts in a component with one of the sign combinations $(+,-)$ or $(-,+)$ and does not converge to a steady state as $t \to \infty$ must enter one of the components with the sign combination $(-,-)$ or $(+,+)$ after a finite time. Once it enters a component of this type, it must stay there and converge to a steady state as $t \to \infty$. Thus, every solution converges to a steady state as $t \to \infty$. It is then straightforward to determine which steady state it converges to in different cases. □

Note that since every solution converges to a steady state, the system exhibits no sustained oscillations. As in the previous section, we can argue that there are no damped oscillations close to the point S_0. Using Proposition 13 of Section 3.5, we get the corresponding conclusion for S_1 and S_2. Consider what happens if β tends to zero while α has a fixed positive value. The polynomial p defined in (3.29) converges. In the limit, there is a unique root, which is S_1. It is a hyperbolic saddle. Thus, it is the limit of a steady state of the system in the general case as $\beta \to 0$. The approximating solution must coincide with the point S_1 in the general system. Let $\gamma = \frac{\alpha^2}{\beta}$ and define $z = \gamma^{-1/2}y$ and $q(z) = p(y)$. If β tends to zero while α has a fixed positive value, the polynomial q converges. Again there is a unique positive root in the limit with $z = 1$. It is approximated by a root for positive $\beta > 0$, which corresponds to the steady state S_2. We conclude that as β tends to zero the coordinates of S_2 have the asymptotic behavior $x = \alpha\beta^{-1} + \cdots$ and $y = \alpha\beta^{-\frac{1}{2}} + \cdots$.

The System with the Fifth Power

In this section, we will study the system where y^2 is replaced in (3.2)-(3.3) by y^5. This is

$$\frac{dx}{dt} = -\alpha x - 2\beta x^2 + 3y^5, \tag{3.33}$$
$$\frac{dy}{dt} = 2\alpha x + 3\beta x^2 - 5y^5 - y. \tag{3.34}$$

The aim is to see to what extent the results obtained for (3.2)-(3.3) generalize to (3.33-(3.34). In the case $\alpha = 0$, the analysis of (3.2)-(3.3) extends without essential changes to (3.33)-(3.34) to give the same qualitative results. When $\alpha > 0$ and $\beta = 0$, the analysis up to and including Proposition 3 extends easily. Of course, the explicit formulae in the definitions of the invariant regions G_i are modified by replacing y^2 by y^5.

Proposition 9 *A solution of (3.33)-(3.34) which is eventually contained in G_4 has, after a suitable translation of t, the asymptotics $x = (\frac{4\alpha}{5})^{\frac{1}{4}}e^{\frac{\alpha t}{5}} + \cdots$, $y = 2^{\frac{1}{20}}\left(\frac{2\alpha}{5}\right)^{\frac{1}{4}}e^{\frac{\alpha t}{25}} + \cdots$ for $t \to \infty$.*

Proof: That the arguments from the case of (3.2)-(3.3) extend easily is also true of the first part of the proof of Proposition 4, which shows that the late time behavior can be analyzed in one of the charts of the Poincaré compactification. In this case, the time coordinate must be rescaled in a different way from what was done previously. Let $\frac{d\tau}{dt} = x^4$. In the case of (3.33)-(3.34), the transformation to this chart gives

$$\frac{dX}{d\tau} = \alpha X^5 - 3XZ^5, \tag{3.35}$$
$$\frac{dZ}{d\tau} = 2\alpha X^4 + (\alpha - 1)X^4 Z - 5Z^5 - 3Z^6. \tag{3.36}$$

The linearization of the system at the origin is identically zero. To get more information, we do a quasi-homogeneous blow-up. The exponents calculated using the Newton polygon are $(5, 4)$. Once again, there are two transformations to be done. The first of these is given by the correspondence $(X, Z) = (u^5, u^4 v)$. We have

$$\frac{dX}{d\tau} = 5u^4\frac{du}{d\tau} = \alpha u^{25} - 3u^{25}v^5 \tag{3.37}$$

and hence,

$$\frac{du}{d\tau} = \frac{1}{5}(\alpha u^{21} - 3u^{21}v^5). \tag{3.38}$$

Furthermore,

$$\frac{dZ}{d\tau} = u^4 \frac{dv}{d\tau} + 4u^3 v \frac{du}{d\tau} = 2\alpha u^{20} - 5u^{20}v^5 + (\alpha - 1)u^{24}v - 3u^{24}v^6 \tag{3.39}$$

and hence,

$$\frac{dv}{d\tau} = 2\alpha u^{16} - 5u^{16}v^5 - (\alpha - 1)u^{20}v + 3u^{20}v^6 - \frac{4}{5}(\alpha u^{20}v - 3u^{20}v^6). \tag{3.40}$$

If we now introduce a new time coordinate s satisfying $\frac{ds}{d\tau} = u^{16}$, then the system becomes

$$\frac{du}{ds} = \frac{1}{5}(\alpha u^5 - 3u^5v^5), \tag{3.41}$$

$$\frac{dv}{ds} = 2\alpha - 5v^2 + (\alpha - 1)u^4v - 3u^4v^6 - \frac{4}{5}(\alpha u^4 v - 3u^4v^6). \tag{3.42}$$

Just as in the case with the quadratic nonlinearity, we see that the solution must eventually be contained in the chart defined by the second transformation, which is given by $(X, Z) = (uv^5, v^4)$. In that case

$$\frac{dZ}{d\tau} = 4v^3 \frac{dv}{d\tau} = 2\alpha u^4 v^{20} - 5v^{20} + (\alpha - 1)u^4v^{24} - 3v^{24}. \tag{3.43}$$

Hence,

$$\frac{dv}{d\tau} = \frac{1}{4}\left(2\alpha u^4 v^{17} - 5v^{17} + (\alpha - 1)u^4 v^{21} - 3v^{21}\right). \tag{3.44}$$

Furthermore,

$$\frac{dX}{d\tau} = v^5 \frac{du}{d\tau} + 5uv^4 \frac{dv}{d\tau} = \alpha u^5 v^{25} - 3uv^{25} \tag{3.45}$$

and hence,

$$\frac{du}{d\tau} = \alpha u^5 v^{20} - 3uv^{20} - \frac{5}{4}\left(2\alpha u^5 v^{16} - 5uv^{16} + (\alpha - 1)u^5v^{20} - 3uv^{20}\right). \tag{3.46}$$

In terms of the time coordinate s with $\frac{ds}{d\tau} = v^{16}$, we get

$$\frac{du}{ds} = \alpha u^5 v^4 - 3uv^4 - \frac{5}{4}\left(2\alpha u^5 - 5u + (\alpha - 1)u^5v^4 - 3uv^4\right), \tag{3.47}$$

$$\frac{dv}{ds} = \frac{1}{4}\left(2\alpha u^4 v - 5v + (\alpha - 1)u^4v^5 - 3v^5\right). \tag{3.48}$$

The axes are invariant and the origin is a hyperbolic saddle. There is a steady state at the point $(u_0, 0)$ with $u_0 = \left(\frac{5}{2\alpha}\right)^{\frac{1}{4}}$. If we transform any solution in the blown-up Poincaré compactification, it must converge to this point. To get more details, we translate the steady state to the origin using a coordinate transformation. Let $w = u - u_0$. Then the equations become:

$$\frac{dw}{ds} = -\frac{1}{2}u_0 v^4 - \frac{5}{4}\left([2\alpha(u_0 + w)^4 - 5](u_0 + w) - \frac{\alpha + 5}{2\alpha}u_0 v^4\right) + \mathcal{O}(v^4 w), \tag{3.49}$$

$$\frac{dv}{ds} = \frac{1}{4}\left([2\alpha(u_0 + w)^4 - 5] - \frac{\alpha + 5}{2\alpha}v^4\right) v + \mathcal{O}(v^5 w). \tag{3.50}$$

Here we have explicitly retained only those terms which are required for the calculation which will now be done. It follows from the definition of the centre manifold that $w = h(v)$ for a function h with $h(v) = \mathcal{O}(v^2)$. The derivative of this relation with respect to time also holds. Hence, $\dot{w} = h'(v)\dot{v}$. It follows from (3.50) that $\dot{v} = \mathcal{O}(v^3)$ and so $\dot{w} = \mathcal{O}(v^4)$. It follows from (3.50) that $w = \mathcal{O}(v^4)$. Hence, $\dot{v} = \mathcal{O}(v^5)$ and $\dot{w} = \mathcal{O}(v^6)$. It can be concluded from the evolution equation for w that

$$[2\alpha(u_0 + w)^4 - 5] - \frac{\alpha+5}{2\alpha}v^4 = -\frac{2}{5}v^4 + \cdots. \tag{3.51}$$

It follows that $\frac{dv}{ds} = -\frac{1}{10}v^5 + \cdots$. We see that the flow on the centre manifold is towards the steady state. After translating s, if necessary, we get $v = \left(\frac{5}{2s}\right)^{\frac{1}{4}} + \cdots$. Substituting this into the defining equation for s gives $s = 5^{\frac{1}{5}}\left(\frac{5}{2}\right)^{\frac{4}{5}}\tau^{\frac{1}{5}} + \cdots$ and $v = \left(\frac{1}{2\tau}\right)^{\frac{1}{20}} + \cdots$. Substituting for the original variables gives $X = u_0\left(\frac{1}{2\tau}\right)^{\frac{1}{4}} + \cdots$ and $Z = \left(\frac{1}{2\tau}\right)^{\frac{1}{5}} + \cdots$. Next we compute the transformation from τ to t. We have $\frac{dt}{d\tau} = \left(\frac{u_0^4}{2\tau}\right) + \cdots$. Hence, $t = \left(\frac{u_0^4}{2}\right)\log\tau + \cdots$ and $\tau = e^{4\alpha t/5} + \cdots$. Finally, we get $x = (\frac{4\alpha}{5})^{\frac{1}{4}} e^{\frac{\alpha t}{5}}$ and $y = 2^{\frac{1}{20}}\left(\frac{2\alpha}{5}\right)^{\frac{1}{4}} e^{\frac{\alpha t}{25}}$. □

Proposition 10 *Any positive solution of (3.33)-(3.34) with $\alpha > 0$ and $\beta = 0$ belongs to one of the following three classes.*

i) It starts below the stable manifold of S_1 and x and y converge to zero as $t \to \infty$.

ii) It starts on the stable manifold of S_1 and converges to S_1 as $t \to \infty$.

iii) It starts above the stable manifold of S_1 and x and y tend to infinity as $t \to \infty$, with the asymptotics given in Proposition 9.

In particular, every bounded solution converges to a steady state as $t \to \infty$.

Proof: The proof is identical to that of Proposition 5 except that Proposition 4 is replaced by Proposition 9. □

It is interesting to compare the asymptotics in Proposition 9 with those obtained in [85] for a more elaborate model of the Calvin cycle. In Proposition 9, we see that both unknowns have growing exponential asymptotics but that the exponent for GAP is one-fifth of that for the other variable. The main system considered in [85] has five unknowns and has solutions for which all unknowns have growing exponential asymptotics. In that case, the exponent for GAP is one-fifth of that for the other four unknowns. These four unknowns satisfy a system of the form $\frac{d\bar{x}}{dt} = A\bar{x} + R$, where R is considered as a remainder term and the larger exponent is an eigenvalue of A. There is a natural analogue of this equation for the system (3.33)-(3.34) with $\beta = 0$. It is the equation $\frac{d}{dt}(5x+3y) = \frac{\alpha}{5}(5x+3y) - 3\left(\frac{\alpha}{5}+1\right)y$. Here the last term is to be considered as the remainder. Note that in the asymptotics of Proposition 9, y is much smaller than x at late times so that this treatment as a remainder term is reasonable. Since there is only one unknown growing at the maximal rate, in this case, the matrix A is replaced by a number and that number is $\alpha/5$. Thus we see that on a heuristic level, the exponents in the two cases agree. The statement of Proposition 10 is stronger than the analogous statement in [85] in the following sense. The description of the asymptotic behavior in [85] is only obtained for some non-empty subset of initial data which is not further characterized, while the set of initial data giving rise to this asymptotic behavior in Proposition 10 is much more explicit. Consider next the case where the coefficients α and β in (3.33)-(3.34) are both positive. The solutions are bounded using the same argument as in the proof of Proposition 6. As in the case of (3.2)-(3.3), the nullclines are of the form $f(x) = g(y)$ for monotone increasing functions f and g. A steady state satisfies the equations

$$y = \frac{1}{3}(\alpha x - \beta x^2), \tag{3.52}$$

$$x = \frac{1}{\alpha}(y^5 + 2y). \tag{3.53}$$

Substituting the second of these equations into the first gives:

$$p(y) = \beta y^{10} + 4\beta y^6 - \alpha^2 y^5 + 4\beta y^2 + \alpha^2 y = 0. \tag{3.54}$$

By Descartes' rule of signs, this equation can have at most two positive solutions. Since the derivative of the polynomial p at zero is positive, $p(y) > 0$ for y slightly larger than zero. Thus, if $p(y) < 0$ for some $y > 0$, the polynomial has two positive roots. Now $p(2) = 1296\beta - 28\alpha^2$. Thus, for fixed β if α is large enough, we have $p(2) < 0$ and p has two positive roots. If we define values of x corresponding to these two values of y, we obtain two positive steady states of the system (3.33)-(3.34). On the other hand, if $\beta > \alpha^2$, there are no positive steady states. We have not succeeded in obtaining information about the hyperbolicity of steady states of this system, which is as complete as the information which we obtained in the case of a quadratic nonlinearity. However, it is possible to show that for generic values of the parameter $\gamma = \frac{\alpha^2}{\beta}$, all steady states are hyperbolic. We can calculate polynomials p and q as in the case with quadratic nonlinearity, but it is impossible to solve explicitly for their common roots y. Instead, we can proceed as follows. For any non-hyperbolic steady state, we obtain equations of the form:

$$\begin{aligned} p(y) &= p_1(y) - \gamma(y-1) = 0, \\ q(y) &= q_1(y) - \gamma(5\gamma^4 - 1) = 0 \end{aligned} \tag{3.55}$$

for certain polynomials p_1 and q_1 which do not depend on γ. Hence,

$$s(y) = (5\gamma^4 - 1)p_1(y) - (y-1)q_1(y) = 0. \tag{3.56}$$

Since the polynomial s is non-constant, this equation has only finitely many solutions y. For any given solution y, there is at most one corresponding value of γ. Hence, for all but finitely many values of γ, all steady states are hyperbolic. With the information on steady states just obtained, we can prove an analog of Proposition 8 for the system with the fifth power using the same techniques. The result is:

Proposition 11 *Any positive solution of (3.33)-(3.34) with $\alpha > 0$ and $\beta > 0$ converges to a steady state as $t \to \infty$. If $\frac{\alpha^2}{\beta} < 1$, there are no points S_1 and S_2 and all solutions converge to S_0. If $\frac{\alpha^2}{\beta}$ is large enough, then points above, on or below the stable manifold of S_1 converge to S_2, S_1 and S_0 respectively.*

By scaling the unknowns x and y by the same factor and t by another factor, it is possible to transform the more general system:

$$\frac{dx}{dt} = -\alpha x - 2\beta x^2 + 3Ay^5, \tag{3.57}$$

$$\frac{dy}{dt} = 2\alpha x + 3\beta x^2 - 5Ay^5 - By. \tag{3.58}$$

for general positive constants A and B into the system (3.33)-(3.34). Thus, the results obtained for (3.33)-(3.34) imply analogous results for (3.57)-(3.58). This observation will be used in the next section.

Derivation from the Three-Dimensional System

The System (3.2)-(3.3) was derived by Hahn from a three-dimensional system but he did not give a mathematical formulation of the relation between the two systems. The three-dimensional system is, in a modified notation,

$$\frac{dx}{dt} = -k_1 x - 2k_2 x^2 + 3k_4 z^5, \tag{3.59}$$
$$\frac{dy}{dt} = 2k_1 x + 3k_2 x^2 - k_3 y, \tag{3.60}$$
$$\frac{dz}{dt} = k_3 y - 5k_4 z^5 - (k_5 + k_6) z. \tag{3.61}$$

We now consider a limit where k_3 becomes large. This means that the reaction producing triose phosphate from PGA is very fast. Let $k_3 = \epsilon^{-1}\tilde{k}_3$ and introduce a new variable by $w = y + z$. Then the equations above are equivalent to the system

$$\frac{dx}{dt} = -k_1 x - 2k_2 x^2 + 3k_4 z^5, \tag{3.62}$$
$$\frac{dw}{dt} = 2k_1 x + 3k_2 x^2 - 5k_4 z^5 - (k_5 + k_6) z, \tag{3.63}$$
$$\epsilon\frac{dz}{dt} = \tilde{k}_3 (w - z) - 5\epsilon k_4 z^5 - \epsilon(k_5 + k_6) z. \tag{3.64}$$

This is a fast-slow system in standard form with fast variable z and slow variables x and w. The critical manifold is given by $z = w$ and the slow system is

$$\frac{dx}{dt} = -k_1 x - 2k_2 x^2 + 3k_4 w^5, \tag{3.65}$$
$$\frac{dw}{dt} = 2k_1 x + 3k_2 x^2 - 5k_4 w^5 - (k_5 + k_6) w. \tag{3.66}$$

Replacing w by y and setting $k_1 = \alpha$, $k_2 = \beta$, $k_4 = A$ and $k_5 + k_6 = B$ gives the System (3.57)-(3.58). The critical manifold is normally hyperbolic and the one normal eigenvalue is negative. We know that for certain values of the parameters the system (3.33)-(3.34) has three steady states S_0, S_1 and S_2. Moreover, for generic values of γ, the steady states S_0 and S_2 are hyperbolic sinks while S_1 is a hyperbolic saddle with a one-dimensional stable manifold. There are heteroclinic orbits connecting S_0 to S_1 and S_1 to S_2. Putting this together with the fact that the normal eigenvalue is negative, shows that for suitable parameters with ϵ small, the three-dimensional system has three steady states S_0, S_1 and S_2, which converge to those with the corresponding names as $\epsilon = 0$. Moreover, S_0 and S_2 are hyperbolic sinks and S_1 is a hyperbolic saddle with a two-dimensional stable manifold. Heteroclinic orbits are connecting S_0 to S_1 and S_1 to S_2.

Nullcline Analysis

In this section, we will discuss how nullclines can be used to obtain information about the global behavior of solutions of a two-dimensional dynamical system. Consider the following system of ordinary differential equations

$$\dot{x} = f(x, y), \tag{3.67}$$
$$\dot{y} = g(x, y), \tag{3.68}$$

where the functions f and g are C^1 and defined on an open subset $U \subset \mathbb{R}^2$. The nullclines N_1 and N_2 are the zero sets of f and g respectively. Let $G = U \setminus (N_1 \cup N_2)$. The open set G is a countable union of connected components G_i. In what follows, we will assert in this case that the following assumption is satisfied.
Assumption 1 The complement of the nullclines has only finitely many connected components.
When the system satisfies Assumption 1, it defines a directed graph as follows: There is one node for each component G_i and there is a directed edge from the node corresponding to G_i to that corresponding to G_j when there is a solution which starts from a point of G_i and later enters G_j without entering any component of G other than G_i and G_j at an intermediate time. Let us call this the succession graph. A cycle in a directed graph is a finite sequence of directed edges such that the initial node of each edge is the final node of the previous one and the final node of the last edge is the initial node of the first one. We now assert in this case that the following assumption is satisfied.
Assumption 2 There exist only finitely many steady states. Whenever a steady state S_i is in the closure of a component G_j, there is a continuous curve joining a point of G_j to S_i which does not intersect any other G_k.

Proposition 12 *Consider a solution $(x(t), y(t))$ on a time interval $[t_0, t_1)$ which lies in G_i for some i when $t = t_0$ and which lies entirely in $\bar{G}_i$. Then $x(t)$ and $y(t)$ are monotone. They are strictly monotone as long as the solution lies in G_i. Suppose that t_1 is maximal. If the solution is bounded then it converges to a point (x^*, y^*) for $t \to t_1$ which is either a point of $N_1 \cup N_2$ or a point of $\bar{G} \setminus G$. If $(x^*, y^*) \in G$, then $(x^*, y^*) \in N_1 \cap N_2$ if and only if $t_1 = \infty$.*

Proof: On a component G_i, the signs of $\dot{x}$ and $\dot{y}$ are constant and this implies the monotonicity statements. It follows that the limits of $x(t)$ and $y(t)$ as $t \to \infty$ exist, either as real numbers or as $\pm\infty$. If the solution is bounded, then these limits are real numbers x^* and y^*. The point (x^*, y^*) belongs to the closure of G. Suppose now that t_1 is maximal and that $(x^*, y^*) \in G$. We claim that if $t_1 = \infty$ then (x^*, y^*) is a point of $N_1 \cap N_2$ and hence, a steady state. Otherwise, at least one of $\dot{x}$ or $\dot{y}$ would tend to a non-zero value, say c, as $t \to t_1$. Suppose w.l.o.g. that $\dot{x}$ has this property and that $c > 0$. It follows that if t_2 is sufficiently large then $\dot{x}(t) \geq \frac{1}{2}ct$ for all $t \geq t_2$. Thus, x is unbounded, a contradiction. We conclude that if the interval $[t_0, t_1)$ is infinite $(x^*, y^*) \in N_1 \cap N_2$. Suppose now conversely that $(x^*, y^*) \in N_1 \cap N_2$. If t_1 were finite, it would be possible to extend the solution beyond $t = t_1$ but then this solution would have to coincide with the time-independent solution $x(t) = x^*$, $y(t) = y^*$, a contradiction. Thus, if $(x^*, y^*) \in N_1 \cap N_2$, the interval $[t_0, t_1)$ is infinite. $\square$

Proposition 13 *Let S_i be a steady state. Suppose that Assumption 2 is satisfied, there is more than one component G_j having S_i as a limit point and no cycle in the succession graph. Then there is no damped oscillation converging to S_i.*

Proof: Suppose there is a solution exhibiting a damped oscillation. Due to Assumption 2, it must intersect each G_j having S_i as a limit point more than once. Hence, the succession graph contains a cycle, a contradiction. □

In this chapter, we have obtained detailed information on minimal models of the Calvin cycle introduced by Hahn in [44]. A rather complete analysis of Hahn's two-dimensional models was given and the relation of the two-dimensional to the three-dimensional model of Hahn was discussed. A comprehensive analysis of the three-dimensional model will be covered in the next chapter. The models in [44] originated by formal simplification of earlier models due to the same author. The first is a model with 19 chemical species defined in [45]. It did not implement a detailed description of photorespiration and a description of this kind was added in the model of [46] with 33 species. It would be desirable to understand the relations between these different models on a better mathematical footing in the future. This should also allow conclusions about the dynamics of the higher-dimensional systems to be obtained. Note that there are some general references in the literature about the inheritance of dynamical features from reduced systems (see, e.g., [7], [26]).

Chapter 4

Hahn's Three-Dimensional Model

In [44], the author has considered a simple model which captures the main events in the Calvin cycle from his perspective: carboxylation, reduction and regeneration. The author also implemented a sink for triose phosphate TP and modeled photorespiration explicitly and not indirectly through the increase of sink reaction flux (i.e., the export of triose phosphate). It was shown in [59] that this approach is favored when validating and correcting many of the models for photosynthesis. Among these models, some incorporate a relatively big number of variables while aiming to simulate in detail the huge number of reactions taking place in the main compartments of the plant leaf. Unfortunately, many of these models (i.e., [67], [82], [80], [118]) made either kinetic mistakes, such as to compute the velocity of some reaction or to recognize the true stoichiometric coefficients. Even some results are not reproducible, perhaps due to technical limitations when these models were studied. This shifts our attention to photosynthesis's simple modeling, which does not promise to produce plausible kinetic parameters when solving the inverse problem. The best option is then to unravel the complex possible but robust qualitative functioning of photosynthesis. This functioning can be either one or many stable steady states or even periodic orbits. This motivates reconsidering a three-dimensional model of [44], whose reduced version was studied already in Chapter 3. This system of reactions generates the differential equations in (3.59-3.61) by using mass action kinetics. The goal in this chapter is then to mathematically unfold the dynamics taking place in the three-dimensional model of Hahn in [44] and to investigate the existence of sustained oscillations as the usual stepping stone toward investigating more complex dynamics. Let's consider the same rescaled model of Hahn in [44]:

$$\frac{dx}{dt} = -ax - 2bx^2 + 3z^5, \tag{4.1}$$

$$\frac{dy}{dt} = 2ax + 3bx^2 - y, \tag{4.2}$$

$$\frac{dz}{dt} = y - 5z^5 - cz. \tag{4.3}$$

where $a = \frac{k_1}{k_3}$, $b = \frac{k_2}{k_3^{\frac{3}{4}} k_4^{\frac{1}{4}}}$ and $c = \frac{k_7}{k_3}$. This model deviates from the one considered in Chapter 3 (3.2-3.3) only in its dimension. The reduction of this model by setting the formation of PGA to equilibrium (i.e., by setting $\frac{dy}{dt} = 0$) regenerates (3.2-3.3). This increase in dimension enables more complex dynamics [96] [97] [95] and consequently a richer bifurcation analysis.

The chapter is organized into four sections. In the first section, we categorize the non-negative orthant in open sets which differ according to the signs of the components of the vector $(\dot{x}, \dot{y}, \dot{z})$. This enables concluding the feasible flows between these sets and finally about positioning the periodic orbit. In the second section, an analysis of the number of equilibria possible for the model is conducted. This includes proving the global boundedness of solutions starting in the non-negative orthant then the analysis is done by using the algebraic properties like the resultant and the discriminant of the generated polynomials. Scaling of the parameters unfolds the number of real solutions. In the third section, the oscillations in the model are studied. A useful realization at this point is that the model satisfies the monotonicity property in a set of relevance. Strong monotonicity has then strong implications for the abstract location of the equilibria and the assumed periodic orbits. A generalization of Bendixson Criterion for manifolds in $\mathbb{R}^3$ disqualify the hypothesis of sustained oscillations. Turning photorespiration off in the fourth section by setting $b = 0$ causes solutions in an unbounded open set to diverge toward infinity. The dynamics are then persistent (i.e., independent of variations in the other parameters). Regarding oscillations, similar conclusions, as in the case when $b > 0$, are proven. The unbounded flow toward infinity was studied in the fifth section with a detailed computation of the species' rates of accumulation, which might influence any future modeling of the Calvin cycle.

Characterization of Dynamics

We examine first the case when $a = b = 0$. One of the equations the system satisfy is $\frac{dy}{dt} = -y$ and therefore y decays exponentially. Consequently, z converges to zero at later time. Let us look at $\frac{dz}{dt}$: $\frac{dz}{dt} = y - 5z^5 - cz$, hence $\frac{d(y+z)}{dt} = -5z^5 - cz$ and then $(y(t) + z(t))$ converges to zero as $t \to \infty$ because of the negative term on the right-hand side and the fact that all solutions do not leave the non-negative orthant $\mathbb{R}^3_{\geq 0}$ if they start there. Therefore, $y(t)$ and $z(t)$ are both non-negative for all $t \geq 0$ and then it follows from $y(t) \xrightarrow[t\to\infty]{} 0$ and $y(t) + z(t) \xrightarrow[t\to\infty]{} 0$ that $z(t) \xrightarrow[t\to\infty]{} 0$. For $z = 0$ and $y = 0$, any $(x_0, 0, 0) \in \mathbb{R}^3_{\geq 0}$ is a steady state. Thus all points on the x-axis are steady states. Let's consider the Jacobian of the system

$$Df(x) = \begin{pmatrix} -a - 4bx & 0 & 15z^4 \\ 2a + 6bx & -1 & 0 \\ 0 & 1 & -25z^4 - c \end{pmatrix}$$

The linearization at any of the steady states $(x_0, 0, 0)$ generates a characteristic polynomial with one zero eigenvalue due to the continuum of equilibria and two negative eigenvalues. Just as in the case of two-dimensional model, any x_0 is then indefinitely approached by some solution $x(t)$.
In the case when $a = 0$ and $b > 0$, the origin is again, as in the two-dimensional model, the only equilibrium and its stability is implied by the Lyapunov function $V(X) = \frac{3}{2}x + y + z$ whose $\dot{V}(X) = -\frac{1}{2}z^5 - cz < 0$ in $\operatorname{int}\mathbb{R}^3_{\geq 0}$. In the case without photorespiration when $b = 0$, the model admits a single positive stationary solution at $C_0 = \left(\frac{3}{a}c^{\frac{5}{4}}, 6c^{\frac{5}{4}}, c^{\frac{1}{4}}\right)$. The characteristic polynomial evaluated at C_0

$$\lambda^3 + (1 + a + 26c)\lambda^2 + (a + 26c + 26ac)\lambda - 4ac = 0$$

One eigenvalue is positive and the other two are of non-positive real part. Moreover, they are of non-vanishing negative real part because the existence of pure imaginary roots of the characteristic polynomial at C_0 requires that $(1+a+26c)(a+26c+26ac)-(-4ac)=0$ which is not satisfied for any choice $a, c > 0$. This condition was proven later in Proposition 22, which is purely technical and independent of the context. The origin O is always attracting with three negative real eigenvalues for $b \geq 0$. Let

$$\Omega := \left\{ X \in \mathbb{R}^3_{\geq 0} \mid (\dot{x}, \dot{y}, \dot{z}) \nleq 0, (\dot{x}, \dot{y}, \dot{z}) \ngeq 0, \dot{x} \neq 0, \dot{y} \neq 0, \dot{z} \neq 0 \right\}, \tag{4.4}$$

where $\nleq$ (respectively $\ngeq$) means not less than or equal (not greater than or equal). Let us define Π by:

$$\Pi := \left\{ X \in \mathbb{R}^3_{\geq 0} \mid (\dot{x}, \dot{y}, \dot{z}) \geq 0 \text{ or } (\dot{x}, \dot{y}, \dot{z}) \leq 0 \right\} \tag{4.5}$$

We will split Ω into six different sets according to the signs of velocities and so we will split Π as well into two different sets. We define:

$$\Omega_1 = (+,+,-) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} > 0, \dot{y} > 0, \dot{z} < 0 \right\} \tag{4.6}$$
$$\Omega_2 = (-,+,-) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} < 0, \dot{y} > 0, \dot{z} < 0 \right\} \tag{4.7}$$
$$\Omega_3 = (-,+,+) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} < 0, \dot{y} > 0, \dot{z} > 0 \right\} \tag{4.8}$$
$$\Omega_4 = (-,-,+) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} < 0, \dot{y} < 0, \dot{z} > 0 \right\} \tag{4.9}$$
$$\Omega_5 = (+,-,+) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} > 0, \dot{y} < 0, \dot{z} > 0 \right\} \tag{4.10}$$
$$\Omega_6 = (+,-,-) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} > 0, \dot{y} < 0, \dot{z} < 0 \right\} \tag{4.11}$$
$$\Pi_1 = (-,-,-) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} < 0, \dot{y} < 0, \dot{z} < 0 \right\} \tag{4.12}$$
$$\Pi_2 = (+,+,+) = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} > 0, \dot{y} > 0, \dot{z} > 0 \right\} \tag{4.13}$$
$$N_1 = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{x} = 0 \right\} \tag{4.14}$$
$$N_2 = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{y} = 0 \right\} \tag{4.15}$$
$$N_3 = \left\{ X \in \mathbb{R}^3_{\geq 0} \mid \dot{z} = 0 \right\} \tag{4.16}$$
$$N_{1,2} = N_1 \cap N_2 \tag{4.17}$$
$$N_{1,3} = N_1 \cap N_3 \tag{4.18}$$
$$N_{2,3} = N_2 \cap N_3 \tag{4.19}$$

Then

$$\Omega = \bigcup_{i=1}^{6} \Omega_i \tag{4.20}$$
$$\Pi = \overline{\Pi}_1 \cup \overline{\Pi}_2 \tag{4.21}$$

The three nullclines are given by N_1, N_2 and N_3 and the union of Ω_i's and Π_i's form the complement of the union of the nullclines. We assert that both Assumptions 1 and 2 from Chapter 3 are satisfied. These assumptions will be evidently satisfied in all the cases discussed later for Hahn's three-dimensional model. Any of the Ω_i's and Π_i's will be at most a finite union of connected components.

Proposition 14 *$\overline{\Pi}_1$ and $\overline{\Pi}_2$ are positively invariant and every solution starting in $N_{1,2}$, $N_{1,3}$ or $N_{2,3}$ enters either Π_1 or Π_2 at a later time. Moreover, every solution starting at $\partial\Pi_j \cap N_i$, $1 \leq j \leq 2, 1 \leq i \leq 3$ enters Π_j, $1 \leq j \leq 2$ immediately.*

Proof: Notice first that $\partial\Pi_1$ and $\partial\Pi_2$, the boundary sets of Π_1 and Π_2 respectively, are subsets of $\bigcup_{1\leq i\leq 3} N_i$. For a solution starting at t_0 in Π_2, we have:

$$(\dot{x}(t_0), \dot{y}(t_0), \dot{z}(t_0)) \gg (0,0,0)$$

We will consider the second and third time derivatives

$$\begin{aligned}\ddot{x} &= -a\dot{x} - 4bx\dot{x} + 15z^4\dot{z}\\ \ddot{y} &= 2a\dot{x} + 6bx\dot{x} - \dot{y}\\ \ddot{z} &= \dot{y} - 25z^4\dot{z} - c\dot{z}\end{aligned} \tag{4.22}$$

$$\begin{aligned}\dddot{x} &= -a\ddot{x} - 4b\dot{x}^2 - 4bx\ddot{x} + 60z^3\dot{z}^2 + 15z^4\ddot{z}\\ \dddot{y} &= 2a\ddot{x} + 6b\dot{x}^2 + 6bx\ddot{x} - \ddot{y}\\ \dddot{z} &= \ddot{y} - 100z^3\dot{z}^2 - 25z^4\ddot{z} - c\ddot{z}\end{aligned} \tag{4.23}$$

Suppose at some $t_1 > t_0$, we have $\dot{x}(t_1) = \dot{y}(t_1) = 0$ and $\dot{z}(t_1) > 0$. That is, the solution lies on $N_{1,2} \cap \partial\Pi_2$ at t_1. It follows then that $\ddot{x}(t_1) = 15z^4(t_1)\dot{z}(t_1) > 0, \ddot{y}(t_1) = 0$, $\dddot{y}(t_1) = 2a\ddot{x}(t_1) + 6bx\ddot{x}(t_1) > 0$. Therefore, there exists $t_2 > t_1$ such that $\dot{x}(t_2), \dot{y}(t_2), \dot{z}(t_2) > 0$ and the solution leaves $N_{1,2} \cap \partial\Pi_2$ and reenters Π_2. In a similar fashion, let there exist $t_1 > t_0 > 0$ such that $\dot{x}(t_1) = \dot{z}(t_1) = 0$ and $\dot{y}(t_1) > 0$. It follows that $\ddot{x}(t_1) = 0, \ddot{y}(t_1) = -\dot{y}(t_1) < 0, \ddot{z}(t_1) = \dot{y}(t_1) > 0$, $\dddot{x}(t_1) = 15z^4(t_1)\ddot{z}(t_1) > 0$.Therefore, there exists $t_2 > t_1$ such that $\dot{x}(t_2), \dot{y}(t_2), \dot{z}(t_2) > 0$ and the solution leaves $N_{1,3} \cap \partial\Pi_2$ and reenters in Π_2. Let for $t_1, t_1 > t_0 > 0$ the velocities $\dot{y}(t_1) = \dot{z}(t_1) = 0$ and $\dot{x}(t_1) > 0$. It follows that $\ddot{y}(t_1) = 2a\dot{x}(t_1) + 6bx(t_1)\dot{x}(t_1) > 0, \ddot{z}(t_1) = 0$, $\dddot{z}(t_1) = \ddot{y}(t_1) > 0$ and therefore there exists $t_2 > t_1$ such that $\dot{x}(t_2), \dot{y}(t_2), \dot{z}(t_2) > 0$ and the solution leaves $N_{2,3} \cap \partial\Pi_2$ and reenters in Π_2.

In an analogous way, every solution which starts in $\partial\Pi_1$ at some time t_0 leaves $N_{i,j} \cap \partial\Pi_1, \forall i,j$ and reenters in Π_1 at future time. It is proven here that every solution staring at Π_1 or Π_2 maximally bounces on the intersection of nullclines and reenters Π_1 and Π_2 respectively.

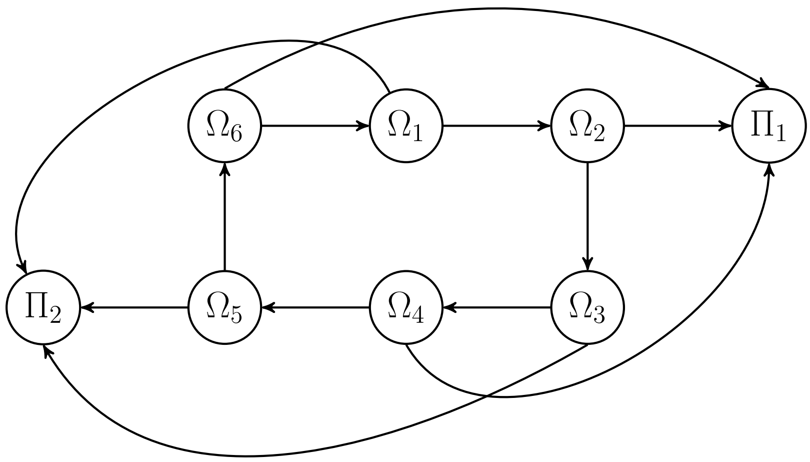
Let us examine now the case when a solution starting at t_0 in Π_2 reaches exactly one of the nullclines at $t_1 > t_0$. We let first $\dot{x}(t_1) = 0, \dot{y}(t_1) > 0, \dot{z}(t_1) > 0$. The solution lies on $N_1 \cap \partial\Pi_2$. It follows from $\ddot{x}(t_1) = 15z^4(t_1)\dot{z}(t_1) > 0$ that the solution immediately reenters Π_2 at $t_2 > t_1$. Now let $\dot{x}(t_1) > 0, \dot{y}(t_1) = 0, \dot{z}(t_1) > 0$ at $t_1 > t_0$. $\ddot{y}(t_1) = 2a\dot{x}(t_1) + 6bx\dot{x}(t_1) > 0$ and the solution moves back from $N_2 \cap \partial\Pi_2$ into Π_2 immediately at some $t_2 > t_1$. Similarly, if we let $\dot{x}(t_1) > 0, \dot{y}(t_1) > 0, \dot{z}(t_1) = 0$ at $t_1 > t_0$ and consider $\ddot{z}(t_1) = \dot{y}(t_1) > 0$, we reach then essentially the same conclusion that $\dot{z}(t_2) > 0$ immediately for some $t_2 > t_1$ and the solution reenters into Π_2 from $N_3 \cap \partial\Pi_2$. $\square$

Proposition 15 *Assume that $\mathbb{R}^3_{\geq 0}$ is positively invariant for the flow of System (4.1-4.3) and that solutions starting in $\mathbb{R}^3_{\geq 0}$ globally exist for all $t \geq 0$. Then, a solution starting in* $\operatorname{int}\Omega$ *at time t_0 belongs to one of the following three classes in future time:*

i) It is a stationary solution.

ii) It changes two velocities' signs simultaneously entering through one of the nullclines into either Π_1 or Π_2. Moreover, any solution starting in Π_1 converges to an equilibrium. The same conclusion holds for solutions starting in Π_2 provided that Π_2 is bounded.

iii) It changes one sign at a time according to the following scheme:



Moreover, if a solution starts in some Ω_i at $t_0 \geq 0$ and remains in it for all $t \geq t_0$, it must eventually converge into a stationary solution. Otherwise, it must leave it in future finite time even if it reentered it again later.

Proof: Suppose that a solution starts at t_0 in Ω_1 (i.e., signs of the differential equations are $(+, +, -)$). Since the nullclines are not tangent, generically, one sign change will take place each time (i.e., $(+, +, -)$ changes to $(-, +, -)$,$(+, -, -)$ or $(+, +, +)$). Consider System (4.22) and suppose that $(+, +, -)$ changes to $(-, +, -)$, then $\exists t_1 > t_0$ such that $\dot{x}(t_1) = 0$ and therefore $\ddot{x}(t_1) = 15z^4(t_1)\dot{z}(t_1) < 0$ and the change is valid. Now suppose that $(+, +, -)$ changes to $(+, -, -)$, this requires similarly that at some time $t_1 > t_0$, $\dot{y}(t_1) = 0$. However, $\ddot{y}(t_1) = 2a\dot{x}(t_1) + 6bx(t_1)\dot{x}(t_1) > 0$, thus the change is not valid. Similarly, if $(+, +, -)$ changes to $(+, +, +)$ then at some time $t_1 > t_0$ we have $\dot{z}(t_1) = 0$. Then $\ddot{z}(t_1) = \dot{y}(t_1) > 0$ and the change is valid. For the non-generic case when $(+, +, -)$ enters into one of the $N_{i,j}$'s at some time $t_1 > t_0$, Proposition 14 shows that a solution starting at some nullcline $N_{i,j}$ enters Π_2 if the third velocity is positive and Π_1 if it is negative.
Suppose that a solution starts at Π_2 at time t_0. This solution may bounce on one of the nullclines at a future time, but then it reenters Π_2. Now suppose that a solution starts in $\overline{\Pi}_2$ at time t_0. Suppose, in addition, that Π_2 is bounded. Then $\overline{\Pi}_2$ is bounded and by Proposition 14, it is positively invariant. Hence, by the generalization of Proposition 12 for solutions in $\mathbb{R}^3$, it must converge into a steady state, located at its boundary. A solution starting in Π_1 has negative velocities $(\dot{x}, \dot{y}, \dot{z}) \ll (0, 0, 0)$. It is decreasing in the non-negative orthant $\mathbb{R}^3_{\geq 0}$ and thus it is bounded from above. Hence, it is bounded since we assume that $\mathbb{R}^3_{\geq 0}$ is positively invariant for the flow of the system. In addition to the assumption that solutions exist for all $t \geq 0$ and that $\overline{\Pi}_1$ is positively invariant (Propositon 14), it follows from the generalization of Proposition 12 for solutions in $\mathbb{R}^3$ that it converges into a steady state, located at its boundary. We prove now that all solutions remaining in some Ω_i for all $t \geq t_0 > 0$ must eventually converge into a steady state. Without loss of generality, we assume that a solution starts in Ω_2. That is, it has the velocities' signs $(-, +, -)$. Assume that the solution is not bounded as $t \to \infty$. Unboundedness must be then in its $y-$component $y(t)$ since both $x(t)$ and $z(t)$ are decreasing and then they remain bounded in $\mathbb{R}^3_{\geq 0}$ as $t \to \infty$. However

$\dot{y}(t) > 0 \Leftrightarrow 2ax(t) + 3bx(t)^2 > y(t)$, which requires that $x(t) \to \infty$ as $t \to \infty$, which contradicts the boundedness of $x(t)$. Therefore, all solutions remaining in Ω_2 for all $t \geq t_0$ must be bounded. In an analogous way, we can prove this property for a solution starting in any of the Ω_i 's and remaining there for all $t \geq t_0$. The boundedness of the solution implies then by the generalization of Proposition 12 for solutions in $\mathbb{R}^3$ that it converges into a steady state in $\overline{\Omega}_2$. This implies, in addition, that all unbounded solutions starting in some Ω_i either interchange between the Ω_i 's for all $t \geq 0$ or they enter Π_2 at some $t_0 > 0$ if it is unbounded. □

Proposition 16 *Any non-empty connected component G of $\overline{\Pi}_1$ or $\overline{\Pi}_2$ has a steady state at its boundary. Moreover, if G is bounded then $G \subseteq [S_1, S_2]$ with S_1 and S_2 steady states at the boundary of G.*

Proof: Any connected component G of $\overline{\Pi}_1$ or $\overline{\Pi}_2$ has by its definition a steady state at its boundary even if this steady state is not a limit point for solutions starting in it. We prove now that G must lie either on the non-negative orthant or the non-positive orthant of the orthonormal system centered at this steady state that we call $S = (x_S, y_S, z_S)$. This is equivalent to say that every point of G is partially ordered with respect to S. Suppose this is not true and let $G \subset \overline{\Pi}_2$. We can assume without loss of generality that a point $R = (x_G, y_G, z_G) \in G$ has $z_G > z_S$. It suffices to consider the interior of G since any solution bounces on one nullcline or on an intersection of two nullclines and reenters Π_2 later as proven in Proposition 14. Then, R has the velocities' signs $(+, +, +)$ which are equivalent to the following inequalities:

$$\begin{aligned} &3z^5 > ax + 2bx^2 \\ &2ax + 3bx^2 > y \\ &y > 5z^5 + cz \end{aligned} \tag{4.24}$$

It follows that the following relations are valid: $y_G > 5z_G^5 + cz_G > 5z_S^5 + cz_S = y_S$, $2ax_G + 3bx_G^2 > y_G > y_S = 2ax_S + 3bx_S^2$. Hence, $R > S$, which contradicts our claim. Similarly, we can show that for $\overline{\Pi}_1$. Therefore, any of these sets must lie either in the non-positive orthant or in the non-negative orthant centered at its bounding steady state. Moreover, if G is bounded, then it lies inside an interval $[S_1, S_2]$ with S_1 and S_2 two steady states. We take G as above and we assume without loss of generality that $G \geq S_1$ and that it is bounded. For $\varepsilon > 0$ arbitrarily small, the set $\overline{\partial(G \setminus B(S_1, \varepsilon))} \subset \overline{\partial(G \setminus B(S_1, \varepsilon))} \cap (\bigcup_{1 \leq i < j \leq 3} N_i)$ and no steady state $S_2 \in \overline{\partial(G \setminus B(S_1, \varepsilon))}$. Any $X = (x, y, z) \in \overline{\partial(G \setminus B(S_1, \varepsilon))}$ is defined by satisfying one of the inequalities in (4.24) since $\overline{\partial(G \setminus B(S_1, \varepsilon))} \cap (\bigcap_{1 \leq i < j \leq 3} N_i) = \varnothing$. Since G is bounded, the following values exist:

$$\begin{aligned} K_3 &:= \sup\left\{z \mid (x, y, z) \in \overline{\partial(G \setminus B(S_1, \varepsilon))}\right\} \\ K_2 &:= \sup\left\{y \mid (x, y, z) \in \overline{\partial(G \setminus B(S_1, \varepsilon))}\right\} \\ K_1 &:= \sup\left\{x \mid (x, y, z) \in \overline{\partial(G \setminus B(S_1, \varepsilon))}\right\} \end{aligned}$$

The point $\overline{(K_1, K_2, K_3)}$ must satisfy all the inequalities in (4.24). Otherwise, it is a steady state at $\overline{\partial(G \setminus B(S_1, \varepsilon))}$, which is assumed false. Then $5K_3^5 + cK_3 < K_2 < 2aK_1 + 3bK_1^2 <$

$2aK_1 + 4bK_1^2 < 6K_3^5$. However, there is a suitable small $\varepsilon' > 0$ such that the inequality $5(K_3+\varepsilon')^5 + c(K_3+\varepsilon') < K_2 < 2aK_1+3bK_1^2 < 2aK_1+4bK_1^2 < 6(K_3+\varepsilon')^5$ holds. This contradicts the definition of K_3. Hence, either G is unbounded, or it is bounded, but with a steady state S_2 at its upper boundary. $\square$ Note that it is not guaranteed that $G \cap \mathbb{R}^3_{\geq 0} \neq \varnothing$.

Number of Positive Steady States

We will consider first the case with photorespiration (i.e., when $b > 0$). It is not obvious how many positive stationary solutions System (4.1-4.3) allows. This is due to the fact that fifth power is present in the system. Determining the number of positive stationary solutions is essential here since it facilitates unfolding the dynamics taking place. In this respect, it is expected that the variation of parameters will lead to a different number of stationary solutions and consequently different phase portraits. A direct outcome of assuming photorespiration is the boundedness of all flows (solutions) through time. This is a very plausible scenario since nothing in plant physiology resembles what could be interpreted mathematically as unboundedness. We begin by stating a famous theorem of LaSalle.

Theorem 8 LaSalle's Lagrange Stability Theorem
Let Θ be a bounded neighborhood of the origin and let $\Theta^{\complement}$ be its complement. Assume that $V(X)$ is a scalar function with continuous first partials in $\Theta^{\complement}$ and satisfying:

i) $V(X) > 0$ *for all* $x \in \Theta^{\complement}$,

ii) $\dot{V}(X) \leq 0$ *for all* $x \in \Theta^{\complement}$,

iii) $V(X) \to \infty$ *as* $\|x\| \to \infty$.

Then each solution of $\dot{X} = f(X)$ *is bounded for all* $t \geq 0$.

(see [69])

Proposition 17 *Solutions of System (4.1-4.3) starting in the non-negative orthant globally exist and remain there for all* $t \geq 0$. *Moreover, (4.1-4.3) has all its solutions starting in the non-negative orthant bounded.*

Proof: Notice first that a solution starting at the origin $O(0,0,0)$ stays at the origin for all $t \geq 0$, hence it cannot escape $\mathbb{R}^3_{\geq 0}$ through the origin. A solution of (4.1-4.3) might leave the non-negative orthant $\mathbb{R}^3_{\geq 0}$ from one of the boundary planes. We consider the case when it leaves through a boundary plane, but not through an axis. For instance, if it leaves $\mathbb{R}^3_{\geq 0}$ through the $y-z$ plane, then there is some $t_0 \geq 0$ such that $x(t_0) = 0$. It is enough then to check $\dot{x}(t_0) = 3z(t_0)^5 > 0$, which is however positive. Then any solution of (4.1-4.3) cannot escape $\mathbb{R}^3_{\geq 0}$ through the $y-z$-plane. Now suppose that a solution escapes through the $x-y$ plane then there is some $t_0 \geq 0$ such that $z(t_0) = 0$. However, it follows from $\dot{z}(t_0) = y(t_0) > 0$ that $z(t)$ the z component of the solution instantly increases and the solution reenters the interior of $\mathbb{R}^3_{\geq 0}$. In an analogous way, a solution of (4.1-4.3) cannot escape through the $x-z$ plane.
A solution of (4.1-4.3) might also leave the non-negative orthant $\mathbb{R}^3_{\geq 0}$ through an axis. Suppose that a solution escapes through the $x-$ axis. There is a moment $t_0 > 0$ such that $y(t_0) = z(t_0) = 0$. Equations $\dot{y}(t_0) = 2ax(t_0) + 3bx(t_0)^2 > 0$, $\dot{z}(t_0) = 0$ and

$\ddot{z}(t_0) = \dot{y}(t_0) > 0$ show that the solution immediately leaves the $x-$ axis toward the interior of $\mathbb{R}^3_{\geq 0}$. Similarly, it might leave through the $y-$ axis and then there exists $t_0 > 0$ such that $x(t_0) = z(t_0) = 0$. However, the following equations $\dot{x}(t_0) = 0$, $\dot{z}(t_0) = y(t_0) > 0$ and $\ddot{x}(t_0) = 15z(t_0)^4\dot{z}(t_0) > 0$ show that it reenters again to the interior of $\mathbb{R}^3_{\geq 0}$. Analogously, a solution of (4.1-4.3) cannot escape through the $z-$ axis. Hence it remains in $\mathbb{R}^3_{\geq 0}$ for all t in its maximal interval of existence.
We prove now that all solutions starting in $\mathbb{R}^3_{\geq 0}$ remain bounded for all finite time t. For instance, if we consider the linear combination of variables $5x+3y+3z$, it satisfies $\frac{d(5x+3y+3z)}{dt} \leq a(5x+3y+3z)$ and from that follows the existence of solutions in the non-negative orthant for all $t \geq 0$ since solutions does not leave it as seen before. This is equivalent to the global existence of solutions for all $t \geq 0$ for ordinary differential equations (see [48]). No blow-up solutions will be present.
Consider the following *Lyapunov-type* function defined by $V : \mathbb{R}^3_{\geq 0} \to \mathbb{R}^3_{\geq 0}$, $V(X) = \frac{31}{10}x + 2y + \frac{19}{10}z$. It has then the following time derivative:
$\dot{V}(X) = (\frac{9a}{10} - \frac{2b}{10}x)x - \frac{1}{5}z^5 - \frac{19c}{10}z - \frac{1}{10}y$. $\dot{V}(X) \leq 0$ for $x \geq \frac{9a}{2b}$. Moreover, $(\frac{9a}{10} - \frac{2b}{10}x)x$ is the only term in $\dot{V}(X)$ which might make it positive since the other terms are non-positive for z and y non-negative. $(\frac{9a}{10} - \frac{2b}{10}x)x \geq 0$ over the interval $[0, \frac{9a}{2b}]$ and it admits its roots at 0 and $\frac{9a}{2b}$. Hence, its maximum is attained when its first derivative with respect to x vanishes (i.e., at $x = \frac{9a}{4b}$ with a maximum value $\frac{81a^2}{80b}$).
Therefore, we have the following upper bound of $\dot{V}(X)$ over the whole $\mathbb{R}^3_{\geq 0}$:

$$\dot{V}(X) \leq \frac{81a^2}{80b} - \frac{1}{5}z^5 - \frac{19c}{10}z - \frac{1}{10}y$$

It follows then that $\dot{V}(X) \leq 0$ whenever $\frac{81a^2}{80b} - \frac{1}{5}z^5 - \frac{19c}{10}z - \frac{1}{10}y \leq 0$. If we now adopt the same notation as in LaSalle's Theorem, we define the following set:

$$\Theta^{\complement} = \left\{(x,y,z) \in \mathbb{R}^3_{\geq 0} \mid x \geq \frac{9a}{2b}, y \geq 0, z \geq 0\right\} \cup \left\{(x,y,z) \in \mathbb{R}^3_{\geq 0} \mid x \leq \frac{9a}{2b}, \frac{81a^2}{80b} \leq \frac{1}{5}z^5 + \frac{19c}{10}z + \frac{1}{10}y\right\}$$

$\Theta^{\complement}$ defines then a complement of a neighborhood of the origin, where $V(X) > 0$ and $\dot{V}(X) \leq 0$. The third condition of the theorem is obvious. It follows then by LaSalle's Theorem that all solutions of (4.1-4.3) starting in the non-negative orthant are bounded. □

Definition 4.2.1 *Given two polynomials $f(x) = a_n x^n + \cdots + a_1 x + a_0$, $g(x) = b_m x^m + \cdots + b_1 x + b_0 \in \mathbb{C}[x]$, their resultant relative to the variable x is a polynomial over the field of coefficients $\mathbb{C}$ of $f(x)$ and $g(x)$ and is defined as:*

$$\mathrm{Res}_x(f,g) := a_n^m b_m^n \prod_{i,j}(\alpha_i - \beta_j),$$

where $f(\alpha_i) = 0$ for all $1 \leq i \leq n$ and $g(\beta_j) = 0$ for all $1 \leq j \leq m$.

Proposition 18 *Number of solutions of Model (4.1-4.3) is equivalent to the number of solutions of the polynomial: $qq(z) = bz^{10} + 4bcz^6 - a^2z^5 + 4bc^2z^2 + a^2cz$. That is, for every $z^* \in \mathbb{R}_{\geq 0}$ root of $qq(z)$ there exists $x^*, y^* \in \mathbb{R}_{\geq 0}$ such that (x^*, y^*, z^*) is a solution of (4.1-4.3) and vice versa.*

Proof: A typical method for solving a system of polynomials is implemented by using the repeated resultant to eliminate $n-1$ variables except x_i from a system with n variables. The result is a polynomial $p(x_i) \in \mathbb{K}[x_i]$. For instance, given the following naming of differential equations of System (4.1-4.3):

$$\begin{aligned} f &:= -ax - 2bx^2 + 3z^5 \\ g &:= 2ax + 3bx^2 - y \\ h &:= y - 5z^5 - cz \end{aligned}$$

We start by eliminating the variable y by considering $\mathrm{Res}_y(h, g) = 2ax + 3bx^2 - 5z^5 - cz$, the resultant of the third and second polynomials with respect to the variable y. Then the resultant of the first and the second $\mathrm{Res}_y(f, g) = -ax - 2bx^2 + 3z^5$. Obtained are now two polynomials with respect to the remaining variables x and z:

$$\begin{aligned} \mathrm{Res}_y(h, g) &= 2ax + 3bx^2 - 5z^5 - cz \\ \mathrm{Res}_y(f, g) &= -ax - 2bx^2 + 3z^5 \end{aligned}$$

In order to eliminate x, we will consider now $\mathrm{Res}_x\left(\mathrm{Res}_y(h, g), \mathrm{Res}_y(f, g)\right)$.

$$\mathrm{Res}_x\left(\mathrm{Res}_y(h, g), \mathrm{Res}_y(f, g)\right) = b\left[bz^{10} + 4bcz^6 - a^2z^5 + 4bc^2z^2 + a^2cz\right] = b\left[qq(z)\right] \quad (4.25)$$

We take advantage of the fact that the resultant of two polynomials is zero, if and only if they have a common root in an algebraically closed field containing the coefficients to generate a solution of the system of polynomials. Generally, these equivalences are proven for polynomials considered existing in $\mathbb{C}[x, y, z]$ (i.e., while working over $\mathbb{C}$). However, they might hold for the polynomials when considered in $\mathbb{R}[x, y, z]$ depending on the geometry of the polynomials (check [102] for a record of theorems concerning the number of real roots of a polynomial). This is the case here, where if $qq(z)$ admits a non-negative root z then a non-negative common root x for $\mathrm{Res}_y(h, g)$ and $\mathrm{Res}_y(f, g)$ is implied and consequently, a non-negative solution (x, y, z) for the whole system exists. The existence of such non-negative x and y could be easily checked by using Descartes' Rule of Signs. Hence, the idea is retracing the steps from a partial solution of a small system back to establish a solution for the whole system. One can easily conclude from Definition 4.2.1 that a double root z^* of $\mathrm{Res}_x\left(\mathrm{Res}_y(h, g), \mathrm{Res}_y(f, g)\right)$ generates (x^*, z^*) a multiple solution of the system of polynomials of $\mathrm{Res}_y(h, g)$ and $\mathrm{Res}_y(f, g)$ and consequently a multiple solution (x^*, y^*, z^*) of the whole system[1]. This is shown in the following proposition: □

Proposition 19 *Let* $F(X, Z, \lambda) = \sum_{i=1}^{n} f_i(X, \lambda)Z^i = 0$ *and* $G(X, Z, \lambda) = \sum_{j=1}^{m} g_j(X, \lambda)Z^j = 0$ *with* F *and* G *smooth enough. If* $\mathrm{Res}_Z(F, G)$ *admits a double root at some* X_0*, then the system of polynomials*

$$\begin{cases} F(X, Z, \lambda) \\ G(X, Z, \lambda) \end{cases}$$

admit a solution (X_0, Z_0) *with at least one zero eigenvalue with respect to the linearization of the system. The converse is true.*

[1] *Notice that equivalence of roots of* $qq(z)$ *and System (4.1-4.3) holds in* $\mathbb{C}$ *in general. However, for non-negative roots it holds also in* $\mathbb{R}_{\geq 0}$.

Proof: As in Definition 4.2.1, the resultant of F and G with respect to Z and its first derivative with respect to X are given by

$$\begin{aligned}
&\mathrm{Res}_Z(F,G) = f_n^m g_m^n \prod_{i,j}(Z_1^i - Z_2^j) \\
&\frac{d\,\mathrm{Res}_Z(F,G)}{dX} = m f_n^{m-1} g_m^n f_n' \prod_{i,j}(Z_1^i - Z_2^j) + n f_n^m g_m^{n-1} g_n' \prod_{i,j}(Z_1^i - Z_2^j) \\
&+ f_n^m g_m^n \left(\sum_{i_0,j_0} \left(\frac{dZ_1^{i_0}}{dX} - \frac{dZ_2^{j_0}}{dX} \right) \prod_{i\neq i_0, j\neq j_0} (Z_1^i - Z_2^j) \right)
\end{aligned}$$

Where Z_1 and Z_2 denote the roots of F and G respectively. That is for each X_0, Z_1 is a root of F and Z_2 is a root of G. We denote by $\frac{dZ_1^{i_0}}{dX}$ and $\frac{dZ_2^{j_0}}{dX}$ the first derivatives of the functions Z_1 and Z_2 at X_0 if they are defined. If the resultant $\mathrm{Res}_Z(F,G)|_{X_0} = 0$ at X_0, then $Z_1^{i_0} = Z_2^{j_0}$ for some $i_0, j_0, 0 \leq i_0 \leq n, 0 \leq j_0 \leq m$. Considering an open bounded interval of Z_1 and Z_2 near $Z_1^{i_0}$ and $Z_2^{j_0}$ respectively and assuming that $\frac{dF}{dZ}|_{(X_0, Z_1^{i_0})} \neq 0$ and $\frac{dG}{dZ}|_{(X_0, Z_2^{j_0})} \neq 0$, the Implicit Function Theorem implies then that Z_1 and Z_2 are described as functions of X locally with $Z_1(X_0) = Z_1^{i_0}$ and $Z_2(X_0) = Z_2^{j_0}$. If we let $\frac{d\,\mathrm{Res}_Z(F,G)}{dX}|_{X_0} = 0$, we get the following identity: $\frac{dZ_1}{dX}(X_0) = \frac{dZ_2}{dX}(X_0)$. Let us denote by Z_0 the common root of F and G at X_0. Consider now the linearization of the system:

$$\begin{cases} F(X,Z,\lambda) \\ G(X,Z,\lambda) \end{cases}$$

at (X_0, Z_0) given by

$$\begin{pmatrix} \frac{\partial F}{\partial X} & \frac{\partial F}{\partial Z} \\ \frac{\partial G}{\partial X} & \frac{\partial G}{\partial Z} \end{pmatrix}_{|(X_0,Z_0)} \tag{4.26}$$

At the same time, we have the following identities for the implicit equations in the system

$$\frac{dF}{dX}|_{(X_0,Z_0)} = \left(\frac{\partial F}{\partial X} + \frac{\partial F}{\partial Z_1}\frac{dZ_1}{dX} \right)|_{(X_0,Z_0)} = 0 \tag{4.27}$$

$$\frac{dG}{dX}|_{(X_0,Z_0)} = \left(\frac{\partial G}{\partial X} + \frac{\partial G}{\partial Z_2}\frac{dZ_2}{dX} \right)|_{(X_0,Z_0)} = 0 \tag{4.28}$$

provided that $Z = Z_1$ in $F = 0$ and $Z = Z_2$ in $G = 0$. This is equivalent to differentiating F and G along the roots functions Z_1 and Z_2 at the point (X_0, Z_0). We denote by $\frac{dZ_1}{dX}|_{(X_0,Z_0)}$ the first derivative of both Z_1 and Z_2 at X_0. The following equality holds:

$$\begin{pmatrix} \frac{\partial F}{\partial X} & \frac{\partial F}{\partial Z} \\ \frac{\partial G}{\partial X} & \frac{\partial G}{\partial Z} \end{pmatrix}_{|(X_0,Z_0)} \begin{pmatrix} 1 \\ \frac{dZ_1}{dX} \end{pmatrix}_{|(X_0,Z_0)} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

which implies that the determinant of the matrix (4.26) is zero. Hence, at least one eigenvalue of the Jacobian is zero at (X_0, Z_0). Similarly, if we let $\frac{dF}{dZ}|_{(X_0,Z_0)} = 0$ and $\frac{dG}{dZ}|_{(X_0,Z_0)} = 0$, the determinant is again zero.

In order to prove the validity of the converse of the forward statement, we suppose that the following matrix has a zero determinant at (X_0, Z_0):

$$\begin{pmatrix} \frac{\partial F}{\partial X} & \frac{\partial F}{\partial Z} \\ \\ \frac{\partial G}{\partial X} & \frac{\partial G}{\partial Z} \end{pmatrix}_{|(X_0,Z_0)} \tag{4.29}$$

It follows then that its rank is less than or equal to one. Let us suppose that the rank of the above matrix is one. The other case is trivial. Without loss of generality let it be that the first row is a multiple of the second row. That is,

$$\begin{pmatrix} \frac{\partial F}{\partial X} & \frac{\partial F}{\partial Z} \end{pmatrix}_{|(X_0,Z_0)} = \eta \begin{pmatrix} \frac{\partial G}{\partial X} & \frac{\partial G}{\partial Z} \end{pmatrix}_{|(X_0,Z_0)} \tag{4.30}$$

If we now reconsider Equations (4.27) and (4.28), the derivatives of F and G along the solutions functions Z_1 and Z_2 respectively, we can easily establish the equality $\frac{dZ_1}{dX}_{|(X_0,Z_0)} = \frac{dZ_2}{dX}_{|(X_0,Z_0)}$, which turns $\frac{d\,\mathrm{Res}_Z(F,G)}{dX}_{|X_0}$ to zero. □

Note that starting from a system of two polynomials, multiple solutions are transferred to a three polynomial system, at least if the system keeps being determined. Equivalence between the number of non-negative roots of $qq(z)$ and System (4.1-4.3) could also be shown using elementary steps. It was proven in [44] that a solution (x^*, y^*, z^*) of (4.1-4.3) is one whose components satisfy the following equations:

$$ax^* = 2y^* - 9z^{*^5} \tag{4.31}$$
$$y^* = 5z^{*^5} + cz^* \tag{4.32}$$
$$bx^{*^2} = 6z^{*^5} - y^* \tag{4.33}$$

We will assume that the first two identities hold and prove the third by regrouping the terms of $qq(z)$ in the following manner:

$$\begin{aligned}
&qq(z^*) = bz^{*^{10}} + 4bcz^{*^6} - a^2z^{*^5} + 4bc^2z^{*^2} + a^2cz^* = 0\\
&= (81bz^{*^{10}} - 180bz^{*^{10}} + 100bz^{*^{10}}) + 4bcz^{*^6} - a^2z^{*^5} + 4bc^2z^{*^2} + a^2(y^* - 5z^{*^5}) = 0\\
&= 81bz^{*^{10}} - 36bz^{*^5}(5z^{*^5}) + 4b(25z^{*^{10}}) + 4bcz^{*^6} - a^2z^{*^5} + 4bc^2z^{*^2} + a^2y^* - 5a^2z^{*^5} = 0\\
&= 81bz^{*^{10}} - 36bz^{*^5}(y^* - cz^*) + 4b(y^{*^2} - c^2z^{*^2} - 10cz^{*^6}) + 4bcz^{*^6} - a^2z^{*^5}\\
&+4bc^2z^{*^2} + a^2y^* - 5a^2z^{*^5} = 0\\
&= 81bz^{*^{10}} - 6a^2z^{*^5} - 36bz^{*^5}y^* + a^2y^* + 4by^{*^2} = 0\\
&= -9bz^{*^5}(2y^* - 9z^{*^5}) - a^2(6z^{*^5} - y^*) + 2by^*(2y^* - 9z^{*^5}) = 0\\
&= b(2y^* - 9z^{*^5})^2 - a^2(6z^{*^5} - y^*) = 0\\
&\implies bx^{*^2} = 6z^{*^5} - y^*
\end{aligned}$$

as required.

According to Descartes' Rule of Signs, $qq(z)$ has maximally two positive solutions counted by multiplicity and a persistent solution for $z = 0$. The zero solution $z^* = 0$ of $qq(z)$ is equivalent to the trivial solution $(0, 0, 0)$ of System (4.1-4.3). We are investigating the existence of positive roots of $qq(z)$, hence we divide by z and consider instead of $qq(z)$, which we will call $q(z) := \frac{qq(z)}{z}$. The geometry of $q(z)$ shows that $\lim\limits_{z\to+\infty} q(z) = +\infty$ and $\lim\limits_{z\to-\infty} q(z) = -\infty$. Moreover, it has maximally two positive solutions, hence there exists an interval where the graph of $q(z)$ resembles a convex curve. If $q(z)$ might ever admit two positive solutions for some choice of parameters, there is then, by the continuous dependence of $q(z)$ on z and its parameters, a parameters choice for which it admits a double root. This double root is then attained for the values of parameters when the local minimum of this convex section of the graph of $q(z)$ touches the x-axis. To make the matter concrete, we define the following function ξ and we call it "depth " function.

$$\begin{aligned} &\xi : \mathbb{R}^3_{\geq 0} \to \mathbb{R}_{\geq 0} \\ &(a, b, c) \to \xi(a, b, c) \end{aligned}$$

$\xi(a, b, c)$ is the orthogonal distance between the local minimum of the convex section of graph of $q(z)$ and the x-axis upon taking the parameters triplet (a, b, c). $\xi(a, b, c) = 0$ for the choice of parameters (a, b, c) exactly when $q(z)$ admits a double root.

Remark 2 Tschirnhaus Transformation
We will use next a transformation of the quintic polynomial in order to write it in its reduced form. Reduced, Principal and Bring-Jerrard are the names of a quintic $P(x)$ after the elimination of $\{x^4\}$, $\{x^4, x^3\}$, $\{x^4, x^3, x^2\}$ respectively. By the end of the seventeenth century, Ehrenfried Walther von Tschirnhaus was able to eliminate the terms x^{n-1} and x^{n-2} from any polynomial $P(x)$ of order n by using a change of variables of the form $y = x^2 + \alpha x + \beta$ [109]. The progress he initiated was like a rain after a long drought in the solving of polynomials. His ability to show this reduction awakened his desire to eliminate one more term, namely x^{n-3}, by means of cubic transformation instead of quadratic. However, we had to wait until the end of the eighteenth century when E.S. Bring [11] (and independently G. B. Jerrard [60], [61]) devised a general transformation which eliminates the mentioned terms from any n-th degree polynomial. The Tschirnhaus Transformation used in the subsequent context is based on the realization that the second term x^{n-1} of any n-th order polyomial $p(x) = x^n + a_{n-1}x^{n-1} + \cdots + a_1 x + a_0$ could be easily removed by the simple change of variable $y = x + \frac{a_{n-1}}{n}$ and this will suffice. (see [47])

Proposition 20 *If (4.1-4.3) has two positive solutions counted by multiplicity, then the following system has exactly one positive solution and no negative solution:*

$$\begin{cases} q(z) + \xi(a, b, c) = 0 \\ \\ \frac{d}{dz}\left(q(z) + \xi(a, b, c)\right) = 0 \end{cases} \tag{4.34}$$

Proof: By definition, the system admitting one positive solution, corresponds to the existence of a positive multiple root of $q(z)$ and consequently to a repeated solution of (4.1-4.3) whenever $\xi(a, b, c) = 0$ or to the existence of two simple positive roots of $q(z)$ and consequently to a two simple solutions of (4.1-4.3) whenever $\xi(a, b, c) > 0$. System (4.34) does not assume negative solutions since otherwise $q(z)$ would have two negative roots counting multiplicity, which is not the case. Same conclusion could have also been drawn, had we

considered the resultant $\mathrm{Res}_z(q, \frac{dq}{dz}) = 0$. Nevertheless, presenting the result in the written scheme is very informative, as we will see soon. □
Substituting one polynomial into the other generates the following quintic:

$$\tilde{q}(z) = 16bcz^5 - 5a^2z^4 + 32bc^2z - 4bc^2 + 9a^2c + 9\xi(a, b, c) = 0$$

Depending on the sign of the last coefficient, $\tilde{q}(z)$ has either one negative root and maximally two positive roots or maximally three positive roots. A solution of System (4.34) is essentially a root of $\tilde{q}(z)$ but not vice versa. The goal is to unfold the case where $\tilde{q}(z)$ has no positive roots (i.e., to determine the parameters' domains where no positive roots of $\tilde{q}(z)$ exist implying that System (4.34) and consequently System (4.1-4.3) has no positive solutions. We can test the equation with some kinds of transformation to realize which relation between the parameters a, b and c is controlling the number of positive roots of $\tilde{q}(z)$ and then of $q(z)$. Consider the deletion of the second term of $\tilde{q}(z)$ using the **Tschirnhaus Transformation** in Remark 2 defined by:

$$\tilde{z} = z - \frac{a^2}{16bc}$$

and generating the following reduced quintic:

$$\tilde{\tilde{q}}(\tilde{z}) = \tilde{z}^5 - (\frac{5a^4}{128b^2c^2})\tilde{z}^3 - (\frac{5a^6}{1024b^3c^3})\tilde{z}^2 + (2c - \frac{15a^8}{65536b^4c^4})\tilde{z} + (\frac{9a^2c + 9\xi}{16bc} + 32bc^2 - 4a^5) = 0 \tag{4.35}$$

In contrary to $\tilde{q}(z)$, the reduced quintic $\tilde{\tilde{q}}(\tilde{z})$ shows a power proportionality relation between the parameters a, b and c which possibly control the number of positive roots it possesses. For instance, if the last two coefficients of $\tilde{\tilde{q}}(\tilde{z})$ are non-positive, it assumes then one positive root, which is probably a solution of System (4.34). The second to last of the coefficients is $2c - \frac{15a^8}{65536b^4c^4} \leq 0 \Leftrightarrow 131072b^4c^5 \leq 15a^8$. That is, the parameters are compared according to the following proportionality ratio $\frac{a^8}{b^4c^5}$. This leads to adopting the ansatz $a^2 = mbc^{\frac{5}{4}}$ and to test it with the resultant of $q(z)$ and $q'(z)$

$$\mathrm{Res}_z(q, q') = -800000a^{24}b^5c^3 + 58342275625a^{16}b^9c^8 + 695784701952a^8b^{13}c^{13} \tag{4.36}$$

Now we substitute the ansatz: $a^2 = mbc^{\frac{5}{4}}$. The resultant simplifies to :

$$\mathrm{Res}_z(q, q') = b^{17}c^{18}m^4\left[-800000m^8 + 58342275625m^4 + 695784701952\right] \tag{4.37}$$

The equation is then solvable for m with one positive solution $m_\circ$ and one negative solution which is not of interest. For $a^2 = m_\circ bc^{\frac{5}{4}}$, where:

$$m_\circ = \sqrt[4]{\left(\frac{143404379}{64000}\sqrt{5}\sqrt{53} + \frac{93347641}{2560}\right)} \tag{4.38}$$

$q(z)$ has a multiple root and consequently by Propositions 18 and 19, System (4.1-4.3) has a single positive stationary solution. Notice that the discriminant of $q(z)$ is given by:

$$\operatorname{Disc}_z(q) = \frac{\operatorname{Res}_z(q, q')}{b}$$

Hence $\operatorname{Disc}_z(q)$ and $\operatorname{Res}_z(q, q')$ have the same sign.

Remark 3 Discriminant and Number of Real Roots of a Polynomial
Let $P \in \mathbb{R}[x]$ be a monic polynomial with real coefficients. P splits into a product of linear factors over $\mathbb{C}$ so that $P = (x - u_1) \cdots (x - u_n)$ for some $u_i \in \mathbb{C}$. Assume that the roots $u_1, \cdots, u_n$ of P are pointwise distinct and denote by r the number of real roots among $u_1, \cdots, u_n$ and by d the discriminant of P. It is a fact that $n - r$ is divisible by 4 if and only if $d > 0$. Suppose this is the case then the number of complex roots denoted by $n_c = n - r$ is divisible by four. If we write $n_c = 4k$ for some non-negative integer k then $k = \frac{n-r}{4}$. However, most of the time r is not known, then k is controlled by the upper bound $\frac{n}{4}$ and by 0 as lower bound. For instance, if a cubic polynomial has a positive discriminant, then $k \leq \frac{3}{4}$ and k is then 0. That is, no pair of complex roots exists. The negation of the proposition i.e. for $d < 0$ implies that $n - r$ is not divisible by four. Hence $n - r \equiv 2 \pmod 4$ i.e. there exists a non-negative integer k such that $n - r = 4k + 2$. Then $k + 1$ designates the number of pairs of complex roots and is controlled by the upper bound $\frac{n-2}{4}$. (see [107])

Proposition 21 *i) For $m > m_\circ$, System (4.1-4.3) has two simple positive stationary solutions.*

ii) For $m = m_\circ$, System (4.1-4.3) has one double positive stationary solution.

iii) For $m < m_\circ$, System (4.1-4.3) has no positive stationary solutions.

Proof: $m > m_\circ \Rightarrow \operatorname{Disc}_z(q) < 0$ hence the number of real roots is not divisible by four (Remark 3). It is a fact in this case that there exists a non-negative integer $k \leq \frac{n-2}{4}$ (n is the degree of the polynomial) such that $2k + 1$ pairs of complex roots exist. Consequently, the number of real roots is $n - 4k - 2$. Therefore, k is bounded above by $\frac{n-2}{4} = \frac{deg(q(z))-2}{4} = \frac{9-2}{4} = \frac{7}{4}$. Hence, k is either zero or one. If $k = 0$ then $q(z)$ assumes one pair of complex roots and seven real roots. However, according to Descartes' Rule of Signs, $q(z)$ has exactly one negative root and allows maximally two positive roots making a sum of maximally three real roots. We conclude that $k \neq 0$ and then $k = 1$. It follows that $q(z)$ has three real roots, one negative and two positive. All the roots are simple in this case since the resultant is negative. For $m = m_\circ$, $\operatorname{Res}_z(q, q') = 0$ and then $q(z)$ admits a double root which is essentially positive because its negative root is persistent (i.e., independent of the choice of m). We then extend this double root to a double solution of (4.1-4.3) as shown in Propositions 18 and 19. Finally, for $m < m_\circ$, $\operatorname{Disc}_z(q) > 0$ and by (Remark 3) there is a non-negative integer $k, k \leq \frac{n}{4} = \frac{9}{4}$ such that $2k$ pairs of complex conjugate roots and $n - 4k$ real roots exist. k is to be chosen from the set $\{0, 1, 2\}$. Only $k = 2$ leads to a feasible scenario, in which $q(z)$ admits a unique real root, a negative root. Hence, $q(z)$ has no positive roots and (4.1-4.3) has no positive solutions. □

Knowing the number of stationary solutions of System (4.1-4.3) is not informative about their nature. There are already known examples for systems that admit as many equilibria as System (4.1-4.3), though none of them is stable. Stability is an essential component of dynamical systems in biology since otherwise, a dynamical system fails to resemble nature, which is robust in its functions. We address this question by considering $q(z)$ and substituting for a^2 by $mbc^{\frac{5}{4}}$ and for z by $\mu c^{\frac{1}{4}}$. The equation simplifies to:

$$q(\mu c^{\frac{1}{4}}) = bc^{\frac{9}{4}} \left(\mu^9 + 4\mu^5 - m\mu^4 + 4\mu + m\right) = 0 \tag{4.39}$$

A further simplification is required and will be done by substituting for m by $k\mu$. It turns out then that $q(\mu c^{\frac{1}{4}})$ is a quadratic polynomial:

$$q(\mu c^{\frac{1}{4}}) = bc^{\frac{9}{4}}\mu \left(\mu^8 + (4-k)\mu^4 + (4+k)\right) = 0 \tag{4.40}$$

Substitute $\eta = \mu^4$, then

$$q(\eta^{\frac{1}{4}} c^{\frac{1}{4}}) = bc^{\frac{9}{4}}\mu \left(\eta^2 + (4-k)\eta + (4+k)\right) = 0 \tag{4.41}$$

and its discriminant

$$\mathrm{Disc}_\eta \left(q(\eta^{\frac{1}{4}} c^{\frac{1}{4}})\right) = k(k-12)$$

The characterization of the parameter m as a function of μ leads to different values of m. That is, solving the system the way it is in (4.41) is in reality finding roots of $q(z)$ for generally two different values of the parameter m. We are obviously finding some and not all of the roots μ's for different values of parameter m. To make the matter more concrete, let's consider the following example: Consider, for instance, the case when $k = 16$, (4.41) has two roots. The first root is $\mu_1 = \sqrt[4]{10}$ when $m = 16\sqrt[4]{10}$ and the second root is $\mu_2 = \sqrt[4]{2}$ when $m = 16\sqrt[4]{2}$. We then complete the roots into stationary solutions of (4.1-4.3) in the following manner: Substitute $\mu_i,\ i \in \{1,2\}$ in $z_i^* = \mu_i c^{\frac{1}{4}}$ then $y_i^* = 5{z_i^*}^5 + cz_i^*$ and $x_i^* = \frac{2}{a}y_i^* - \frac{9}{a}z_i^*$. Considering the characteristic polynomial of (4.1-4.3) at both $(x_i^*, y_i^*, z_i^*)\,,\ i \in \{1,2\}$. It admits three eigenvalues with negative real part at (x_1^*, y_1^*, z_1^*) and two eigenvalues of negative real part and one eigenvalue with positive real part at (x_2^*, y_2^*, z_2^*). Hence, the first is asymptotically stable, while the second is unstable. We conclude that there are some values of m for which $q(z)$ has two roots ($m > m_0$), where at least one of them is stable or unstable. Generally, this does not suffice to conclude that for $m > m_0$, always one of the roots is stable and the other is unstable because each of these roots might undergo a bifurcation and changes its stability nature as m changes. Here, a plausible bifurcation is that which does not induce a change in the number of positive stationary solutions since a maximal number of two positive roots counting multiplicity was proven in Proposition 21. Hopf bifurcation is, for example, plausible here when one of the equilibria changes its nature from stable to unstable or vice versa.

Proposition 22 *Let $P(z) := a_0 z^3 + a_1 z^2 + a_2 z + a_3$ with $a_0 \neq 0$ then $P(z)$ admits pure imaginary roots if and only if $a_2 \neq 0$, $a_0 a_3 - a_1 a_2 = 0$, $\operatorname{sign} a_2 = \operatorname{sign} a_0$. Moreover if $a_3, a_1 \neq 0$ then $\operatorname{sign} a_3 = \operatorname{sign} a_1$.*

Proof: Let ib and $-ib$, $b \in \mathbb{R}^*$ be the two imaginary roots of $P(z)$, it follows then:

$$\begin{aligned} P(ib) &= -a_0 ib^3 - a_1 b^2 + a_2 ib + a_3 = 0 \\ P(-ib) &= a_0 ib^3 - a_1 b^2 - a_2 ib + a_3 = 0 \end{aligned}$$

In both cases, the assumption requires that:

$$\begin{aligned} a_3 - a_1 b^2 &= 0 \\ b(a_2 - a_0 b^2) &= 0 \end{aligned}$$

Simultaneously, $a_3, a_1 = 0$ or $a_3, a_1 \neq 0$. $b(a_2 - a_0 b^2) = 0 \Rightarrow a_2 - a_0 b^2 = 0 \Rightarrow a_2 \neq 0$. Suppose $a_3, a_1 \neq, 0$, it follows then that $b^2 = \frac{a_3}{a_1} = \frac{a_2}{a_0}$ and both > 0. Consequently, $\operatorname{sign} a_2 = \operatorname{sign} a_0$, $\operatorname{sign} a_3 = \operatorname{sign} a_1$ and $a_0 a_3 - a_1 a_2 = 0$. Proving the other direction, given that $a_2 \neq 0$, $a_0 a_3 - a_1 a_2 = 0$, $\operatorname{sign} a_2 = \operatorname{sign} a_0$. It follows that $a_3 = \frac{a_1 a_2}{a_0}$ and

$$\begin{aligned} P(z) &= a_0 z^3 + a_1 z^2 + a_2 z + \frac{a_1 a_2}{a_0} \\ &= (a_0 z + a_1)\left(z^2 + \frac{a_2}{a_0}\right) \end{aligned}$$

and then $-\frac{a_1}{a_0}$ is one root and $\pm\sqrt{-\frac{a_2}{a_0}}$ are the two other roots. The existence of pure imaginary roots require then that $a_2 \neq 0$ and $\operatorname{sign} a_2 = \operatorname{sign} a_0$, which are given. It follows then $a_1 = 0 \Leftrightarrow a_3 = 0$. Suppose now that $a_1, a_3 \neq 0$ then from $a_0 a_3 - a_1 a_2 = 0$ follows the relation $\frac{a_0}{a_2} = \frac{a_1}{a_3}$ as a natural consequence and implies that $\operatorname{sign} a_3 = \operatorname{sign} a_1$. The proof is complete. $\square$

Proposition 23 *Only fold-type bifurcation can occur in System (4.1-4.3).*

Proof: Consider the characteristic polynomial of System (4.1-4.3) at some positive equilibrium (x^*, y^*, z^*)

$$\begin{aligned} P(\lambda) = {} & \lambda^3 + (1 + \underbrace{a + c + 25z^{*^4} + 4bx^*}_{\mu_1})\lambda^2 \\ & + (\underbrace{a + c + 25z^{*^4} + 4bx^*}_{\mu_1} + \underbrace{ac + 25az^{*^4} + 100bx^* z^{*^4} + 4bcx^*}_{\mu_2})\lambda \\ & + (\underbrace{ac + 25az^{*^4} + 100bx^* z^{*^4} + 4bcx^*}_{\mu_2} - (\underbrace{30az^{*^4} + 90bx^* z^{*^4}}_{\mu_3})) \end{aligned}$$

The coefficients of the characteristic polynomial are now:

$$a_0 = 1 \qquad a_1 = 1 + \mu_1 \qquad a_2 = \mu_1 + \mu_2 \qquad a_3 = \mu_2 - \mu_3$$

Moreover, $a_0, a_1, a_2 > 0$ because $\mu_1, \mu_2, \mu_3 > 0$. Only the last term a_3 can be signed. Suppose $P(\lambda)$ admits pure imaginary roots at (x^*, y^*, z^*), it follows then by Proposition 22 that $a_3 > 0$ and $a_0 a_3 - a_1 a_2 = 0$. However,

$$a_0 a_3 - a_1 a_2 = \begin{vmatrix} a_0 & a_1 \\ a_2 & a_3 \end{vmatrix} = \begin{vmatrix} 1 & 1 + \mu_1 \\ \mu_1 + \mu_2 & \mu_2 - \mu_3 \end{vmatrix} = \mu_2 - \mu_3 - \mu_1 - \mu_1^2 - \mu_2 - \mu_1 \mu_2 < 0$$

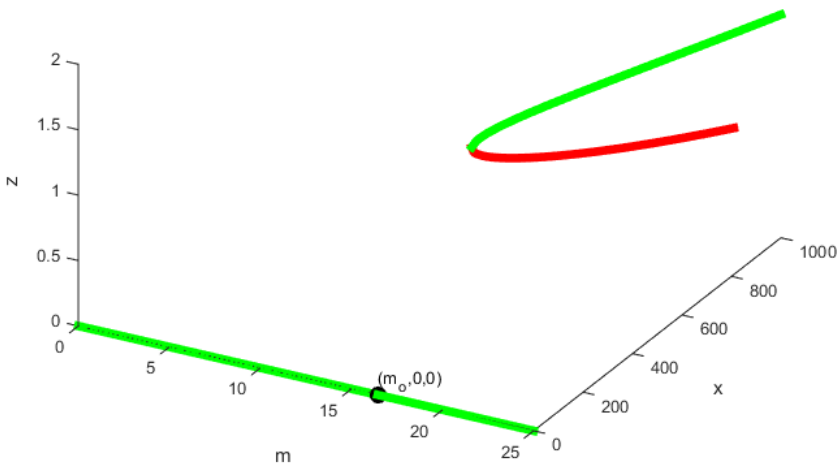


Figure 4.1: The bifurcation diagram of Hahn's model. Green plots represent stable steady states, while red plots represent unstable steady states

Therefore, a stable equilibrium (x^*, y^*, z^*), for which the last coefficient $a_3 > 0$ by Descartes' Rule of Signs, can never change stability by a Hopf bifurcation because a Hopf bifurcation occurs when the eigenvalues of the characteristic polynomial passes through the imaginary axis to the other half-plane. For an unstable positive equilibrium (x^*, y^*, z^*), the last coefficient $a_3 < 0$. Therefore, the characteristic polynomial at this equilibrium cannot admit pure imaginary roots by Proposition 22. We conclude that no Hopf bifurcation can occur in System (4.1-4.3). In addition, no double zero eigenvalue can occur due to the positivity of a_0, a_1 and a_2. The only plausible scenario is then when the last coefficient a_3 vanishes. Here, we talk about simple fold bifurcation or cusp bifurcation (i.e., fold-type bifurcation). □

In fact, we can already conclude from the existence of the two equilibria with different stability nature in the aforementioned example that fold bifurcation will occur. This is because a simple stable positive equilibrium implies that the other existing positive equilibrium is unstable and vice versa. Moreover, for some range of parameters, System (4.1-4.3) has no positive equilibria, which shows that for some parameters' values the equilibria disappear. Since only fold-type bifurcation can occur, then it will eventually occur, then the existing equilibria blend and disappear. Therefore, we can already conclude from Proposition 23 and a concrete example that System (4.1-4.3) experiences a fold-type bifurcation.

Proposition 24 *Model (4.1-4.3) has the following spectrum of non-negative stationary solutions for the ansatz representation $a^2 = mbc^{\frac{5}{4}}$:*

i) $m < m_\circ$*:* $O(0,0,0)$ *asymptotically stable equilibrium.*

ii) $m = m_\circ$*:* O *asymptotically stable equilibrium and* $F > 0$ *fold equilibrium.*

iii) $m > m_\circ$*: O, A and B such that O, B are asymptotically stable equilibria. A is an unstable equilibrium. Moreover, $O < A < B$.*

Proof: It is easy to check from the characteristic polynomial of (4.1-4.3) that O the origin is always an asymptotically stable stationary solution. Model (4.1-4.3) admits a number of positive stationary solutions, which coincides with the number of positive roots of $q(z)$ as the ratio of parameters $m = \frac{a^2}{bc^{\frac{5}{4}}}$ varies. For $m > m_\circ$, (4.1-4.3) has two positive stationary solutions, while for $m < m_\circ$ no positive stationary solution exists. It remains to explicitly validate the conclusion that at $m = m_\circ$, there exists exactly one positive stationary solution with exactly one zero eigenvalue. Consider the last coefficient in the characteristic polynomial $P(\lambda)$ at any equilibrium (x^*, y^*, z^*)

$$\begin{aligned}
a_3 &= ac - 5az^{*^4} + 10bx^*z^{*^4} + 4bcx^* \\
&= ac - 5az^{*^4} + 10b\left(\frac{1}{a}z^{*^5} + 2\frac{c}{a}z^*\right)z^{*^4} + 4bc\left(\frac{1}{a}z^{*^5} + 2\frac{c}{a}z^*\right) \\
&= \frac{10b}{a}z^{*^9} + \frac{24bc}{a}z^{*^5} - 5az^{*^4} + \frac{8bc^2}{a}z^* + ac \\
&= \frac{1}{a}(q(z^*) + z^*q'(z^*))
\end{aligned}$$

For $m = m_\circ$, a_3 vanishes and then $P(\lambda)$ admits zero root. The other roots have a negative real part. Hence, for $m = m_\circ$, a fold equilibrium exists and then a fold-type bifurcation occurs as m varies in the margin of $m_\circ$. The fold bifurcation is simple. That is, it is not a cusp bifurcation. The latter implies the existence of *hysteresis* phenomenon, for which the two stable equilibria alternatively meet with the unstable equilibrium at some parameters' values and disappear, undergoing a fold bifurcation each time. This is excluded here since, for all choices of positive parameters, O persists as an asymptotically stable equilibrium. Notice that the nullclines set to zero generate the following functions of z

$$\begin{aligned}
y &= 5z^5 + cz \\
x &= \frac{-a + \sqrt{a^2 + 24bz^5}}{4b}
\end{aligned}$$

which are obviously monotone with respect to z. Hence all equilibria are ordered following the total order in $\mathbb{R}_{\geq 0}$. Specifically, we have $O < A < B$ since all equilibira are connected to each other by a one-dimensional manifold, which is the centre manifold for $m = m_0$. $\square$

At $m_\circ$ a fold equilibrium is born with one zero eigenvalue as seen in Figure 4.1. For $m > m_\circ$, two stable equilibria exist and are shown in green and one unstable equilibrium lies between them is shown in red. We will focus in the next sections on the case when photorespiration is present and $m > m_\circ$. Later we study the case when photorespiration is set to zero. The latter case analysis is independent of m and is characterized by the existence of a single positive steady state, which is unstable and persistent.

Oscillations in the Model

Throughout the discussion, we denote by $\phi_t(x)$ the unique solution of $\dot{x} = f(x),\ f \in C^1(\Omega), \Omega \subset \mathbb{R}^n$ in x at time $t \in I(x)$, where $I(x) = [0, \infty[$ is the maximal interval of

existence of any solution starting in $\mathbb{R}^3_{\geq 0}$ for Hahn's three-dimensional model (Proposition 17). It is common to write $\phi_t x$ instead of $\phi_t(x)$ and this we follow here. The stable manifold at some equilibrium S is a $k-$dimensional (with $k \leq n$) invariant manifold with k corresponding to the number of eigenvalues with a negative real part of the Jacobian matrix of the system at point S. It is invariant with respect to the flow. For example, if we denote this manifold by U then $\phi_t(U) \subset U, t \geq 0$. Moreover, it is tangent to the stable subspace usually denoted by E^s. The stable subspace of a steady state in $\mathbb{R}^n$ is the space spanned by the set of eigenvectors corresponding to the eigenvalues with a negative real part of the linearization at the steady state. Additionally, we define the set $B(S)$ as the set of all points in $\mathbb{R}^n$ that converge later in time toward the steady state S. We call this set the basin of attraction of S. Naturally, we confine the definitions on the non-negative orthant of $\mathbb{R}^n$. Analogously, we might define the unstable manifold at some equilibrium S as the $k'-$dimensional (with $k' \leq n$) invariant manifold with k' corresponding to the number of eigenvalues with a positive real part of the Jacobian at S. It is tangent to the unstable subspace denoted by E^u.
We consider here Hahn's three-dimensional model for $m > m_0$. As proven in Section 4.2, three equilibria are present in this case: O, A and B. In addition to an eigenvalue of a positive real part, the linearization at the steady state A admits two eigenvalues with negative real parts. Hence, A possesses a two-dimensional stable manifold $W^s(A)$. We define the extension of $W^s(A)$ named $\tilde{W}^s(A)$ as the intersection of all solutions starting within the closure of basins of attraction of O and B. Explicitly, $\tilde{W}^s(A) = \overline{B(O)} \cap \overline{B(B)}$, where $B(B)$ (respectively $B(O)$) designates the subspace of all points in $\mathbb{R}^3_{\geq 0}$ that converge to B (respectively to O) later in forward time. Besides solutions converging to A over $W^s(A)$, solutions starting on $\tilde{W}^s(A)$ are those not converging to A yet forming a geometric extension to its stable manifold. For example, solutions converging to periodic orbits lying on the boundary of $W^s(A)$. We assume for the moment that this equivalence between $\tilde{W}^s(A) = \overline{B(O)} \cap \overline{B(B)}$ and the geometric extension of $W^s(A)$ does make sense. We will call it the geometric extension of the stable manifold $W^s(A)$ of A, knowing that none of the next propositions appearing before establishing this definition depends necessarily on it.
For $m > m_0$, the complement of the nullclines for System (4.1-4.3) is the union of Ωs and Πs. That is, the intersections of $\Omega_i \cap \mathbb{R}^3_{\geq 0} \neq \varnothing,\ 1 \leq i \leq 6$ and $\Pi_i \cap \mathbb{R}^3_{\geq 0} \neq \varnothing,\ i = 1, 2$.

Proposition 25 *i) A solution starting in $\overline{\Pi}_1 \cap]O, A[$ converges to O. A solution starting in $\overline{\Pi}_1 \cap]B, \infty[$ converges to B.*

ii) A solution starting in $\overline{\Pi}_2 \cap]A, B[$ converges to B.

Proof: Notice first that for $m > m_0$, Π_1 is the union of two connected components:

$$\left(\overline{\Pi}_1 \cap]O, A[\right) \bigcup \left(\overline{\Pi}_1 \cap]A, B[\right).$$

Notice also that $O, A \in \overline{\Pi}_1 \bigcap [O, A]$ and $A, B \in \overline{\Pi}_2 \bigcap [A, B]$. Both conclusions are profited from Proposition 16. By Proposition 14, a solution starting in $\overline{\Pi}_1$ is positively invariant. Then, each of $\overline{\Pi}_1 \cap]O, A[$ and $\overline{\Pi}_1 \cap]B, \infty[$ is positively invariant since they are disjoint sets. Hence, a solution starting in $\overline{\Pi}_1 \cap]O, A[$ remains bounded as $t \to \infty$ and has either all velocities negative or immediately all of velocities will be negative at any time t_0. Hence, by the generalization of Proposition 12 for solutions in $\mathbb{R}^3$ and as $t \to \infty$, all solutions converge into a steady state at the boundary of $\overline{\Pi}_1 \cap]O, A[$. That is, solutions converge either to A or to O. However, A is unstable while O is asymptotically stable. Hence, all solutions

starting there converge into O.
Any solution starting in $\overline{\Pi}_1 \cap]B, \infty[$ remains bounded because of its non-positive velocities' signs and the positive invariance of $\overline{\Pi}_1$. It must then converge to B as $t \to \infty$.
Now suppose that a solution starts in $\overline{\Pi}_2 \cap]A, B[$ and notice that for $m > m_0$ we have $\overline{\Pi}_2 \subset [A, B]$, a unique connected component of non-negative velocities' signs. Therefore, $\overline{\Pi}_2 \cap]A, B[$ is positively invariant as proven in Proposition 14. Any solution starting there other than A and B has all velocities either positive or immediately positive. Hence, any solution converges to a limit point, which is a steady state at the boundary by the above mentioned generalization of Proposition 12. It must then converge to the upper boundary of $\overline{\Pi}_2 \bigcap]A, B[$ namely to B. These sets are drawn in Figure 4.2. $\square$

Corollary 8.1 *A periodic orbit of (4.1-4.3) with $m > m_0$ if it exists, it revolves over all the Ω_i's. Moreover, the two-dimensional stable manifold $W^s(A)$ of A belongs to $\overline{\Omega} = \bigcup_{i=1}^{6} \overline{\Omega_i}$.*

Proposition 26 *The stable manifold $W^s(A)$ (or rather its extension $\tilde{W}^s(A)$) intersects all the axes and all the planes $x - y$, $y - z$ and $x - z$ in a bounded region.*

Proof: Let x be bounded. A solution starting in $W^s(A)$ for x small enough, starts either in Ω_5 where the velocities have the following signs $(+, -, +)$ or in Ω_6 with the signs $(+, -, -)$. Without loss of generality, assume that a solution starts in $W^s(A)$ in Ω_5. It follows sign $\frac{\dot{y}}{\dot{x}} = -1$ and sign $\frac{\dot{z}}{\dot{x}} = +1$. That is both y and z can be locally written as functions $h(x)$ and $g(x)$ respectively. Notice that $\frac{dy}{dx} = \frac{2ax+3bx^2-y}{-ax-2bx^2+3z^5}$ and $\frac{dz}{dx} = \frac{y-5z^5-cz}{-ax-2bx^2+3z^5}$. Any point in $W^s(A)$ except for A is at a positive Euclidean distance from any of the nullclines. Therefore, the denominator of both $\frac{dy}{dx}$ and $\frac{dz}{dx}$ is bounded away from zero. In reality, this denominator is bounded by $2z^5$ for z large enough (i.e., $|-ax - 2bx^2| < |z^5|$ for z large enough). Then as x decreases over that side of $W^s(A)$, both $y = h(x)$ and $z = g(x)$ must intersect the $y - z$ plane. By analogy, it follows that $W^s(A)$ intersects the $x - z$ plane and the $x - y$ plane. Hence it is bounded in $\mathbb{R}^3_{\geq 0}$. The result holds for any existing invariant two-dimensional manifold belonging to $\overline{\Omega}$ for the given model. In particular, it holds for $\tilde{W}^s(A)$. $\square$

Proposition 27 *The directed graph $\Gamma(A)$ of a matrix $A \in M_n(\mathbb{R})$ is strongly connected if and only if A is irreducible.*

(see [58],[12]) We call a system $\dot{x} = f(x)$ irreducible in an open set $D \subset \mathbb{R}^n$ whenever its Jacobian matrix $Df(x)$ is an irreducible matrix for all $x \in D$.

Proposition 28 *Let $\dot{x} = f(x)$ be cooperative and irreducible over a p-convex domain $\Omega \subset \mathbb{R}^n$ then it generates a strongly monotone positive semi-flow in D when the latter is defined.*

Consider the Jacobian matrix of System (4.1-4.3)

$$Df(x) = \begin{pmatrix} -a - 4bx & 0 & 15z^4 \\ 2a + 6bx & -1 & 0 \\ 0 & 1 & -25z^4 - c \end{pmatrix} \tag{4.42}$$

The matrix has all its non-diagonal entries positive for $(x, y, z) \in \Upsilon = \left\{(x, y, z) \in \mathbb{R}^3_{\geq 0} \mid z \neq 0\right\}$ for both cases when $b = 0$ or when $b > 0$. The digraph of $Df(x)$ over Υ with vertices $1, 2$ and 3 corresponding to the vertices v_1, v_2 and v_3 respectively:

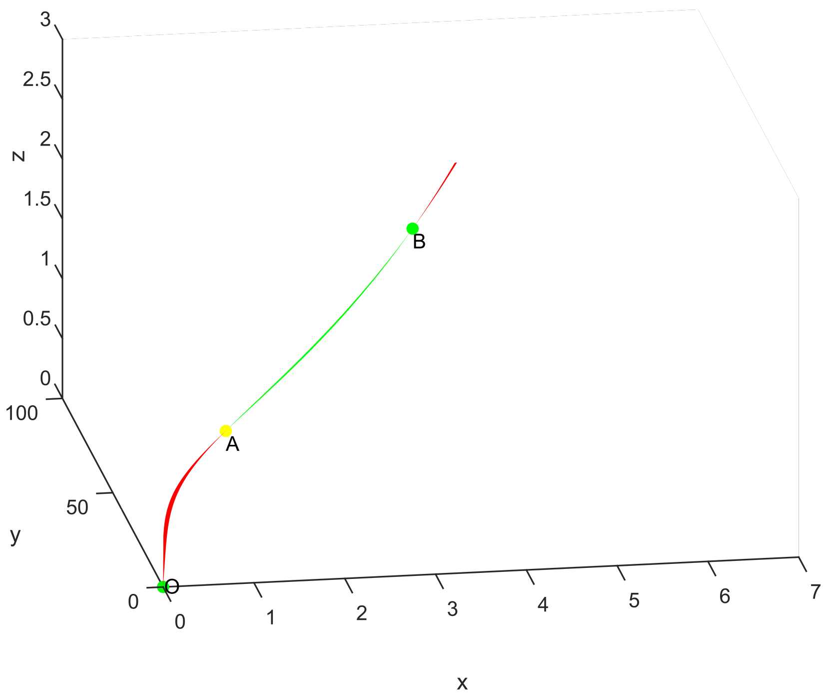
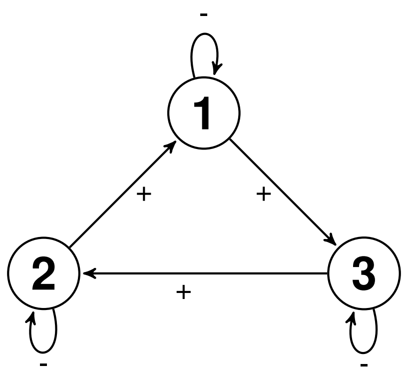


Figure 4.2: The equilibria are shown in the figure. In green, O designates the stable equilibrium at $(0, 0, 0)$ and B is another stable equilibrium. Drawn in yellow in between is the unstable equilibrium A. In green is the set Π_2, while in red are the two connected components of Π_1



Proposition 29 *System (4.1-4.3) is strongly monotone over* $\Upsilon = \{(x, y, z) \in \mathbb{R}_{\geq 0} \mid z \neq 0\}$.

Proof: We notice that $\frac{\partial f_i}{\partial x_j} \geq 0,\ i \neq j$, hence System (4.1-4.3) is cooperative. In addition, the digraph of the Jacobian matrix $Df(x)$ is strongly connected over Υ, it is then irreducible over this set. Besides the fact that Υ is p-convex, it follows from Proposition 28 that System (4.1-4.3) is strongly monotone over Υ. If we consider a point $(x, y, 0) \in \mathbb{R}^3_{\geq 0}$ then $\dot{z}|_{(x,y,0)} = y \geq 0$. Therefore, for any solution starting at $(x, y, 0) \in \mathbb{R}^3_{\geq 0}$, the solution leaves this set and enters Υ in a finite time. $\square$

We can now recollect the definition $\tilde{W}^s(A) = \overline{B(O)} \cap \overline{B(B)}$ and check Theorem 3. After establishing the fact that (4.1-4.3) is strongly monotone, which is stronger than the property strongly order preserving, we state the fact that any point in $\operatorname{int} \mathbb{R}^3_{\geq 0}$ can be approximated from below and above. Knowing that any solution starting at the boundary $\partial\mathbb{R}^3_{\geq 0} \backslash \{O\}$ leaves it instantly toward the interior and knowing also that O itself is a stable steady state, we can easily see based on the mentioned theorem that $\mathbb{R}^3_{\geq 0} = \operatorname{int} Q \cup \overline{\operatorname{int} C}$. That is, the interiors of quasiconvergent points and convergent points are dense in $\mathbb{R}^3_{\geq 0}$. The equilibrium A being the unstable steady state with a two-dimensional unstable manifold splitting a dense subset of $B(B)$ from a dense subset of $B(O)$ and whose stable manifold is nowhere dense in $\mathbb{R}^3_{\geq 0}$, must lie eventually on the boundary of their closures. Therefore, $\tilde{W}^s(A)$ is indeed the geometric extension of $W^s(A)$ especially that the former describes by its definition a Lipschitz two-dimensional manifold. This will be shown later. Notice that the set of quasiconvergent points is the set of all points $x \in \mathbb{R}^3_{\geq 0}$, whose $\omega(x)$ contains more than one point. In general, $\omega(x)$ is not simply $\lim\limits_{t\to\infty} \phi_t x$ since it is not guaranteed that this limit exists. It might be the case that for two different time sequences $\{t_n\}_n$ and $\{t'_n\}_n$, $\lim\limits_{n\to\infty} \phi_{t_n} x \neq \lim\limits_{n\to\infty} \phi_{t'_n} x$. This is not the case in Hahn's model. By the total order of the set of equilibria $E = \{O, A, B\}$ with $O < A < B$, it is true, based on Non-ordering of Limit Sets in Theorem 1, that $Q = C$. Hence, in reality $\mathbb{R}^3_{\geq 0} = \overline{\operatorname{int} C}$. Next, we illustrate this order of equilibria $O < A < B$, which we have shown already in Proposition 24, by using trichotomy (Theorem 4).

Proposition 30 *All equilibria of System (4.1-4.3) are partially ordered (i.e., $O < A < B$).*

Proof: It is obvious that $A > 0$ and $B > 0$. Consider now the interval $[O, B]$ and suppose that $A \notin [O, B]$, it follows then by trichotomy (Theorem 4) that for all $x \in]O, B[$, either $\phi_t x \xrightarrow[t\to\infty]{} O$ or $\phi_t x \xrightarrow[t\to\infty]{} B$. In both cases, one of the equilibria is unstable, which contradicts the fact that both O and B are asymptotically stable. Hence, $A \in [O, B]$. $\square$

Proposition 31 *The following sets are positively invariant:*

$$S_L^A := \left\{x \in \mathbb{R}^3_{\geq 0} \mid x \leq A\right\} = [O, A] \tag{4.43}$$
$$S_U^A = \left\{x \in \mathbb{R}^3_{\geq 0} \mid x \geq A\right\} = [A, \infty[\tag{4.44}$$
$$S_L^B := \left\{x \in \mathbb{R}^3_{\geq 0} \mid x \leq B\right\} = [O, B] \tag{4.45}$$
$$S_U^B = \left\{x \in \mathbb{R}^3_{\geq 0} \mid x \geq B\right\} = [B, \infty[\tag{4.46}$$
$$[A, B] = S_U^A \cap S_L^B \tag{4.47}$$

Moreover,

$$\begin{aligned} \phi_t x &\xrightarrow[t\to\infty]{} O \quad \forall x \in [O, A[\\ \phi_t x &\xrightarrow[t\to\infty]{} B \quad \forall x \in]A, B] \\ \phi_t x &\xrightarrow[t\to\infty]{} B \quad \forall x \in [B, \infty[\end{aligned}$$

Proof: By dichotomy from Theorem 1, the results follow:

$$\begin{aligned} \forall x \in S_L^A,\ x \leq A &\implies w(x) \leq w(A) = A \\ \forall x \in S_U^A,\ x \geq A &\implies w(x) \geq w(A) = A \\ \forall x \in S_L^B,\ x \leq B &\implies w(x) \leq w(B) = B \\ \forall x \in S_U^B,\ x \geq B &\implies w(x) \geq w(B) = B \end{aligned}$$

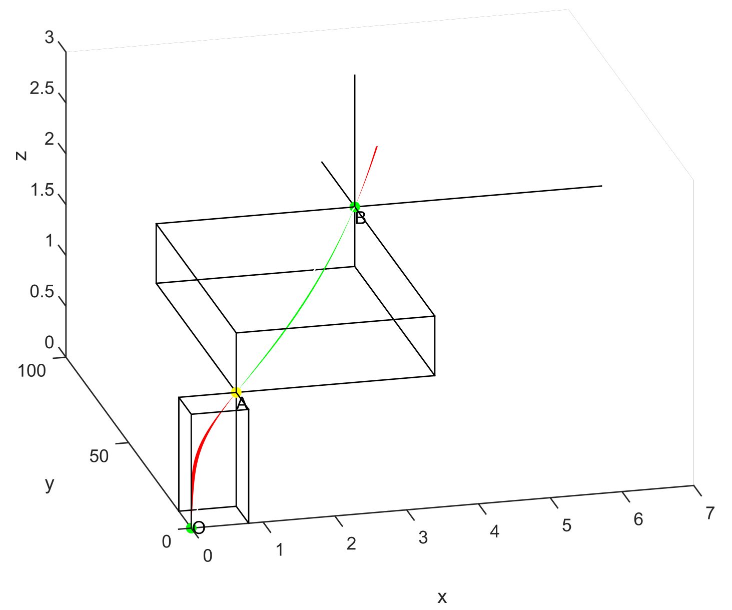


Figure 4.3: The dynamics in the box with verticies O and A are well-known. All points except A converge to O. Similarly, all solutions starting in the box with verticies A and B converge to B except for A. All solutions starting in non-negative orthant centered at B converge to B

This implies then that the mentioned sets are positively invariant. $\forall x \in [O, A], \nexists e \in [O, A]$ such that $e \in E$. It follows then by trichotomy from Theorem 4 that at any $x \in]O, A[$ either $\phi_t x \xrightarrow[t\to\infty]{} O$ or $\phi_t x \xrightarrow[t\to\infty]{} A$. However, O is asymptotically stable whereas A is unstable, hence $\phi_t x \xrightarrow[t\to\infty]{} O$, $\forall x \in]O, A[$. By a similar argument, we conclude that $\forall x \in]A, B[$, $\phi_t x \xrightarrow[t\to\infty]{} B$.
The set $[B, \infty[$ is positively invariant under the flow of System (4.1-4.3). Therefore, if we translate B to the origin, it follows that B is the unique equilibrium in the non-negative orthant $\mathbb{R}^3_{\geq 0}$ and by boundedness of orbits at any $x \in \mathbb{R}^3_{\geq 0}$ follows the asymptotic stability of B in $\mathbb{R}^3_{\geq 0}$ (see *Theorem 3.1 p.18 in [96]*). The sets are illustrated in Figure 4.3. $\square$

Proposition 32 *Let $\Psi := \{x \in \mathbb{R}_{\geq 0} \mid x \not\leq A, x \not\geq A\}$ denoting the set of incomparable points to A in $\mathbb{R}^3_{\geq 0}$. Suppose the model admits a periodic orbit P then $P \in \Psi \cap [0, B]$.*

Proof: Suppose for some $p \in P$ the inequality $X_p = (x_p, y_p, z_p) \leq X_A = (x_A, y_A, z_A)$ holds. By strong monotonicity, we have :

$$\phi_t(X_p) \ll \phi_t(X_A) = X_A,\ \forall t > t_\circ \implies w(X_p) \leq w(X_A) = X_A$$

Hence, all points of the periodic orbit P are less than A. Therefore, $P \in [0, A]$, which is false since $[O, A[$ belongs to the basin of attraction of O. By a similar argument, we conclude that $X_p \not\geq X_B = (x_B, y_B, z_B)$ since $[B, \infty[$ belongs to the basin of attraction of B.
Suppose now that $\forall p \in P,\ \ X_p \not\leq B$. That is, all points of the periodic orbit are incomparable with B. However, P is a bounded set of points then $\exists M \in [B, \infty[$ such that $X_p < X_M$ for some $p \in P$. By dichotomy (Theorem 1) and the unidirectional flow in $[B, \infty[$, we conclude: $\omega(X_p) \leq \omega(X_M) = X_B$ a contradiction.
Therefore, $\forall p \in P,\ \ X_p < X_B$. Now if we suppose $X_p > X_A$ for some $p \in P$, we get that

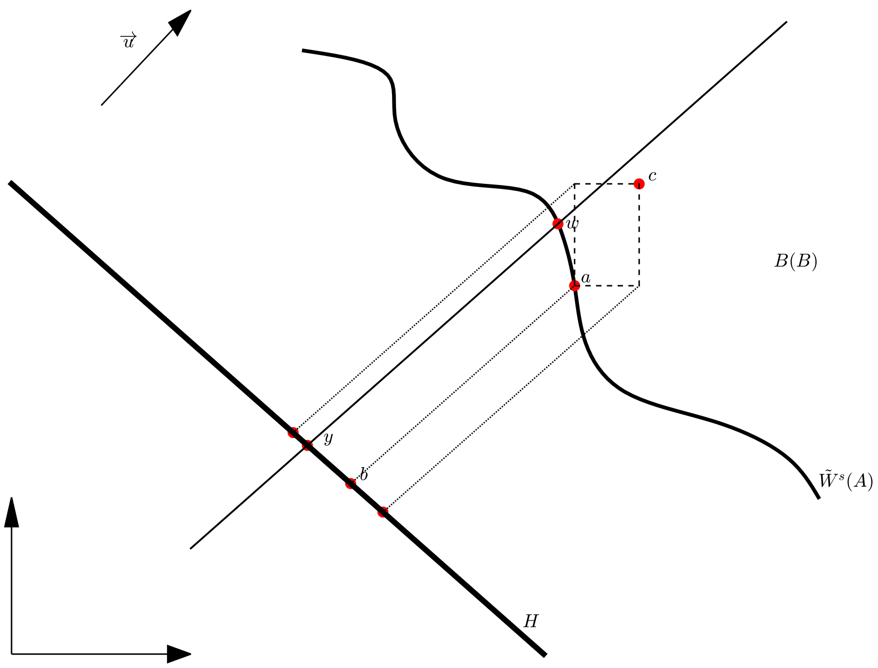


Figure 4.4: The construction shows that the projection into the hyperplane H defines a homeomorphism

$P \in [A, B]$, whereas in $[A, B]$ by trichotomy from Theorem 4, the solution at any $x \in]A, B]$ converges to B (i.e., a contradiction). Therefore, $P \in \Psi \cap [O, B]$. $\square$

Definition 4.3.1 *A set S is called balanced if no two distinct points of S are related.*

We mimic here a proof by Morris Hirsch in [54].

Proposition 33 *$W^s(A)$ (or rather its extension $\tilde{W}^s(A)$) is balanced.*

Proof: Suppose two points of $W^s(A)$, X and Y are related by $X < Y$. Recall that $W^s(A)$ lies on the boundary of the basin of attraction of the equilibrium B (i.e., $W^s(A) \subset \partial B(B)$). This is because of the density of convergent points in $\mathbb{R}^3_{\geq 0}$ as it is clear by Theorem 3 for Hahn's model. Especially convergent points to O or B form a dense set in $\mathbb{R}^3_{\geq 0}$. Therefore, there are sequences $\{x_n\}_n$ and $\{y_n\}_n$, both in $B(B)$, such that $x_n \underset{n\to\infty}{\to} X$ and $y_n \underset{n\to\infty}{\to} Y$. For n large enough, there is $n_\circ$ such that $x_{n_\circ} < X_0 < y_{n_\circ}$ for some $X_0 \in W^s(A)$ such that $X \leq X_0 \leq Y$. For solutions starting at $x_{n_\circ}$, X_0 and $y_{n_\circ}$ respectively, we have $\phi_t x_{n_\circ} \ll \phi_t X_0 \ll \phi_t y_{n_\circ}$ for all $t > 0$, implied by strong monotonicity. However, $\phi_t x_{n_\circ} \underset{t\to\infty}{\to} B$ and $\phi_t y_{n_\circ} \underset{t\to\infty}{\to} B$ and then $\phi_t X_0 \underset{t\to\infty}{\to} B$, which is false since $X_0 \in W^s(A)$. Therefore, no two points on $W^s(A)$ are related. $\square$

Proposition 34 *$\tilde{W}^s(A)$ defines a Lipschitz manifold in $\mathbb{R}^3_{\geq 0}$.*

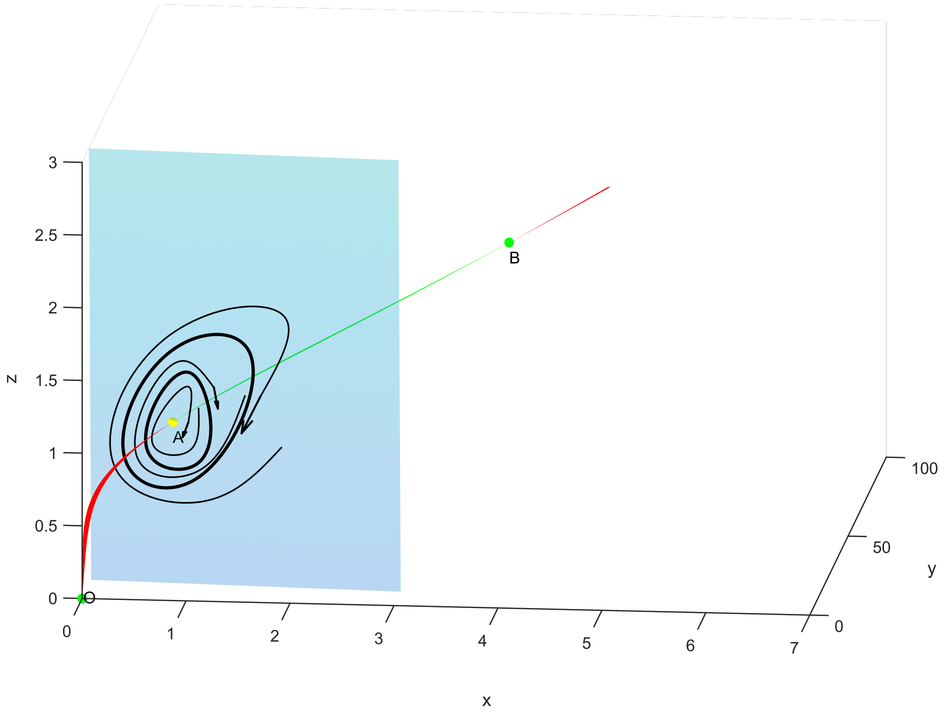


Figure 4.5: The unstable equilibrium A possesses a two-dimensional stable manifold seen in cayenne. Periodic orbits, if they exist, exist evenly on $\tilde{W}^s(A)$

Proof: We will use the unrelatedness of $\tilde{W}^s(A)$ proved in Proposition 33 to show that it is homeomorphic to a two-dimensional manifold. Moreover, the homeomorphism is Lipschitz. It follows from this that $\tilde{W}^s(A)$ defines a two-dimensional Lipschitz manifold in $\mathbb{R}^3_{\geq 0}$. Here, we mimic a construction by Hirsch [54] in a rather variant situation. Let us denote by $P_H : \mathbb{R}^3 \to H$ the orthogonal projection into hyperplane H. That is, $H \subset \mathbb{R}^3$ is the orthogonal hyperplane of some vector $\overrightarrow{u} > 0$. We want to show that $g = P_H|_{\tilde{W}^s(A)}$ is a homeomorphism onto an open subset of H.

We prove first that g is a bijection. Evidently, g is a surjection from $\tilde{W}^s(A)$ onto its image. It suffices to show that g is injective. Suppose $s, r \in \tilde{W}^s(A)$ with $g(s) = g(r)$. By definition of the projection, there exists $\alpha, \beta > 0$ such that $g(s) = s - \alpha\overrightarrow{u}$ and $g(r) = r - \beta\overrightarrow{u}$. It follows that $s = r + (\alpha - \beta)\overrightarrow{u}$. However, $\overrightarrow{u} > 0$ and then it follows that s and r are ordered to each other, which contradicts the balanced property proved in Proposition 33. Hence, g is injective and then bijective.

We show now that the image of g is open. Suppose for instance that $g(a) = b$. Choose $c \gg a$ then $P_H(]a, c[)$ forms a neighborhood around b. This is shown for the two-dimensional case in Figure 4.4. Now let $y \in P_H(]a, c[)$ and consider the line parallel to $\overrightarrow{u}$ through y and let us denote it by L_y. This line meets $]a, c[$ because of the way it is defined. The intersection of L_y with $\overline{B(B)}$ has a greater lower bound w, which lies eventually on $\tilde{W}^s(A)$. Hence $y = g(w)$ and then $g(N_\varepsilon(a)) = N_{\varepsilon'}(b)$ and the map is open. Hence, g^{-1} is continuous. Additionally, g is continuous by construction.

We conclude then that g is a homeomorphism. g has a Lipschitz constant 1 since it is just the restriction of the orthogonal projection P_H. We could also show that g^{-1} has a Lipschitz constant $1 + \mu$ for some $\mu > 0$ (see Proposition 2.6 in [54]). Hence g is a Lipschitz homeomorphism. The conclusion follows. $\square$

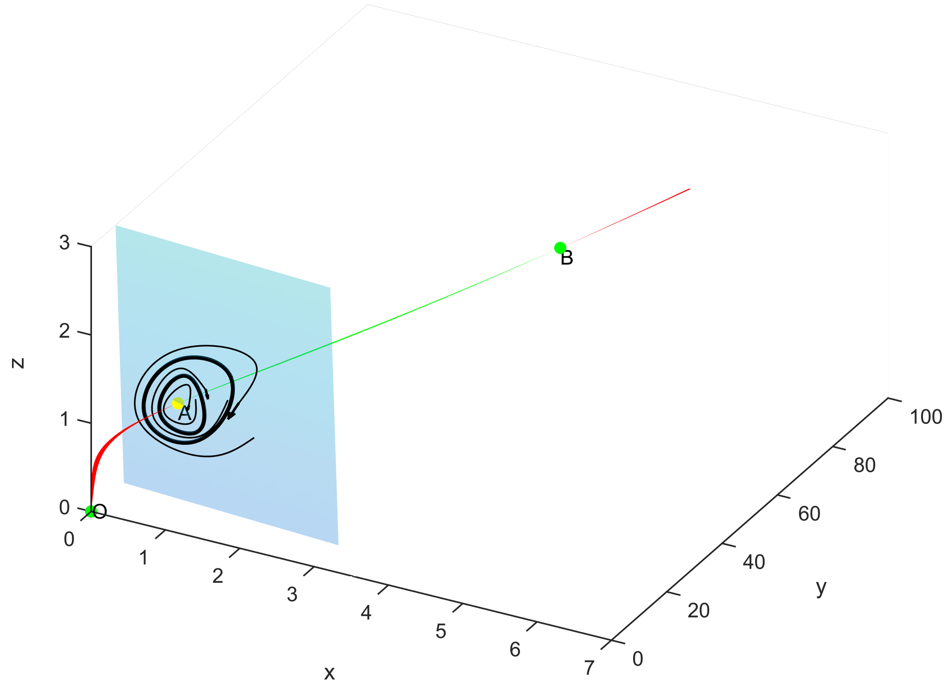


Figure 4.6: The stable manifold of A with the possible periodic orbits seen from different angle

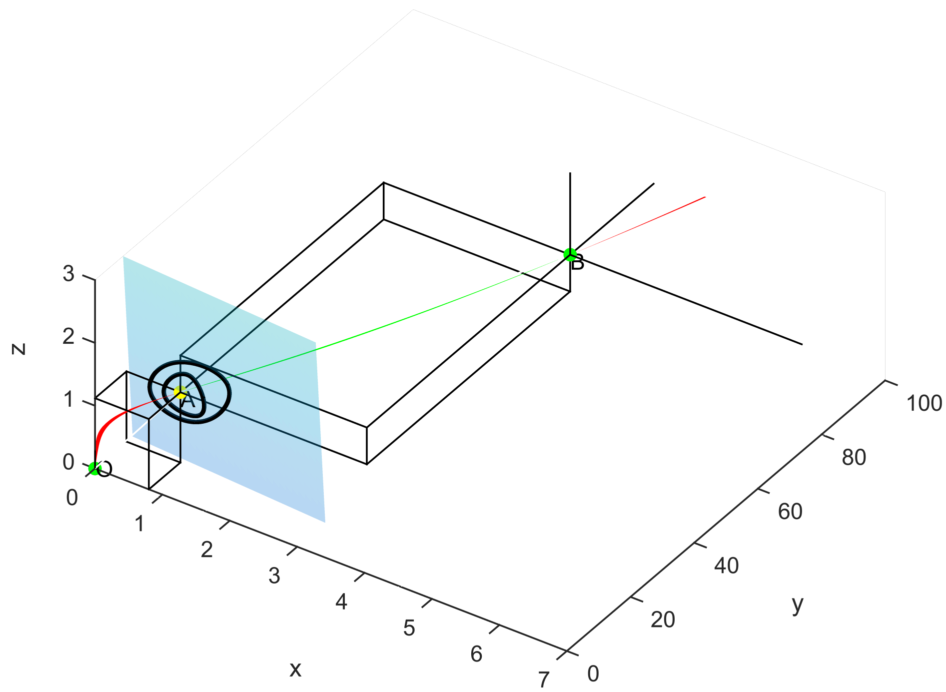


Figure 4.7: The stable manifold of A does not intersect any of the neighboring boxes except at A itself

Proposition 35 *There lies maximally an even number of periodic orbits counting multiplicity on $\tilde{W}^s(A)$ and the existence of a periodic orbit in $\tilde{W}^{s^\complement}(A)$ implies the existence of another periodic orbit on $\tilde{W}^s(A)$.*

Proof: We refer to *Theorem 4.1* in [52]. Under the assumption of cooperativity, no compact limit set of a cooperative or competitive system can be an annulus of closed orbits. Let Q_A^+ and Q_A^- represent respectively the non-negative and non-positive orthants centered at A. Suppose that a periodic orbit γ exists above the extension $\tilde{W}^s(A) \setminus W^s(A)$, it belongs to $\tilde{\Omega} := \Omega \cap Q_A^{+^\complement} \cap Q_A^{-^\complement}$. This is equivalent to saying: There exists $p \in \gamma$ and $q \in \tilde{W}^s(A)$ such that $q < p$. By strong monotonicity follows that $\phi_t q \ll \phi_t p$, $\forall t \geq 0$. Because $q \in \tilde{W}^s(A) \setminus W^s(A)$ and $O(q)$ is bounded, $\omega(q) \in \tilde{W}^s(A) \setminus W^s(A)$. The generalized Poincaré-Bendixson Theorem can be applied. It's application for two-dimensional manifolds is conditioned by the applicability of Jordan Curve Theorem (see [48], p. 182), which is valid for the Lipschitz two-dimensional manifold $\tilde{W}^s(A)$. The theorem guarantees that an $\omega-$limit set on a two-dimensional Lipschitz manifold is a periodic orbit, a homoclinic or heteroclinic connection of equilibria, or an equilibrium. By definition, no equilibria are in $\tilde{W}^s(A) \setminus W^s(A)$, then any $\omega(q) \in \tilde{W}^s(A) \setminus W^s(A)$ must be eventually a periodic orbit. Hence, $\omega(q)$ is a periodic orbit. If we call it ι, then $\iota \ll \gamma$. Now choose any point $x \in \tilde{\Omega}$ such that $q \ll x \ll p$ with $q \in \iota$ and $p \in \gamma$. Then $\phi_t q \ll \phi_t x \ll \phi_t p$ for all $t \geq 0$. Hence, $\omega(x)$ is then either a periodic orbit since all equilibria are identified and $E = \{O, A, B\}$, or $\omega(x) \in \{\iota, \gamma\}$. In the latter case, solutions spiral from either ι or γ toward the other periodic orbit. Hence, there are two possibilities: Either a cylinder of periodic orbits or spiraling solutions bounded from below by ι and from above by γ. The important consequence is that in both cases, a periodic orbit $\iota \in \tilde{W}^s(A)$ is implied. Analogously, a periodic orbit existing below $\tilde{W}^s(A)$ implies the existence of periodic orbit above it in $\tilde{W}^s(A)$.
That any periodic orbit of the model does not lie directly above or below $W^s(A)$ is clear by the limit set dichotomy from Theorem 1. Let's look at this in a little more detail: Suppose there is a periodic orbit γ disjoint from $W^s(A)$, roughly saying above $W^s(A)$ then: $\exists p \in \gamma$ and $\exists q \in W^s(A)$ such that $q < p \implies A = \omega(q) < \omega(p) = \gamma$ and then implies that A is comparable to every point in γ, which is false. Actually, no point in γ is comparable to A (Proposition 32). This establishes that periodic orbits if they exist, are to be traced on an extension of $W^s(A)$. There is a generalization of this feature in *Theorem 6.1* in [103].
Suppose the existence of exactly one periodic orbit on $\tilde{W}^s(A)$ and call it ι. ι revolves around A over $W^s(A)$. ι splits the extension of $W^s(A)$ into two subsets: inner and outer. The inner set is defined by $W^s(A)$ is the only set of initial data which converges to A in forward time. The outer part is the intersection of closures of all basins of attraction of O, A and B. All solutions starting in the outer part converge to ι at a later time and all solutions starting in the inner part converges to A at a later time. Thus, ι is semi-stable over the extension of $W^s(A)$. Hence one of its eigenvalues (Floquet multiplier) is exactly one. ι occurs then for some parameters' values, when two periodic orbits undergo a saddle-node bifurcation. Hence, two periodic orbits exist generically revolving around A. If we assume the existence of an odd number of periodic orbits, analogous to the case above, one of the periodic orbits is semi-stable with respect to $\tilde{W}^s(A)$. All existing subsequent periodic orbits must have a periodic-to-periodic connection between each other since a direct connection to A is impossible as the stable manifold $W^s(A)$ is two-dimensional. The proof is complete. □

Theorem 9 Busenberg and van den Driessche

Let $f : \mathbb{R}^3 \longmapsto \mathbb{R}^3$ be a Lipschitz vector field and let $\gamma(t)$ be a closed piecewise C^1 curve bounding an orientable C^1 surface $S \subset \mathbb{R}^3$ with unit normal vector $\vec{n}$. If there is a vector field $g : \mathbb{R}^3 \longmapsto \mathbb{R}^3$, defined and C^1 in a neighborhood of S such that:

i) $g \cdot f \leq 0 \quad (\geq 0)$ *on* γ,

ii) $(curl\ g) \cdot \vec{n} \geq 0 \quad (\leq 0)$ *on* S,

iii) either $g \cdot f \not\equiv 0$ *on* γ *or* $(curl g) \cdot \vec{n} \not\equiv 0$ *on* S,

then $\gamma(t)$ is not a cycle of $\dot{x} = f(x)$ traversed in the positive direction with respect to $\vec{n}$.

(see [13])

Proposition 36 *System (4.1-4.3) with $m > m_0$ does not admit a periodic orbit.*

Proof: Theorem 9 can be fairly applied to Lipschitz manifolds since the proof in [13] depends on Stoke's Theorem, which applies eventually to Lipschitz manifolds. This is then a direct generalization which follows from the fact the Lipschitz functions are almost everywhere differentiable. Consider $\tilde{W}^s(A)$, which is a compact Lipschitz orientable manifold (see Proposition 34) and suppose that $\tilde{W}^s(A)$ has a normal vector $\vec{n} = (n_1, n_2, n_3)$ with negative and positive components simultaneously.
Without loss of generality, let $n_1 > 0, \quad n_2, n_3 < 0$. The vector $\vec{\tau} = (n_2 + n_3, -n_1, -n_1)$ is perpendicular to $\vec{n}$:

$$\vec{\tau} \cdot \vec{n} = (n_2 + n_3, -n_1, -n_1) \cdot (n_1, n_2, n_3) = 0$$

However, $\vec{\tau} < 0$ and $\vec{\tau} \in T_p$ for some $p \in \tilde{W}^s(A)$, where T_p denotes the tangent space of $\tilde{W}^s(A)$ at some point $p \in \tilde{W}^s(A)$. Hence, $\exists x, y \in \tilde{W}^s(A)$ such that $x < y$, which is false because $\tilde{W}^s(A)$ is balanced by Proposition 35. Therefore, depending on the orientation of $\tilde{W}^s(A)$, only positive or negative normal vector $\vec{n}$ of $\tilde{W}^s(A)$ exists.
Introduce the function $g : \mathbb{R}^3 \longmapsto \mathbb{R}^3$ defined by $g(X) = f(X) \times v(X)$, where :

$$v(X) = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Assume that $\vec{n} > 0$. The first condition of Busenberg's Theorem is evident as $g \cdot f \equiv 0$. Moreover,

$$\text{curl } g(X) = \begin{pmatrix} 1 + c + 15z^4 + 25z^4 \\ 3a + c + 10bx + 25z^4 \\ 2 + a + 4bx \end{pmatrix}$$

which implies that $(\text{curl } g) \cdot \vec{n} > 0$ on $\tilde{W}^s(A)$ and thus no periodic orbit lies on $\tilde{W}^s(A)$. In Proposition 35, a periodic orbit of System (4.1-4.3) implies the existence of a periodic orbit over $\tilde{W}^s(A)$. Hence, the model admits no periodic orbit. Here ends the proof. □
Since the fact is interesting by itself, we prove here that the neighboring surface on which the assumed periodic orbit γ lies is indeed C^1 smooth hence fulfilling the exact requirements of Busenberg's theorem. A 3×3 non-singular matrix satisfying the system $\phi'(t, x) =$

$Df(x)\phi(t,x)$ with $Df(x)$ being the Jacobian matrix of Hahn's model is called a fundamental matrix solution of System (4.1-4.2) (see [79]). Since System (4.1-4.2) is autonomous, this matrix is given by $H(t,x) = \exp(Df(x)t)$. This matrix characterizes the derivative of the Poincaré map at a point $x_0 \in \gamma$ by the following identity $\|DP(x_0)\| = \|H(T,x_0)\|$ with T the period of γ and $\|\cdot\|$ denoting the determinant. We have $\|H(T,x_0)\| = \exp(\sum_{i=1}^{3} \lambda_i T) = \exp(\text{Trace}(Df(x_0))T)$ with λ_is the eigenvalues of $Df(x_0)$. However, $\text{Trace}(Df(x)) < 0, \forall (x,y,z) \in \mathbb{R}^3_{\geq 0}$. Hence, $\|DP(x_0)\| < 1$ and then at least one of the characteristic multipliers of $\gamma(t)$ is less than one. This property guarantees that any periodic orbit γ of Hahn's model possesses a two-dimensional C^1 surface of solutions converging to it in forward time (Theorem 11.2, p. 255 in [48], see also [94]).

Proposition 37 *A solution of (4.1-4.3) with $m > m_0$ belongs to one of the following:*

i) It starts below $W^s(A)$ and converges then to O.

ii) It starts above $W^s(A)$ and converges then to B.

iii) It starts on $W^s(A)$ and converges then to A.

Proof: The result is an outcome of the combination of Propositions 31, 32 and 36. Solutions starting in $]O,A[$ converge to O, while solutions starting in $]A,B[$ and $]B,+\infty[$ converge to B. A solution starting at x with $x \nleq B$ and $x \ngeq B$ (i.e., at an incomparable point with B) is bounded from above by some $q \in]B,+\infty[$. It follows then by strong monotonicity that $\omega(x) \leq B$. Hence, at some time $t_1 > 0$, the solution enters $[O,B]$. The solution will be then above $\tilde{W}^s(A)$ at some future time. All non-trivial limit sets[1] above or below $\tilde{W}^s(A)$, including periodic orbits, are projected into non-trivial limit sets over $\tilde{W}^s(A)$ as shown in Proposition 35. $\tilde{W}^s(A)$ is a two-dimensional Lipschitz manifold, on which the generalized Poincaré-Bendixson Theorem can be applied since Jordan Curve Theorem is applicable on $\tilde{W}^s(A)$. The theorem guarantees that an $\omega-$limit set of an orbit on $\tilde{W}^s(A)$ is either (1) a periodic orbit, (2) a homoclinic or heteroclinic connection of equilibria or (3) an equilibrium. There are no equilibria except A on $\tilde{W}^s(A)$. Hence, heteroclinic connection is not an option. Moreover, A is asymptotically stable on its stable manifold $W^s(A)$. Hence, no homoclinic connection is possible. (1) is precluded in Proposition 36. Hence, the $\omega-$limit set of any solution on $\tilde{W}^s(A)$ is eventually the equilibrium A. That is, $\tilde{W}^s(A) = W^s(A)$. It follows that all solutions converge to equilibria. For solutions starting above $W^s(A)$, it must be then that $\omega(x) = B$. Similarly, for solutions starting below $W^s(A)$, they converge to O. □

In reality, Proposition 37 explains the meaning of Theorem 4. While the proof of Theorem 4 considers a general projection to a hyperplane perpendicular to a radial vector, the proof of Proposition 37 considers a projection of non-trivial dynamics into $\tilde{W}^s(A)$ by a radial positive vector, a normal vector of $\tilde{W}^s(A)$. This projection shows that non-trivial dynamics are projected particularly into periodic orbits. Hence, non-trivial dynamics of a cooperative system in $\mathbb{R}^3$ are equivalent to periodic orbits that do not form an annulus. This is the tenor of Theorem 4. Its proof uses a very significant property of limit sets, namely Non-Ordering of Limit sets mentioned in Theorem 1.

The dynamics in the case when $m < m_\circ$ are given by the next proposition.

[1] we mean by non-trivial limit sets all limit sets that are not equilibria or connections of equilibria.

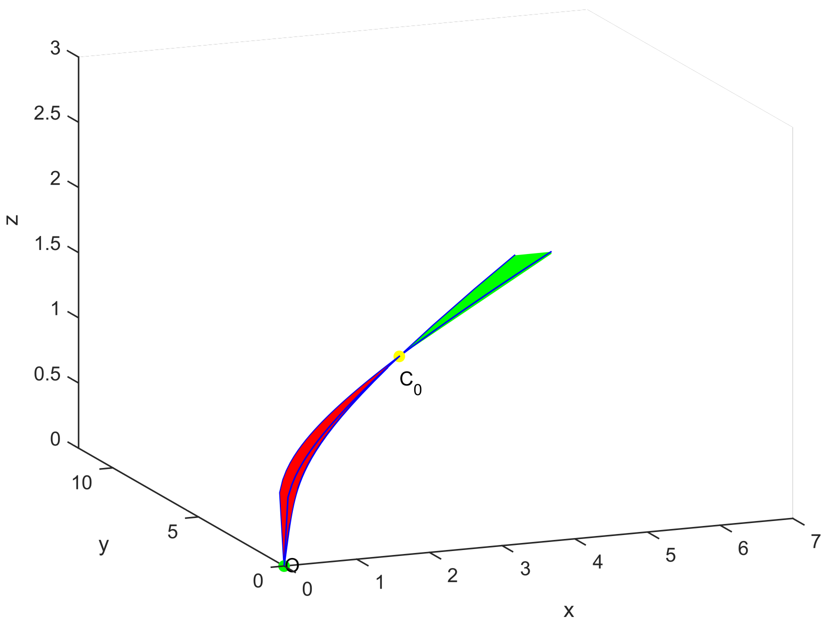


Figure 4.8: The set of non-negative velocities Π_2 is in green. The set of non-positive velocities Π_1 is in red. C_0 is the unique positive equilibrium and it is unstable, whereas O is the stable equilibrium at $(0,0,0)$. The nullclines are apparent in the figure

Proposition 38 *Let $m < m_\circ$ then System (4.1-4.3) admits a single steady state $O(0,0,0)$ in the non-negative orthant $\mathbb{R}^3_{\geq 0}$ and it is globally asymptotically stable.*

Proof: It was already shown in Proposition 24 that for $m < m_\circ$, System (4.1-4.3) admits a single steady state $O(0,0,0)$, which is asymptotically stable. It follows by Theorem 2 that O is globally asymptotically stable in $\mathbb{R}^3_{\geq 0}$. Then all solutions starting in $\mathbb{R}^3_{\geq 0}$ converge to O later in forward time. $\square$

Notice that for $m < m_0$, not all the Ωs or the Πs have a non-empty intersection with $\mathbb{R}^3_{\geq 0}$. At least $\Pi_2 \cap \mathbb{R}^3_{\geq 0} = \varnothing$ since otherwise a solution starting in an arbitrarily small neighborhood of O, leaves it at $t > t_0$ for some $t_0 > 0$. This is false since O is asymptotically stable.

The Model without Photorespiration

We will let $b = 0$ and $a > 0$. It is clear then that the complement of the union of the nullclines has eight components denoted by Ω_i, $1 \leq i \leq 6$ and Π_i, $1 \leq i \leq 2$. Figure 4.8 shows the intersection of the nullclines $N_{1,2}$, $N_{1,3}$ and $N_{2,3}$. While the Ω_is, $1 \leq i \leq 6$ lie in the complement of Π_is, $1 \leq i \leq 2$ and the nullclines; It was already shown by Proposition 14 that a solution entering Π_1 or Π_2 never leaves it except to bounce on the nullclines. In this section, we carry the definition of the extension of the unstable steady state's two-dimensional stable manifold. Since the name of this steady state here is C_0, we call it $\tilde{W}^s(C_0)$. We abuse the notation as in [54] and we treat ∞ as an equilibrium defining the basin of attraction of ∞ by the set of all solutions that diverge (notationally converge) toward infinity later in time. This will be denoted by $B(\infty)$. $\tilde{W}^s(C_0)$ is then defined as the intersection of all solutions starting within the closure of the basins of attraction of O and ∞. Explicitly $\tilde{W}^s(C_0) = \overline{B(O)} \cap \overline{B(\infty)}$.

For $b = 0$, the complement of the nullclines for System (4.1-4.3) is still the union of Ωs and Πs. That is, the intersections of $\Omega_i \cap \mathbb{R}^3_{\geq 0} \neq \varnothing,\ 1 \leq i \leq 6$ and $\Pi_i \cap \mathbb{R}^3_{\geq 0} \neq \varnothing,\ i = 1, 2$.

Proposition 39 $\mathbb{R}^3_{\geq 0} = \overline{\operatorname{int} C}$ *for System (4.1-4.3) with* $b = 0$*.* C *is the set of convergent points, possibly toward infinity. It is given by:*

$$C := \left\{X = (x, y, z) \in \mathbb{R}^3_{\geq 0} \mid \omega(X) \in E = \{O, C_0, \infty = (\infty, \infty, \infty)\}\right\}.$$

Proof: Let $X_0 \in \operatorname{int} \mathbb{R}^3_{\geq 0} \setminus \operatorname{int} Q$. Since the set of all convergent points $C \subset Q$, we have $O(X_0)$ is bounded. By closedness of Q, there must be a sequence $\{Y_n\}_n \in \operatorname{int} \mathbb{R}^3_{\geq 0} \setminus Q$ such that $Y_n \underset{n\to\infty}{\to} X_0$. We assume that for every n, Y_n can be approximated from below. Then, for every n, Y_n is the limit point of a sequence $X^n_m \to Y_n$ with $X^n_m < X^n_{m+1} < Y_n$. However, $O(Y_n), \forall n$ is bounded since $Y_n \notin Q$. Hence, $O(X^n_m), \forall m, n$ is bounded by dichotomy (Theorem 1). By Sequential Limit Set Trichotomy (Theorem 4.1 in [96]), it follows that $\omega(X^n_m) = U_0 < \omega(Y_n), \forall m$. That is, $\{X^n_m\} \in C, \forall m$, particularly $\omega(X^n_m) \in \{O, C_0\}$. Hence $Y_n \in \overline{\operatorname{int} C}, \forall n$. Hence, $X_0 \in \overline{\operatorname{int} C}$. Same argument holds if Y_n is approximated from above except that $\omega(X^n_m)$ might be equal to ∞. Solutions that start on $\partial\mathbb{R}^3_{\geq 0}$ except for O, the persistent stable steady state, leave it immediately toward the interior of $\mathbb{R}^3_{\geq 0}$. Therefore, it suffices considering $X_0 \in \operatorname{int} \mathbb{R}^3_{\geq 0} \setminus \operatorname{int} Q$. □

We conclude from Proposition 39 that $\tilde{W}^s(C_0)$ is a nowhere-dense set in $\mathbb{R}^3_{\geq 0}$. It extends $W^s(C_0)$ in $\mathbb{R}^3_{\geq 0}$ if it defines a two-dimensional sufficiently smooth manifold in $\mathbb{R}^3_{\geq 0}$. We will show later this.

Proposition 40 *i) A solution starting in* $\overline{\Pi}_1 \cap]O, C_0[$ *converges to* O*.*

ii) A solution starting in $\overline{\Pi}_2 \cap]C_0, \infty[$ *diverges toward infinity.*

Proof: Notice that for $b = 0$, each of Π_1 and Π_2 has a single connected component. Moreover, $\Pi_1 \subset [O, C_0]$ and $\Pi_2 \subset [C_0, +\infty[$. Notice also that $O, C_0 \in \overline{\Pi}_1$, profited from Proposition 16. By Proposition 14, a solution starting in $\overline{\Pi}_1$ is positively invariant. Any solution starting there remains bounded for all $t \geq 0$ and it has negative velocities' signs. Hence, by the generalization of Proposition 12 for solutions in $\mathbb{R}^3$ and as $t \to \infty$, all solutions converge into a steady state at the boundary of $\overline{\Pi}_1$. The solution must then converge either to O or to C_0. However, O is asymptotically stable while C_0 is unstable. Hence it converges to O as $t \to \infty$.
Now, consider a solution starting in $\overline{\Pi}_2$, which is positively invariant. Hence, this solution does not leave it for all $t_0 > 0$. Moreover, it has positive velocities' signs. It increases then indefinitely and diverges toward infinity. If we suppose it converges to some limit point S, which is then a steady state, it requires then that $S \gg C_0$. However, no other steady state, other than O and C_0 is identified for System (4.1-4.3) when $b = 0$. Hence, it eventually diverges. □

Proposition 41 *The stable manifold of* C_0 *(respectively its extension* $\tilde{W}^s(C_0)$*) intersects the planes* $x - y$*,* $y - z$ *and* $x - z$*.*

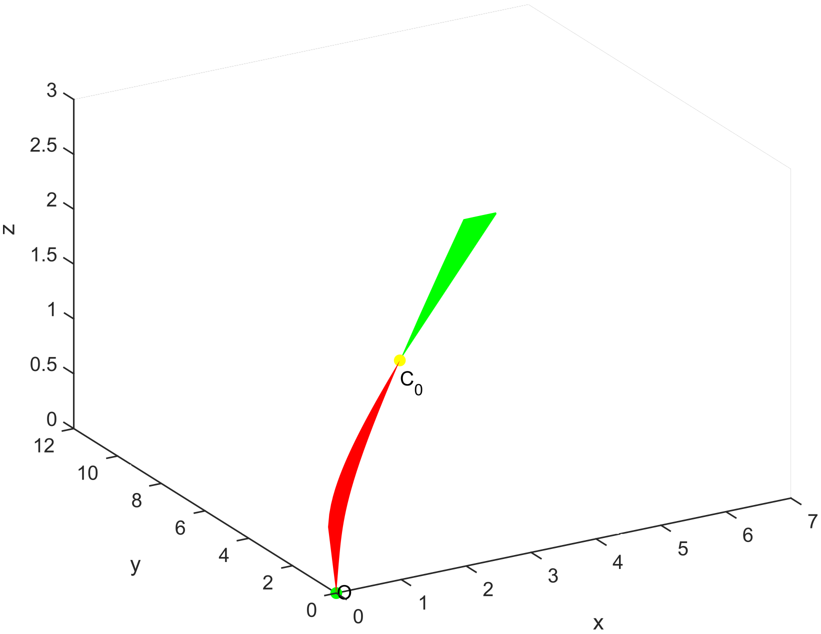


Figure 4.9: The set of non-negative velocities Π_2 is in green. The set of non-positive velocities Π_1 is in red

Proof: Consider System (4.1-4.3) with $b = 0$. Let z be bounded and let $W^s(C_0)$ be having an unbounded branch in the $x - y$ directions. A solution traveling this branch is in Ω_3 or in Ω_4. In both cases, $\frac{dz}{dx}$ and $\frac{dy}{dx}$ are signed and thus bounded away from zero. It could then be concluded that a solution on $W^s(C_0)$ is locally described by $y = h(x)$ and $z = g(x)$. Consider the derivative

$$\frac{d(y+z)}{dx} = \frac{2ax - 5z^5 - cz}{-ax + 3z^5}$$

It has a growth rate equivalent to $\mathcal{O}(-2)$. This implies that x decreases whenever y increases since z is bounded. A contradiction to the assumption that $W^s(C_0)$ has an unbounded branch in x and y directions simultaneously. Now let x be bounded and suppose that $W^s(C_0)$ has an unbounded branch near the $y - z$ plane. The solutions belong then either to Ω_5 with $(+,-,+)$ velocities' signs or to Ω_6 with $(+,-,-)$ velocities' signs. In both cases, $\frac{dz}{dx}$ and $\frac{dy}{dx}$ are signed. Hence y and z can be locally written as functions $h(x)$ and $g(x)$ of x over this branch. Both $\frac{dz}{dx} = \frac{y-5z^5-cz}{-ax+3z^5}$ and $\frac{dy}{dx} = \frac{2ax+3bx^2-y}{-ax+3z^5}$ have the same denominator, which is bounded away from zero since this branch must be at a positive Euclidean distance from C_0, the single intersection point of it with the different nullclines. Hence both $h'(x) = \frac{dy}{dx}$ and $g'(x) = \frac{dz}{dx}$ are bounded from above and then the solution given by the parametrization $(x(t), h(x), g(x))$ must intersect the $y - z$ plane in a finite time. This contradicts our assumption. In an analogous way, no unbounded branch near the $x - z$ plane can exist and then $W^s(C_0)$ or rather its extension are bounded in $\mathbb{R}^3_{\geq 0}$. $\square$

Notice that writing two of the solution components in terms of the third is an outcome of the Implicit Function Theorem.

Proposition 42 *System (4.1-4.3) for $b = 0$ is strongly monotone over $\Upsilon = \{(x, y, z) \in \mathbb{R}_{\geq 0} \mid z \neq 0\}$.*

Proof: We notice that $\frac{\partial f_i}{\partial x_j} \geq 0,\ i \neq j$, hence System (4.1-4.3) is cooperative. In addition, the digraph of the Jacobian matrix $Df(x)$ is strongly connected over Υ and is then irreducible over this set. Besides the fact that Υ is p-convex, it follows from Proposition 28 that System (4.1-4.3) for $b = 0$ is strongly monotone over Υ. If we consider a point $(x, y, 0) \in \mathbb{R}^3_{\geq 0}$, then $\dot{z}|_{(x,y,0)} = y \geq 0$. Therefore, for any solution starting at $(x, y, 0) \in \mathbb{R}^3_{\geq 0}$, the solution leaves this set and enters Υ in a finite time. □

Proposition 43 *The following sets are positively invariant*

$$S_L^{C_0} := \left\{(x,y,z) \in \mathbb{R}^3_{\geq 0} \mid (x,y,z) \leq (x_{C_0}, y_{C_0}, z_{C_0})\right\} = [O, C_0] \quad (4.48)$$
$$S_U^{C_0} := \left\{(x,y,z) \in \mathbb{R}^3_{\geq 0} \mid (x,y,z) \geq (x_{C_0}, y_{C_0}, z_{C_0})\right\} = [C_0, +\infty[\quad (4.49)$$

Proof: $\forall x \in [O, C_0], \nexists e \in]O, C_0[$ such that $e \in E$ (E is the set of equilibria). Therefore it follows by trichotomy (Theorem 4) that any $x \in]O, C_0[$ either converges to O (i.e., $\phi_t x \xrightarrow[t\to\infty]{} O$ or $\phi_t x \xrightarrow[t\to\infty]{} C_0$). Since O is asymptotically stable in $\mathbb{R}^3_{\geq 0}$, it follows that $\phi_t x \xrightarrow[t\to\infty]{} O$. In any case, $\phi_t x \in [O, C_0]$, $\forall t \geq 0$ and then $[O, C_0]$ is positively invariant. Now if $x \in]C_0, +\infty[$ then $x > C_0$ and by strong monotonicity $\phi_t x \gg \phi_t(C_0)$, $\forall t \geq 0$ and then $[C_0, +\infty[$ is positively invaraint. □

Let $Q^+_{C_0}$ and $Q^-_{C_0}$ represent respectively the non-negative and non-positive orthants centered at C_0.

Proposition 44 *A solution starting in $\left(Q^+_{C_0} \cap \Pi_2^\complement\right) \setminus \{C_0\}$ diverges to infinity.*

Proof: Clearly, $\Pi_2 \subset Q^+_{C_0}$ (Proposition 16). Let $p_1 \in \left(Q^+_{C_0} \cap \Pi_2^\complement\right) \setminus \{C_0\}$ with coordinates (x_1, y_1, z_1). Points belonging to Π_2 satisfy the following relation:

$$\begin{gathered} \frac{5}{2a}z^5 + \frac{c}{2a}z < x < \frac{3}{a}z^5 \\ 5z^5 + cz < y < 6z^5. \end{gathered}$$

Therefore, suitably changing z considered as our parameter, $\exists p_2, p_3 \in \Pi_2$ satisfying

$$p_2 < p_1 < p_3.$$

Consequently, due to strong monotonicity of the flow if $\phi_{t_0}(p_i) = p_i \;\; i \in \{1, 2, 3\}$, then:

$$\phi_t(p_2) < \phi_t(p_1) < \phi_t(p_3) \quad \forall t > t_0 \quad (4.50)$$

Suppose $\phi_t(p_1)$ remains in $Q^+_{C_0} \cap \Pi_2^\complement$ for infinity of time. Both $\phi_t(p_2)$ and $\phi_t(p_3)$ approaches (∞, ∞, ∞) as $t \to \infty$, which implies that $\phi_t(p_1) \to (\infty, \infty, \infty)$ as $t \to \infty$. Notice that $\phi_t(p_2) \to \infty$ and $\phi_t(p_3) \to \infty$ as $t \to \infty$. Otherwise, if we assume they converge, we have by strong monotonicity and positive invariance shown in the previous proposition that they must converge into a steady state $S \gg C_0$. However, no steady states other than O and C_0 exist for the system. Hence, they diverge toward infinity.

We do not profit from this implication to know whether the solution enters Π_2 at a later time. It might be the case that a solution starting in $Q^+_{C_0} \cap \Pi_2^\complement$ keeps revolving around Π_2 through all the Ω_i's without entering it in future time. However, if it does, it must then do it after a finite time according to the same analysis done in Section 3.5 of the previous chapter. □

Corollary 9.1 *A periodic orbit of (4.1-4.3), if it exists, lies in $\overline{\Omega}$ and revolves through all the Ω_i's*

Proposition 45 *$W^s(C_0)$ (respectively $\tilde{W}^s(C_0)$) is balanced.*

Proof: Same analysis as in Proposition 33 holds here. The only difference here in comparison with Proposition 33 is that there are two sequences with $\{x_n\}_n$ and $\{y_n\}_n$, both in $B(\infty)$, such that they converge to X and Y respectively with $X, Y \in W^s(C_0)$, $X < Y$. Then $\exists n_0 \in \mathbb{N}$ and X_0 with $X \leq X_0 \leq Y$ such that $x_{n_0} < X_0 < y_{n_0}$. Because of strong monotonicity, $\phi_t x_{n_0} \ll \phi_t X_0 \ll \phi_t y_{n_0}$ for all $t \geq t_0$. However, $\phi_t x_{n_0}, \phi_t y_{n_0} \to (\infty, \infty, \infty)$ as $t \to \infty$ by Proposition 47. Hence, $\phi_t X_0 \to (\infty, \infty, \infty)$ as $t \to \infty$, which contradicts the fact that $X_0 \in W^s(C_0)$. Notice that the extension $\tilde{W}^s(C_0)$ inherits this property from $W^s(C_0)$ by a similar argument. □

Proposition 46 *$\tilde{W}^s(C_0)$ defines a Lipschitz manifold in $\mathbb{R}^3_{\geq 0}$.*

Proof: The proof is identical to that done in Proposition 34 except that we substitute here $B(B)$ by $B(\infty)$. By abuse of notation, $B(\infty)$ defines the basin of attraction of ∞. This is the set of all solutions that diverge toward infinity in forward time. □

Proposition 47 *A periodic orbit of (4.1-4.3), if it exists, implies the existence of a periodic orbit in $\tilde{\Omega} = \Omega \cap Q_{C_0}^{+^{\complement}} \cap Q_{C_0}^{-^{\complement}}$ over $\tilde{W}^s(C_0)$ and any periodic orbit switches between all the Ω_i's.*

Proof: It is clear that $W^s(C_0) \subset \tilde{\Omega}$ since almost all solutions starting outside $\tilde{\Omega}$ either converges to O or diverges to infinity. We present here a proof similar to that of Proposition 35. If we suppose there is a periodic orbit γ disjoint from $W^s(C_0)$, roughly saying above $W^s(C_0)$, then: $\exists p \in \gamma$ and $\exists q \in W^s(C_0)$ such that $q < p$ and $\phi_t(q) \to X_{C_0}$ as $t \to \infty$. It follows by strong monotonicity that $\exists t_0 > 0$ such that $\phi_t(p) > X_{C_0}$ for all $t \geq t_0$ (i.e., $\phi_t(p) \notin \tilde{\Omega}$ for all $t \geq t_0$), but $\omega(p) = \gamma$ then $\gamma \in Q^+_{C_0}$, which is a contradiction.
Now suppose that a periodic orbit γ exists above the extension $\tilde{W}^s(C_0) \backslash W^s(C_0)$, it belongs to $\tilde{\Omega}$. This is equivalent to say: There is $p \in \gamma$ and $q \in \tilde{W}^s(C_0)$ such that $q < p$. By strong monotonicity, it follows that $\phi_t q \ll \phi_t p$, $\forall t \geq 0$. Since $q \in \tilde{W}^s(C_0) \setminus W^s(C_0)$ and $O(q)$ is bounded, it follows that $\omega(q)$ is a periodic orbit. If we call the periodic orbit ι, then $\iota \ll \gamma$. Now choose any point $x \in \tilde{\Omega}$ such that $q \ll x \ll p$ with $q \in \iota$ and $p \in \gamma$. Then $\phi_t q \ll \phi_t x \ll \phi_t p$ for all $t \geq 0$. Hence, $\omega(x)$ is then either a periodic orbit since all equilibria are identified and $E = \{O, C_0\}$, or $\omega(x) \in \{\iota, \gamma\}$. In the latter case, solutions spiral from either ι or γ toward the other periodic orbit. Hence, there exists a cylinder of either periodic orbits or of spiraling solutions bounded from below by ι and from above by γ. The important consequence is that in both cases, a periodic orbit $\iota \in \tilde{W}^s(C_0)$ is implied. In an analogous way, a periodic orbit existing below $\tilde{W}^s(C_0)$ implies the existence of periodic orbit above it in $\tilde{W}^s(A)$. As in Proposition 35, the dynamics over $\tilde{W}^s(C_0)$ allows exclusively the existence of an even number of periodic orbits. □

Proposition 48 *There lies an even number of Periodic orbits over $\tilde{W}^s(C_0)$ counting multiplicity.*

Proof: Same analysis as in Proposition 35 holds here. We see the dynamics in Figures 4.10 and 4.11. □

Proposition 49 *No periodic orbit exists for (4.1-4.3) with $b = 0$.*

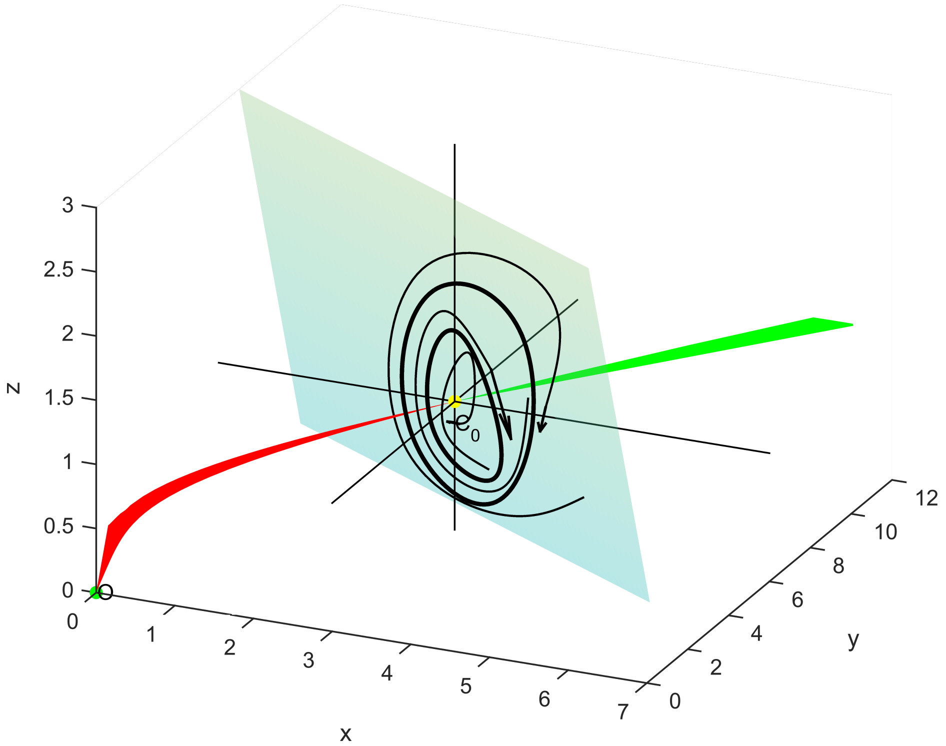


Figure 4.10: For $b = 0$, C_0 possesses a two-dimensional stable manifold which lies in the complement of the negative and positive orthants centered at C_0. There is the possibility of existence of an even number of periodic orbits over this stable manifold

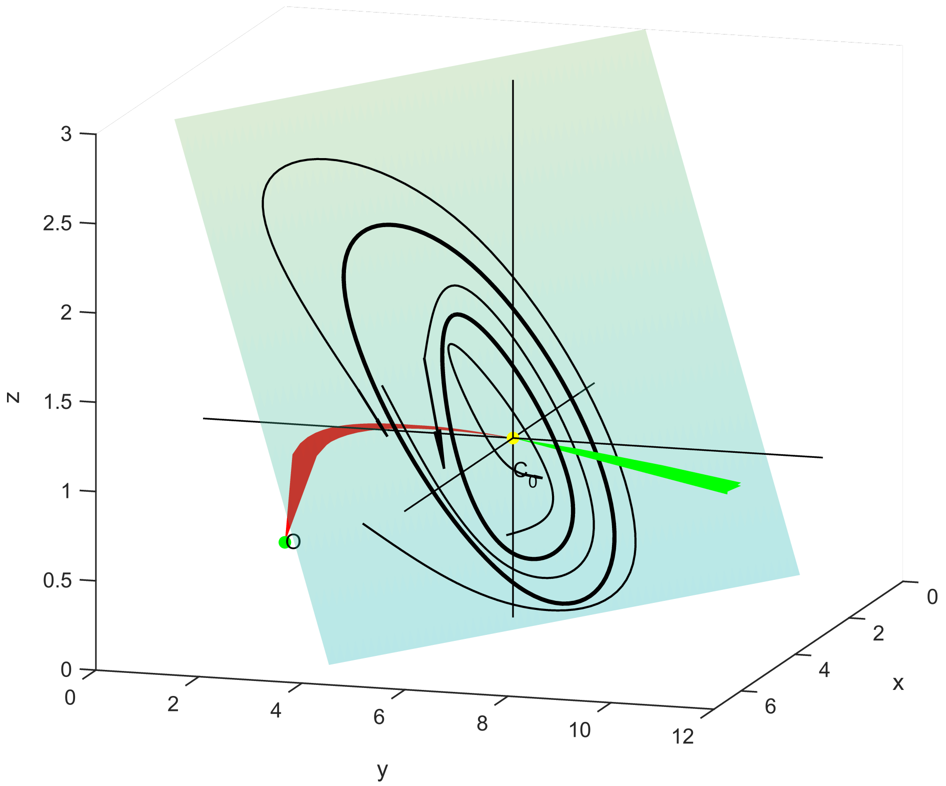


Figure 4.11: The possible periodic orbits over the stable manifold of C_0 seen from a different angle. The dynamics should flow from outside to inside

Proof: The conclusion is just an outcome of the previous Propositions 47, 45, 48 together with Proposition 36. Consider the proof of Proposition 36 and substitute $b = 0$. The same conclusions holds. □

Proposition 50 *A solution of (4.1-4.3) with* $b = 0$ *belongs to one of the following:*

i) It converges to C_0.

ii) It converges to O.

iii) It diverges to infinity.

Proof: There are no non-trivial limit sets for System (4.1-4.3) except periodic orbits (Theorem 4). Periodic orbits above $\tilde{W}^s(C_0)$, if they exist, are projected into periodic orbits on $\tilde{W}^s(C_0)$ as shown in Proposition 47. $\tilde{W}^s(C_0)$ is a two-dimensional Lipschitz manifold, on which the generalized Poincaré-Bendixson Theorem can be applied (see [48], p. 182). Then an $\omega-$limit set on $\tilde{W}^s(C_0)$ is a periodic orbit, a heteroclinic or a homoclinic connection, or an equilibrium. No heteroclinic connection exists over $\tilde{W}^s(C_0)$ since a single equilibrium is there, namely C_0. C_0 is asymptotically stable on $\tilde{W}^s(C_0)$ and then there is no homoclinic orbit connecting it to itself. This orbit is the intersection of the stable and unstable manifolds of an equilibrium and since C_0 is just stable over the extension of its stable manifold, there is no such an orbit then. The existence of periodic orbits was precluded in Proposition 49. Hence, an $\omega-$limit set on $\tilde{W}^s(C_0)$ is C_0. It follows that $\tilde{W}^s(C_0) = W^s(C_0)$. There are then no non-trivial limit sets in $B(\infty)$ or $B(O)$. That is, a solution starting above $W^s(C_0)$ is eventually in $B(\infty)$ and it diverges toward infinity and a solution starting below $W^s(C_0)$, converges to O. □

Notice that solutions diverging to infinity either start from $\bigcup_{i=1}^{6} \Omega_i$ or from Π_2. It is, however, not known whether solutions starting in $\bigcup_{i=1}^{6} \Omega_i$ do enter Π_2 at a later time.

The Behavior near Infinity

Proposition 51 x, y *and* z *of a solution of (4.1-4.3) with* $b = 0$ *starting in* Π_2 *diverges toward infinity with the following bounded limits:*

$$\frac{5}{2a} \leq \liminf_{t\to\infty} \frac{x(t)}{z(t)^5} \leq \limsup_{t\to\infty} \frac{x(t)}{z(t)^5} \leq \frac{3}{a}$$
$$5 \leq \liminf_{t\to\infty} \frac{y(t)}{z(t)^5} \leq \limsup_{t\to\infty} \frac{y(t)}{z(t)^5} \leq 6$$
$$\frac{5}{3}a \leq \liminf_{t\to\infty} \frac{y(t)}{x(t)} \leq \limsup_{t\to\infty} \frac{y(t)}{x(t)} \leq 2a.$$

Proof: We notice first that x, y and z of a solution might grow toward infinity either with strictly positive velocities or with velocities unrelated to $(0, 0, 0)$, interchanging signs upon entering and leaving the Ω_i's. Proposition 15 tells that a solution starting in any of the Ω_i's must leave it in a future finite time if it does not converge into a steady state. It either enters the next Ω_i according to the scheme in the mentioned proposition, or it might enter

Π_2. Certainly, there will be a solution starting in Ω, which diverges later toward infinity by Proposition 50. Though, it is not known if this solution enters Π_2 later or if it remains in the Ω's. Therefore, we restrict the claim for solutions starting in Π_2. Knowing that $\overline{\Pi}_2$ is positively invariant as proven in Proposition 14, it suffices to consider solutions in Π_2. A solution starting in Π_2 has the velocities' signs $(\dot{x}(t), \dot{y}(t), \dot{z}(t)) \gg (0,0,0)$. This inequality generates the following inequalities:

$$5z^5 + cz < 2ax < 6z^5 \tag{4.51}$$
$$5z^5 + cz < y < 6z^5 \tag{4.52}$$
$$\frac{5}{3}ax < y < 2ax \tag{4.53}$$

A solution starting in Π_2 is monotone increasing hence if it does not converge toward infinity, it must eventually converge into a steady state $S \in \overline{\Pi}_2$ with $S \gg C_0$. However, no steady states other than O and C_0 exist for the system. Hence, it diverges toward infinity. The solution is bounded away from the boundaries of $\mathbb{R}^3_{\geq 0}$ and we can safely divide by $z(t)$ in the Inequalities (4.51), (4.52) and by $x(t)$ in the Inequality (4.53). We obtain the result upon taking the limits for $t \to \infty$. □

Hence, if we consider the Poincaré compactification $(x, y, z) \to (X = \frac{1}{x}, Y = \frac{y}{x}, Z = \frac{z}{x})$, a flow diverging to infinity is mapped to a flow entering a neighborhood of some $(0, K_0 > 0, 0)$. That is, it is far from a neighborhood near the $z-$axis. If we consider this compactification and let $\frac{d\tau}{dt} = x^4$, then:

$$\frac{dX}{d\tau} = aX^5 - 3Z^5X \tag{4.54}$$
$$\frac{dY}{d\tau} = 2aX^4 - YX^4 + aYX^4 - 3Z^5Y \tag{4.55}$$
$$\frac{dZ}{d\tau} = YX^4 - 5Z^5 - 3Z^6 + aZX^4 - cZX^4 \tag{4.56}$$

The linearization at a point $(0, K_0, 0)$ is a zero matrix. Therefore, it is again necessary to blow up to get more information about the flow near this point. We will again use the Newton polygon scheme in order to desingularize this point (see [100], [101]), Knowing that a degenerate singularity of a smooth two-dimensional vector field is desingularizable after a finite number of 'blowing ups' (i.e., trasnformations that include those directional transformations carried out in the Newton polygon scheme (see [20])). Then, we are aware that Newton polygon is used usually for two polynomials of two variables corresponding to the right-hand sides in the above equations. Therefore, we will use this method with each two polynomials while considering the third variable as a parameter. The computed transformation does not involve then the third variable. The fact is that the only plausible transformation upon considering the right-hand sides of $\frac{dX}{d\tau}$ and $\frac{dY}{d\tau}$ is $(X, Y) \to (u, v)$. That is, it changes nothing. Let us consider the Newton polygons of transformations right-hand sides of $\frac{dX}{d\tau}$ and $\frac{dZ}{d\tau}$ and then of $\frac{dY}{d\tau}$ and $\frac{dZ}{d\tau}$. The following transformations are computed:

$$(X, Y, Z) \to (u, v, w) \tag{4.57}$$
$$(X, Y, Z) \to (uw^5, v, w^4) \tag{4.58}$$
$$(X, Y, Z) \to (u^5, v, u^4w) \tag{4.59}$$
$$(X, Y, Z) \to (u, vw, w^2) \tag{4.60}$$
$$(X, Y, Z) \to (u, v, v^2w) \tag{4.61}$$

(4.57) changes nothing. Upon applying the transformations (4.60) and (4.61) and considering the linearization at the images of $(0, K_0, 0)$ due to each mapping, we notice that the relevant point is not desingularized, but it possesses a zero matrix linearization. It remains then to consider the transformations (4.58) and (4.59), for which the linearization at the relevant point reveals a negative eigenvalue and two zero eigenvalues in both. A further computation shows then that both transformations lead essentially to the same result. Therefore, we will consider only (4.58): $(X, Y, Z) \to (uw^5, v, w^4)$ and we let $\frac{ds}{d\tau} = w^{16}$.

$$\frac{du}{ds} = \frac{25}{4}u + \frac{3}{4}uw^4 - \frac{5}{4}u^5v - \frac{1}{4}au^5w^4 + \frac{5}{4}cu^5w^4 \tag{4.62}$$
$$\frac{dv}{ds} = 2au^4w^4 - u^4w^4v - 3w^4v + au^4w^4v \tag{4.63}$$
$$\frac{dw}{ds} = \frac{1}{4}u^4wv - \frac{3}{4}w^5 - \frac{5}{4}w + \frac{1}{4}au^4w^5 - \frac{1}{4}cu^4w^5 \tag{4.64}$$

Notice that in this case $u = \frac{X}{Z^{\frac{5}{4}}} = \frac{x^{\frac{1}{4}}}{z^{\frac{5}{4}}}$, $v = Y = \frac{y}{x}$ and $w = Z^{\frac{1}{4}} = \frac{z^{\frac{1}{4}}}{x^{\frac{1}{4}}}$. The dynamics near infinity are then tracked in a neighborhood near some $(u_0, v_0, 0)$ (i.e., for $w = 0$). Let $w = 0$. The system is then

$$\frac{du}{ds} = \frac{25}{4}u - \frac{5}{4}u^5v \tag{4.65}$$
$$\frac{dv}{ds} = 0 \tag{4.66}$$
$$\frac{dw}{ds} = 0 \tag{4.67}$$

and there exists then a continuum of equilibria described by the curve $v = \frac{5}{u^4}$ on the $u - v$ plane. The linearization at any point is then:

$$J|_{(u, v = \frac{5}{u^4}, 0)} = \begin{pmatrix} -25 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

with a zero eigenvalue corresponding to the continuum itself and another zero eigenvalue. Hence, the centre manifold, whose existence is evident due to the Centre Manifold Theorem, is two-dimensional. In order to compute the centre manifold, we transform an arbitrary point $(u_0, y_0 = \frac{5}{u_0^4}, 0)$ to zero and we calculate the time derivative. Let $U := u - u_0$ then $\dot{U} = \dot{u} - \dot{u}_0$ and let $V := v - v_0$ then $\dot{V} = \dot{v} - \dot{v}_0$. Recall that $u_0^4 v_0 = 5$ and therefore, $\dot{u}_0 = \frac{5^{\frac{1}{4}}}{4v_0^{\frac{5}{4}}}\dot{v}_0$, where $\dot{v}_0 = \dot{v}|_{(u_0, v_0, w)}$.The triplet $(U, V, W = w)$ satisfies the following differential equations:

$$\begin{aligned}\frac{dU}{ds} = \Bigg(&\frac{3}{4}u_0 + \frac{3}{4}U - \frac{1}{20}u_0^5(3v_0 + v_0u_0^4 - 2au_0^4 - av_0u_0^4) \\ &- \frac{1}{4}a(u_0+U)^5 + \frac{5}{4}c(u_0+U)^5\Bigg)W^4 \\ &+ (\frac{25}{4}u_0 + \frac{25}{4}U - \frac{5}{4}(V + v_0)(u_0 + U)^5)\end{aligned} \tag{4.68}$$

$$\frac{dV}{ds} = \left(2a(u_0+U)^4 - (V+v_0)(u_0+U)^4 - 3(V+v_0) + a(V+v_0)(u_0+U)^4\right)W^4 \tag{4.69}$$

$$\begin{aligned}\frac{dW}{ds} &= \left(\frac{1}{4}a(u_0+U)^4 - \frac{1}{4}c(u_0+U)^4 - \frac{3}{4}\right)W^5 \\ &\quad + \left(\frac{1}{4}(V+v_0)(u_0+U)^4 - \frac{5}{4}\right)W\end{aligned} \tag{4.70}$$

Proposition 52 *The centre manifold is described by $U = kW^4 + h.o.t.$, where h.o.t. means higher order terms in W.*

Proof: Suppose $U \sim \mathcal{O}(W^2)$ + h.o.t., it follows $\dot{U} \sim \mathcal{O}\left(2W\dot{W}\right)$ + h.o.t.. However, $\dot{W} \sim \mathcal{O}(UW)$ + h.o.t. $\sim \mathcal{O}(W^3)$ + h.o.t.. In this case, the lowest term in $\dot{U}$ is a multiple of U since all other terms in $(\frac{25}{4}u_0 + \frac{25}{4}U - \frac{5}{4}(V+v_0)(u_0+U)^5)$ vanish. Consequently, no non-zero coefficient k exists. As a generalization, if we let $U \sim \mathcal{O}(W^m)$ + h.o.t. then again $\dot{U} \sim \mathcal{O}\left(mW^{m-1}\dot{W}\right)$ + h.o.t. and $\dot{W} \sim \mathcal{O}(UW)$ + h.o.t. $\sim \mathcal{O}(W^{m+1})$ + h.o.t. and then $\dot{U} \sim \mathcal{O}(W^{2m})$ + h.o.t.. However, from the equation of $\dot{U}$, we conclude that $\dot{U} \sim \mathcal{O}(U, W^4)$ + h.o.t. $\sim \mathcal{O}\left(\min_m (W^m, W^4)\right)$ + h.o.t.. The case when $\min_m (W^m, W^4) = W^m$ requires that $m = 2m$, which is false for integers. The case when $\min_m (W^m, W^4) = W^4$ requires that $2m = 4$, which contradicts minimality of power. In both cases, the power of W from the time derivative of the centre manifold ansatz does not equate with that from the original differential equation of U. Therefore, it is not possible to calculate a non-zero k from equating both equations. The only remedy is then to set $U = kW^4$ + h.o.t.. We substitute in the original differential equation of U. The least power in W is then four and the coefficient of this least power is a linear function of k but not a multiple of it, hence k is not zero. Further discussion shows that k is non-zero.

$\square$

Substitute $U = kW^4$ + h.o.t. in $\dot{U}$, we get:

$$\begin{aligned}\frac{dU}{ds} &= \left(\frac{25}{4}u_0 - \frac{5}{4}u_0^5(V+v_0)\right) + \left(\left[\frac{25}{4} - \frac{25}{4}u_0^4(V+v_0)\right]k + \frac{3}{4}u_0 - \frac{1}{4}au_0^5\right. \\ &\quad \left. + \frac{5}{4}cu_0^5 - \frac{1}{20}u_0^5(3v_0 - 2au_0^4 + u_0^4v_0 - au_0^4v_0)\right)W^4 \\ &\quad + \mathcal{O}(W^8)\end{aligned} \tag{4.71}$$

The first two terms are zero and then $V = 0$. The second equation solves for k

$$k = \frac{1}{250}au_0^9 + \frac{1}{20}cu_0^5 - \frac{1}{100}u_0^5 \tag{4.72}$$

After substitution in the differential equations of the triplet (U, V, W)

$$\frac{dU}{ds} = \mathcal{O}\left(W^8\right) \tag{4.73}$$

$$\frac{dV}{ds} = \frac{1}{u_0^4}\left[2au_0^8 + (5a-5)u_0^4 - 15\right]W^4 + \mathcal{O}(W^8) \tag{4.74}$$

$$\frac{dW}{ds} = \frac{1}{100}\left[2au_0^8 + (25a-5)u_0^4 - 75\right]W^5 + \mathcal{O}(W^9) \tag{4.75}$$

Rescale time by $\frac{d\tilde{s}}{ds} = W^4$. It contributes to dividing the right-hand sides of the differential equations by W^4. Now the stationary solution is computed by setting $W = 0$ and solving the right-hand side of $\dot{V}$. The relevant u_0 is then

$$u_0 = \left(\frac{5 - 5a + \sqrt{25a^2 + 70a + 25}}{4a} \right)^{\frac{1}{4}} \tag{4.76}$$

and consequently, $v_0 = \frac{5}{u_0^4}$. This equality generates the following relations:

$$v_0 > v_0^* \Leftrightarrow u_0 < u_0^* \Leftrightarrow \big(2au_0^8 + (5a-5)u_0^4 - 15\big) < 0$$
$$v_0 < v_0^* \Leftrightarrow u_0 > u_0^* \Leftrightarrow \big(2au_0^8 + (5a-5)u_0^4 - 15\big) > 0$$

Therefore, the dynamics are attracting in the V-direction. In the W-direction, we have after the substitution of u_0:

$$\frac{dW}{d\tilde{s}} = \underbrace{\left[\frac{a{u_0^*}^4 - 3}{5} \right]}_{<0} W + \mathcal{O}(W^5) \tag{4.77}$$

Hence, $(0,0,0)$ is an attracting stationary solution in the positive orthant $\mathbb{R}^3_{\geq 0}$, concluded by the suspension to the dynamics of the centre manifold.

Proposition 53 *x,y and z of an unbounded solution in Π_2 diverging to infinity satisfy the following equations for all t > t_0: $x(t) = \frac{1}{u_0}(20K)^{\frac{1}{4}} e^{\frac{5K}{u_0^4}t} + \cdots$, $y(t) = \frac{v_0}{u_0}(20K)^{\frac{1}{4}} e^{\frac{5K}{u_0^4}t} + \cdots$ and $z(t) = \frac{1}{u_0}(\frac{1}{20K})^{\frac{1}{20}} e^{\frac{K}{u_0^4}t} + \cdots$.*

Proof: Consider (4.75) and let $\frac{1}{100}\left(2au_0^8 + (25a-5)u_0^4 - 75\right)$ be denoted by $-K$ for some $K > 0$. If we solve for W, we get $W(s) = (\frac{1}{4Ks})^{\frac{1}{4}} + \cdots$. We substitute in $ds = W^{16}d\tau$ we have then $s = 5^{\frac{1}{5}}(\frac{1}{4K})^{\frac{4}{5}}\tau^{\frac{1}{5}} + \cdots$ and hence, $W(\tau) = (\frac{1}{20K\tau})^{\frac{1}{20}} + \cdots$. Substituting in $X = u_0W^5 + \cdots = u_0(\frac{1}{20K\tau})^{\frac{1}{4}} + \cdots$. Similarly, $Z = W^4 = (\frac{1}{20K\tau})^{\frac{1}{5}} + \cdots$ and $V = v_0$. If we now compute τ in terms of the original time t, we have $d\tau = x^4dt$ (i.e., $d\tau = \frac{1}{X^4}dt$) and it follows then $\tau = e^{\frac{20K}{u_0^4}t} + \cdots$. Consider now $x = \frac{1}{X}$, $y = \frac{Y}{X}$ and $z = Z$ and substitute τ by $e^{\frac{20K}{u_0^4}t} + \cdots$, we conclude the following time equations

$$x(t) = \frac{1}{u_0}(20K)^{\frac{1}{4}} e^{\frac{5K}{u_0^4}t} + \cdots \tag{4.78}$$

$$y(t) = \frac{v_0}{u_0}(20K)^{\frac{1}{4}} e^{\frac{5K}{u_0^4}t} + \cdots \tag{4.79}$$

$$z(t) = \frac{1}{u_0}(\frac{1}{20K})^{\frac{1}{20}} e^{\frac{K}{u_0^4}t} + \cdots \tag{4.80}$$

The proof is complete. □

In this chapter, we have studied a third model for the Calvin cycle, according to Hahn [44]. This model implements photorespiration explicitly. Upon setting the flux of photorespiration to zero, all solutions starting from an open unbounded set tend to infinity, essentially

not biological. In this sense, photorespiration plays the role of the stabilizer of the cycle. Without it, RuBP, PGA and TP accumulate indefinitely. It was shown that a key feature for the analysis here is the strong monotonicity of the model. This character helps identify the possible dynamics and their region of occurrence. Although in (3.2-3.3) this feature is also satisfied, it was not urgently needed to draw conclusions. It was shown that sustained oscillations (i.e., periodic orbits if they are present) would be extremely unstable to the point that they will not be noticed. The geometric region where these oscillations might exist was recognized and this conclusion is not special for the model discussed. It is the negation of the existence of periodic orbits, which could be called a special character of the model since it is the direct outcome of the differential equations in (4.1-4.3). It could have been interesting had we proved the existence of sustained oscillations in the model since it is still not anticipated that the Calvin cycle works in an oscillatory mode. At least it was shown in [86] [32] [90] [66] [30] that photosynthesis admits damped oscillations.
Another interesting task is to relate Hahn's models to other models of the Calvin cycle in the literature. Possible relations to a model of Grimbs et al.[41] studied in [85] were already mentioned in Section 3.3 and perhaps these could be extended so as to give a wider view of runaway solutions of models for the Calvin cycle (i.e., Those solutions where all concentrations tend to infinity). One task is to obtain some characterization of models admitting solutions of this type. Another is to obtain formulae for the asymptotics of these solutions in the case that they do occur. This kind of behavior can be ruled out if the model admits a suitable conservation law. This is, for instance, the case in a model of [80], whose mathematical properties were studied in [72]. In Hahn's model with photorespiration, boundedness of solutions is obtained without there being a conservation law. A model gives another example of this studied in Section 6 of [85], where the original model of Grimbs et al. is modified by including the concentration of ATP explicitly. It also remains to obtain a comprehensive understanding of solutions when some concentrations tend to zero at late times. As discussed in [72], we can relate this to the biological phenomenon of overload collapse. This means intuitively that the production of sugar by the cycle cannot meet the demand for export from the chloroplast. In [72], it was shown that there are solutions to the model of [80] which admit this phenomenon while in a modification of the model due to Poolman [82], these solutions are eliminated. The model of [82] does not include photorespiration but does include the mobilization of glucose from starch.

Chapter 5

A New Model for Photosynthesis

As it is clear for many biochemical processes, inhibition is also one property of the carboxylation of ribulose 1,5-bisphosphate (RuBP). There is not one but many phosphates that compete with RuBisCO on the active site of RuBP. These ligands bind to both carbamylated and un-carbamylated sites of RuBP, reducing the efficiency of RuBisCO both in carboxylation and in oxygenation reactions (see [114], [6]). Among the different phosphate inhibitors, inorganic phosphate P_i is characterized by a relatively high binding constant. It diffuses through a triose phosphate translocator channel into the chloroplast in an exchange of triose phosphate diffusing in the reverse direction (see [112]). We will implement this fact in a new model for photosynthesis because it resembles one of the significant inhibitions on RuBisCO's work. Also it defines together with the other species a conserved quantity, something very natural. Again, we are not considering any sudden transients such as a sudden light intensity change or CO_2 concentration change. We are assuming a homogenous light environment, CO_2 concentration and RuBisCO concentration. This is based on precedent models of photosynthesis, which show a high and fast adaptation of photosynthetic rates (see [66], [91]) to similar changes. In Section 5.1, we reconsider Hahn's three-dimensional model and we introduce a new non-dimensionalization. This leads to applying the Singular Perturbation Theory and then shows the equivalence between the dynamics taking place on a two-dimensional manifold with those studied in Chapter 4. In Section 5.2, we introduce our new model for photosynthesis, a four-dimensional model with conserved quantity. Again, we utilize the Singular Perturbation Theory and we reduce the model into a three-dimensional model with a conserved quantity. In Section 5.3, we thoroughly study the dynamics of the reduced new model and we demonstrate the existence of two stable equilibria in some parameters' domains. In other domains of parameters, we show that the model exhibits the hysteresis phenomenon. This allows the coexistence of three stable equilibria and asserts the switch between two of them upon raising or lowering a control parameter. We record that this behavior is new for models describing photosynthesis. In Section 5.4, we conclude the new finding and we reflect on our new model and our perspective for any new photosynthesis modeling.

parameter	unit
k_1	sec^{-1}
k_2	$(mol\, m^{-3})^{-1} sec^{-1}$
k_3	sec^{-1}
k_4	$(mol\, m^{-3})^{-4} sec^{-1}$
k_5	sec^{-1}
k_6	sec^{-1}

Table 5.1: Table of units of reactions' rates of Hahn's model

Hahn's Three-Dimensional Model in Singular Perturbation Theory

This section finds a suitable non-dimensionalization of Hahn's three-dimensional model given by the following system of differential equations.

$$\begin{aligned}\frac{d[\text{RuBP}]}{dt} &= -k_1[\text{RuBP}] - 2k_2[\text{RuBP}]^2 + 3k_4[\text{TP}]^5 \\ \frac{d[\text{PGA}]}{dt} &= 2k_1[\text{RuBP}] + 3k_2[\text{RuBP}]^2 - k_3[\text{PGA}] \\ \frac{d[\text{TP}]}{dt} &= k_3[\text{PGA}] - 5k_4[\text{TP}]^5 - (k_5 + k_6)[\text{TP}] \end{aligned} \tag{5.1}$$

The non-dimensionalization is motivated by the factor m governing bifurcation upon writing $a^2 = mbc^{\frac{5}{4}}$ (i.e we assume that $m = \frac{bc^{\frac{5}{4}}}{a^2} = \frac{k_4^{\frac{1}{4}} k_1^2}{k_2 k_7^{\frac{5}{4}}}$). We consider the following non-dimensionalization:

$$[\text{RuBP}] = \frac{k_1}{k_2}X, \;\; [\text{PGA}] = \frac{k_1^2}{k_2 k_3}Y, \;\; [\text{TP}] = \frac{k_1^2}{k_2 k_7}Z. \tag{5.2}$$

In addition, we rescale time by setting $t = \frac{1}{k_1}\tau$. If we adopt the following naming: $e = m^4$, $\delta = \frac{k_3}{k_1}$, $\gamma = \frac{k_7}{k_1}$, the generated non-dimensionalized system is then

$$\frac{dX}{d\tau} = -X - 2X^2 + 3eZ^5 \tag{5.3}$$

$$\frac{dY}{d\tau} = \delta\left(2X + 3X^2 - Y\right) \tag{5.4}$$

$$\frac{dZ}{d\tau} = \gamma\left(Y - 5eZ^5 - Z\right) \tag{5.5}$$

Recall that reaction rates are written in the units given in Table 5.1. Hence, all parameters and variables in the new system are unitless and hence the non-dimensionalization is valid. Although the non-dimensionalization is not trivial, it is found to be useful to pose the problem in the Singular Perturbation Theory settings. We remark that k_3 is the rate of transformation of PGA into TP, which could have been easily lumped by connecting RuBP directly to TP. This lumping reduces the model into a two-dimensional model. A counter-argument to this is that three-dimensional models allow more sophisticated dynamics than two-dimensional ones. However, if we recognize that $\delta = \frac{k_3}{k_1}$ and that k_3 is the rate of a reaction, which is purely linear reaction connecting a substrate to a product of the Calvin cycle and where the substrate is not involved in any other reaction and it does not resemble any of the key processes (i.e., neither photosynthesis nor photorespiration or starch and sucrose production), we might be convinced that this reaction does not influence the dynamics. It could then be considered working in an arbitrarily fast mode, implying that $\delta = \frac{1}{\varepsilon}$ with ε being arbitrarily small. We now write the system in fast-slow settings whose slow formulation is

$$\frac{dX}{d\tau} = -X - 2X^2 + 3eZ^5 \tag{5.6}$$
$$\varepsilon\frac{dY}{d\tau} = \left(2X + 3X^2 - Y\right) \tag{5.7}$$
$$\frac{dZ}{d\tau} = \gamma\left(Y - 5eZ^5 - Z\right) \tag{5.8}$$

Choosing $\gamma = \frac{k_7}{k_1}$ as too small or too big contributes to favoring photosynthesis over starch and sucrose production, or vice versa. This will be studied later. The critical manifold of the above system is the set $C = \left\{(X, Y, Z) \in \mathbb{R}^3_{\geq 0} \mid 2X + 3X^2 - Y = 0\right\}$.

Proposition 54 *The critical manifold C of the system is normally hyperbolic attracting manifold.*

Proof: Let $g(X, Y, Z, \varepsilon) = 2X + 3X^2 - Y$. It suffices to check the derivative of g with respect to Y. It is the matrix $D_Y(g(X, Y, Z, 0)) = -1 < 0$. The conclusion follows. □

We are left then with a two-dimensional flow taking place over the critical manifold C. It is given by:

$$\frac{dX}{d\tau} = -X - 2X^2 + 3eZ^5 \tag{5.9}$$
$$\frac{dZ}{d\tau} = \gamma\left(2X + 3X^2 - 5eZ^5 - Z\right) \tag{5.10}$$

This system, when set to zero, shares the same resultant as that of Hahn's three-dimensional model (see (4.37)). We conclude that Hahn's three-dimensional model behaves dynamically as a two-dimensional model for ε small enough. Hence, dynamically no essential gain is added by considering the transformation of PGA into TP since, in both systems, all solutions converge to equilibria at a later time and we witness the same bifurcation in both. It is convenient then to assume that inner reactions within the Calvin cycle, which do not contribute to outer processes, like photorespiration or starch and sucrose synthesis, work fast enough and could then be lumped into one fast reaction.

If we consider now the other variants of fast-slow setting first by assuming that $\gamma = \frac{1}{\varepsilon}$ (i.e., starch and sucrose production yields much faster than carboxylation), we have then the following system:

$$\frac{dX}{d\tau} = -X - 2X^2 + 3eZ^5 \tag{5.11}$$
$$\frac{dY}{d\tau} = \delta\left(2X + 3X^2 - Y\right) \tag{5.12}$$
$$\varepsilon\frac{dZ}{d\tau} = \left(Y - 5eZ^5 - Z\right) \tag{5.13}$$

The critical manifold is again normally hyperbolic attracting and is given by

$$C = \left\{(X, Y, Z) \in \mathbb{R}^3_{\geq 0} \mid Y - 5eZ^5 - Z = 0\right\}$$

Z of a point belonging to C is then the root of a fifth degree polynomial, which is not analytically easy to solve if it is solvable at all. Therefore, we have to switch to numerical simulation of its dynamics. We notice that setting $\gamma = \frac{1}{\varepsilon}$ makes e itself singular since then $e = \frac{k_4 k_1^8}{k_2^4 k_7^5} = \left(\frac{k_1}{k_7}\right)^4 = \varepsilon^4 \frac{k_4 k_1^4}{k_7 k_2^4}$. In order to keep $e \sim \mathcal{O}(1)$, we have to let, for example, $\frac{k_4}{k_7} = \frac{1}{\varepsilon^4}$ or $\frac{k_1}{k_2} = \frac{1}{\varepsilon}$ thus the loss in yield of carboxylation is compensated by a weaker photorespiration in the second ratio or that regeneration is extremely more efficient than starch and sucrose production in the first ratio. In the latter case, although one of the cycle's breakage reactions is very efficient compared to carboxylation, carboxylation improves at another point. When TP is formed, it is almost all incorporated in regeneration. Such compulsory scaling to keep e in a non-singular range is not encountered in the first fast-slow setting when $\delta = \frac{k_1}{k_3} = \frac{1}{\varepsilon}$ because k_3 is not present in any other parameter except in δ. Reducing a model in the light of Singular Perturbation Theory will prove very helpful when considering more detailed models of photosynthesis. We will use this approach in the next section.

A New Model for Photosynthesis

This model will serve as a substitute for Hahn's three-dimensional model studied in Chapter 4. It includes, in addition to the previous model, a conservation value of the whole concentrations in the cycle. The reaction network reads:

$$\underset{\text{Ribulose 1,5-bisphosphate}}{\text{RuBP}} \xrightarrow{k_1} \underset{\text{Phosphoglycerate}}{\text{2 PGA}}$$

$$\underset{\text{Ribulose 1,5-bisphosphate}}{\text{2 RuBP}} \xrightarrow{k_2} \underset{\text{Phosphoglycerate}}{\text{3 PGA}} + \underset{\text{Inorganic phosphate}}{\text{P}_i}$$

$$\underset{\text{Phosphoglycerate}}{\text{PGA}} \xrightarrow{k_3} \underset{\text{Triose phosphate}}{\text{TP}}$$

$$\underset{\text{Inorganic phosphate}}{\text{P}_i} + \underset{\text{Triose phosphate}}{\text{5 TP}} \xrightarrow{k_4} \underset{\text{Ribulose 1,5-bisphosphate}}{\text{3 RuBP}}$$

$$\underset{\text{Triose phosphate}}{\text{TP}} \xrightarrow{k_7} \underset{\text{Inorganic phosphate}}{\text{P}_i} + \text{Sucrose} + \text{Starch}$$

The differential equations written in mass action kinetics read:

$$\begin{aligned}
\frac{d[\text{RuBP}]}{dt} &= -k_1[\text{RuBP}] - 2k_2[\text{RuBP}]^2 + 3k_4[\text{TP}]^5[\text{P}_i] \\
\frac{d[\text{PGA}]}{dt} &= 2k_1[\text{RuBP}] + 3k_2[\text{RuBP}]^2 - k_3[\text{PGA}] \\
\frac{d[\text{TP}]}{dt} &= k_3[\text{PGA}] - 5k_4[\text{TP}]^5[\text{P}_i] - k_7[\text{TP}] \\
\frac{d[\text{P}_i]}{dt} &= k_2[\text{RuBP}]^2 - k_4[\text{TP}]^5[\text{P}_i] + k_7[\text{TP}]
\end{aligned} \tag{5.14}$$

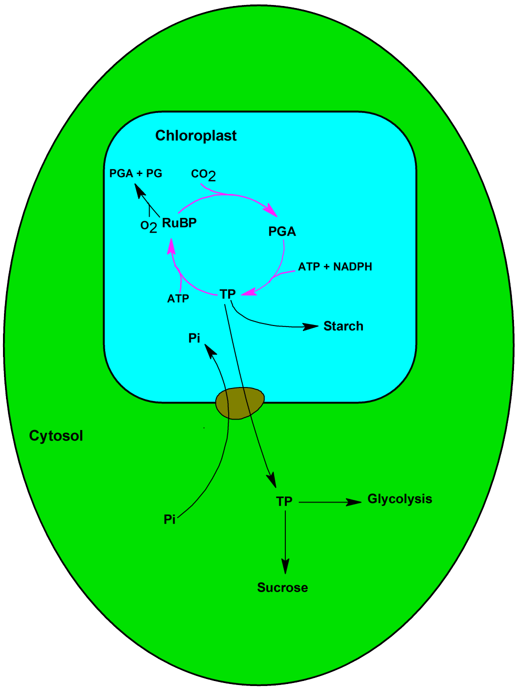


Figure 5.1: The main reactions in photosynthesis according to the new model

The system has the following conserved quantity:

$$2[\text{RuBP}] + [\text{PGA}] + [\text{TP}] + [\text{P}_i] = k \tag{5.15}$$

Additionally, we have the following relations at stationary solutions:

$$\frac{1}{3}k_1[\text{RuBP}] - \frac{1}{3}k_2[\text{RuBP}]^2 - k_7[\text{TP}] = 0 \tag{5.16}$$

$$2k_1[\text{RuBP}] + 3k_2[\text{RuBP}]^2 - k_3[\text{PGA}] = 0 \tag{5.17}$$

As in the previous section, we consider the same non-dimensionalization:

$$[\text{RuBP}] = \frac{k_1}{k_2}X, \;\; [\text{PGA}] = \frac{k_1^2}{k_2k_3}Y, \;\; [\text{TP}] = \frac{k_1^2}{k_2k_7}Z, \;\; [\text{P}_i] = \frac{k_1}{k_2}W \tag{5.18}$$

If we adopt the following parameters: $a = \frac{k_7}{k_1}$, $b = \frac{kk_2}{k_1}$, $c = \frac{k_7}{k_3}$, $\delta = \frac{k_3}{k_1}$ and $e = \tilde{m}^5 = \frac{k_4k_1^{10}}{k_2^5k_7^6}$, we have the following non-dimensionalized system

$$\begin{aligned}
\frac{dX}{d\tau} &= -X - 2X^2 + 3abeZ^5 - 3eZ^6 - 6aeXZ^5 - 3ceYZ^5 \\
\frac{dY}{d\tau} &= \delta\left(2X + 3X^2 - Y\right) \\
\frac{dZ}{d\tau} &= aY - aZ - 5a^2beZ^5 + 5aeZ^6 + 10a^2eXZ^5 + 5aceYZ^5 \\
\frac{dW}{d\tau} &= X^2 + Z + 2aeXZ^5 - abeZ^5 + eZ^6 + ceYZ^5
\end{aligned} \tag{5.19}$$

The conservation law reads now:

$$b = 2X + \frac{1}{\delta}Y + \frac{Z}{a} + W \tag{5.20}$$

Recall that an equilibrium of the system satisfies the following equalities:

$$Z^* = \frac{1}{3}\left(X^* - {X^*}^2\right) \tag{5.21}$$

$$Y^* = 2X^* + 3{X^*}^2 \tag{5.22}$$

This requires that any solution (X^*, Y^*, Z^*, W^*) satisfies the following bounds:

$$0 \leq X^* \leq \min\left\{1, \frac{b}{2}\right\} \tag{5.23}$$

$$0 \leq Z^* \leq \min\left\{\frac{1}{12}, ab\right\} \tag{5.24}$$

$$0 \leq W^* \leq b \tag{5.25}$$

Motivated by the discussion in the previous section, we set $\delta = \frac{k_3}{k_1} = \frac{1}{\varepsilon}$. In order to keep $e \sim \mathcal{O}(1)$, we additionally set $\frac{k_3}{k_7} = \frac{1}{\varepsilon}$ (i.e., $c = \frac{k_7}{k_3} = \varepsilon$). The critical manifold $C := \left\{(X, Y, Z, W) \in \mathbb{R}^4_{\geq 0} \mid Y = 2X + 3X^2\right\}$ is normally hyperbolic attracting manifold.

Proposition 55 *The critical manifold* $C := \left\{(X, Y, Z, W) \in \mathbb{R}^4_{\geq 0} \mid Y = 2X + 3X^2\right\}$ *is normally hyperbolic attracting manifold.*

Proof: Submitting to the fast-slow systems' notation, the critical manifold is given by the equation $g(X, Y, Z, W, \varepsilon = 0) = 0$. For System 5.19, this is $g(X, Y, Z, W, 0) = 2X + 3X^2 - Y = 0$. We consider the matrix $D_Y g|_{(X,Y,Z,W,0)} = -1 < 0$. Hence, the critical manifold defined above is normally hyperbolic attracting manifold. □

Now setting $\varepsilon = 0$, the system reduces into the three-dimensional system

$$\dot{X} = -X - 2X^2 + 3abeZ^5 - 3eZ^6 - 6aeXZ^5 \tag{5.26}$$

$$\dot{Z} = 2aX + 3aX^2 - aZ - 5a^2beZ^5 + 5aeZ^6 + 10a^2eXZ^5 \tag{5.27}$$

$$\dot{W} = X^2 + Z + 2aeXZ^5 - abeZ^5 + eZ^6 \tag{5.28}$$

It suffices to study the right-hand sides of $\dot{X}$ and $\dot{Z}$. If we consider the resultant of the right-hand sides of (5.26) and (5.27), we have

$$\mathrm{Res}_Z(\dot{X}, \dot{Z}) = a^6e^5X\left[eX^4(X-1)^5\left(X^2 + (-6a-1)X + 3ab\right) + 243(2X+1)\right] \tag{5.29}$$

Note that solutions of (5.29) in $\mathbb{R}_{\geq 0}$ are in one-to-one correspondence to solutions of System (5.26-5.28) in $\mathbb{R}^3_{\geq 0}$. Note also that the conservation law (5.20) reads now $b = 2X + \frac{Z}{a} + W$, while (5.21), (5.22), (5.23), (5.24) and (5.25) keep being satisfied. Besides $X = 0$, which solves the resultant and generates the trivial solution $(0, 0, b)$ of System (5.26-5.28), solving the resultant for positive X means solving a polynomial of degree eleven. Therefore, we switch to the inverse problem, searching for a parameter value e, for which positive roots X of the Resultant (5.29) exist. The root X^* is then completed into a relevant solution of System (5.26-5.28) if the right-hand sides of the Equations (5.21) and (5.22) are non-negative. The intervals of X, where this completion is valid, are called the intervals of relevance. If we set the resultant to zero and solve for e, we get the following continuous rational function:

$$e = \frac{243\,(2X+1)}{X^4\,(X-1)^5\,(-X^2+(6a+1)X-3ab)} \tag{5.30}$$

whose derivative with respect to X is:

$$\frac{de}{dX} = \frac{243\,(20X^4+(-108a-17)\,X^3+(48ab-12a-8)\,X^2+(30a+9ab+5)\,X-12ab)}{X^5\,(X-1)^6\,(-X^2+(6a+1)X-3ab)^2} \tag{5.31}$$

Let us name the significant polynomials in $\frac{de}{dX}$ in the following way:

$$\begin{aligned} P(X) &:= 20X^4+(-108a-17)\,X^3+(48ab-12a-8)\,X^2+(30a+9ab+5)\,X-12ab \\ Q(X) &:= (X-1) \\ R(X) &:= -X^2+(6a+1)X-3ab \end{aligned}$$

We compute the resultants

$$\mathrm{Res}_X(P(X),Q(X)) = 45a(b-2) \tag{5.32}$$

$$\mathrm{Res}_X(P(X),R(X)) = -27a^2b\,(b-2)\,(4a+4ab+1)\,\big((6a+1)^2-12ab\big) \tag{5.33}$$

Notice that $W^* = \frac{-1}{3a}R(X^*)$ and it is eventually non-negative for $X<1$ and e positive. We notice also that the discriminant of $R(X)$ is $\mathrm{Disc}_X(R(X)) = (6a+1)^2-12ab$. Moreover, we notice that $P(X)$ admits exactly one negative root. For $b=2$, $P(X)$ admits a simple common root with $Q(X)$ and $R(X)$ exactly at $X=1$. Otherwise for $b=\frac{(6a+1)^2}{12a}$, $P(X)$ shares a common root with $R(X)$ at $X=\frac{6a+1}{2}$, which is simple for $P(X)$ and double for $R(X)$. The simplicity of the common roots of $P(X)$ with respect to the product of the other polynomials leaves the poles of $\frac{de}{dX}$ unchanged since they depend then on the roots of the product of polynomials in the denominator of $e=f(X)$. Knowing that $Q(X)$ admits a unique root at $X=1$, we will classify the relevant domains of X according to the roots of $R(X)$. We mean by relevant domains of X, those domains, for which a steady state in the non-negative orthant in $\mathrm{int}\,\mathbb{R}^3_{\geq 0}$ exists if we choose a suitable value of e. We consider two main cases: Case(I) for $b<\frac{(6a+1)^2}{12a}$ and case(II) for $b>\frac{(6a+1)^2}{12a}$. Note that in case(II), $R(X)$ admits no real roots and note also that $\frac{(6a+1)^2}{12a}>2$.

Case (I): In this case, $R(X)$ has two positive roots since its discriminant is positive. In between these roots, $R(X)$ is positive and consequently e is negative, which is not of interest. At this point, we make a difference between two sub-cases, which infer the position of these roots. (I)(a) when in addition to the given inequality $b<\frac{(6a+1)^2}{12a}$, we assume that $b<2$. Then the roots of $R(X)$ to be called r_1 and r_2 are positioned in this way $r_1<\frac{b}{2}<1<r_2,\ 6a<r_2$. In the second sub-case (I) (b), while assuming $b>2$, the roots of $R(X)$ are in the following order $1<r_1<r_2<6a$ and the schematic Figure 5.2 for e holds for both sub-cases. We mean by a u-shaped curve, a curve that either looks like a U or a tipped over U. Concretely, a curve $f(x)$ looks like a U over an interval $]r,s[$ if its

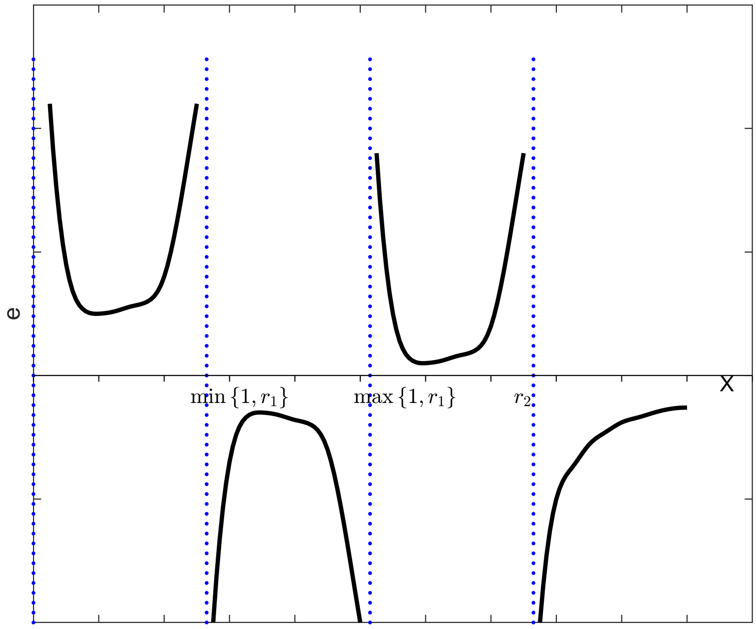


Figure 5.2: The schematic figure of sub-cases (I)(a) and (I)(b). The difference between the sub-cases occur when $\min\{1, r_1\}$ is r_1 in (I)(a) and is 1 in (I)(b)

	Case(I)(a)	Case(I)(b)	Case(I)(c)
	$b < \frac{(6a+1)^2}{12a}$	$b < \frac{(6a+1)^2}{12a}$	$b < \frac{(6a+1)^2}{12a}$
	$b < 2$	$b > 2$	$b = 2$
IOR	$]0, r_1[$	$]0, 1[$	$]0, 1[$
	Case(II)(a)	Case(II)(b)	Case(II)(c)
	$b = \frac{(6a+1)^2}{12a}$	$b = \frac{(6a+1)^2}{12a}$	$b > \frac{(6a+1)^2}{12a}$
	$\frac{6a+1}{2} > 1$	$\frac{6a+1}{2} < 1$	$\frac{6a+1}{2} < 1$
IOR	$]0, 1[$	$]0, \frac{6a+1}{2}[\cup]\frac{6a+1}{2}, 1[$	$]0, 1[$

Table 5.2: The conditions of the different discussed cases and the interval of relevance (IOR) of X in each case

limits are $\lim_{x\to r^+} f(x) = +\infty = \lim_{x\to s^-} f(x)$ and admits a global minimum over this interval. It looks like a tipped over U if $\lim_{x\to r^+} f(x) = -\infty = \lim_{x\to s^-} f(x)$ and it admits a global maximum over the interval. We can be sure that the graph of e is a u-shaped curve in the first interval $X \in]0, \min\{1, r_1\}[$ based on two things: First $e = f(X)$ tends either to $+\infty$ or to $-\infty$ at the sections $X = 0$, $X = 1$, $X = r_1$ and $X = r_2$ (i.e., where the poles are encountered). For instance, in sub-case (I) (a), there must exist at least one extremum in each of the sections $]0, r_1[$, $]r_1, 1[$ and $]1, r_2[$. However, $\frac{de}{dX}$ admits maximally three positive roots. Hence, exactly one extremum will be present in each of the aforementioned sections including $]0, r_1[$, the interval of relevance of X, where e exclusively takes relevant values. Similarly, in the sub-case (I)(b), e is plausibly defined for $X \in]0, 1[$ where only one extremum (minimum) exists and the function is u-shaped. We add another sub-case (I)(c) when $b = 2 < \frac{(6a+1)^2}{12a}$, the boundary case between (I)(a) and (I)(b). Here, the graph of e is u-shaped over the intervals $]0,1[$ and $]1,r_2[$. No change concerning the maximal number of positive roots in this sub-case. The schematic graph of e is illustrated in Figure 5.3. We sub-

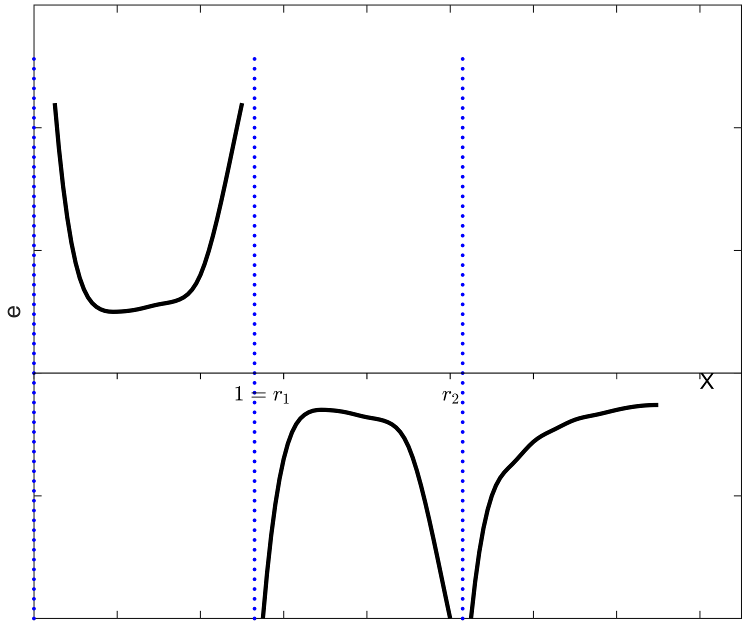


Figure 5.3: The schematic figure of the sub-case (I)(c)

classify case (II) into three sub-cases: (II)(a) $b = \frac{(6a+1)^2}{12a}$ and $\frac{(6a+1)}{2} > 1$. (II)(b) $b = \frac{(6a+1)^2}{12a}$ and $\frac{(6a+1)}{2} < 1$ and (II)(c) $b > \frac{(6a+1)^2}{12a}$ and $\frac{(6a+1)}{2} < 1$. The first sub-case (II)(a) is described by the schematic Figure 5.4, where the graph of e is u-shaped in the interval of relevance $]0,1[$. We notice that in all the cases yet discussed maximally two positive stationary soluti-

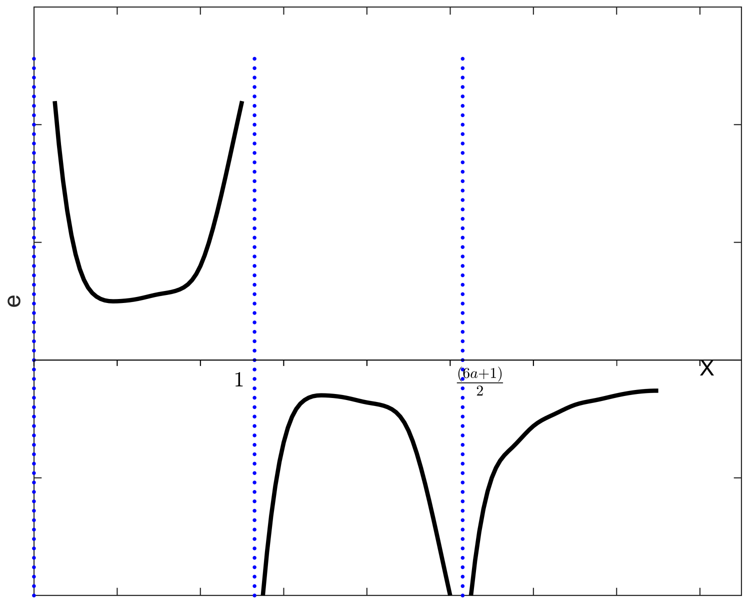


Figure 5.4: The schematic figure of the sub-case (II)(a)

ons appear as e changes in a seemingly simple fold bifurcation scenario. This will not be the case in the last two sub-cases (II)(b) and (II)(c). (II)(b) is described by the schematic Figure 5.5 and the graph of e is u-shaped in $]0, \frac{6a+1}{2}[$ and $]\frac{6a+1}{2}, 1[$, the intervals of relevance. The

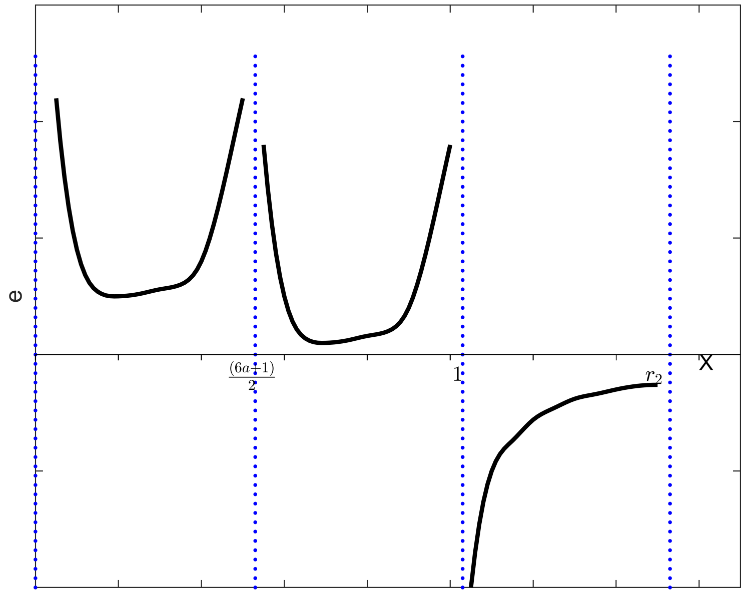


Figure 5.5: The schematic figure of the sub-case (II)(b)

latter sub-case (II)(c) has the schematic Figure 5.6. Notice that the conditions describing each case and the interval of relevance of X in each case are listed in Table 5.2. In (II)(b)

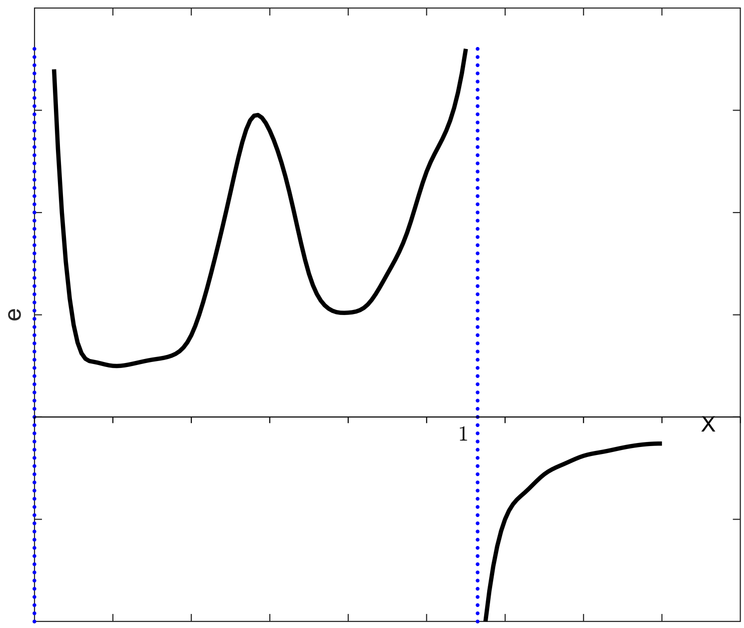


Figure 5.6: The schematic figure of the sub-case (II)(c)

and upon varying e, there occur two seemingly fold bifurcations not known whether simultaneously or in succession. The two u-shaped curves are within the interval of relevance of X. This leads to the coexistence of four positive stationary solutions upon sufficiently elevating the value of e. The bifurcation taking place must be a simple fold bifurcation since

one of the three existing stationary solutions, the trivial steady state $(0,0,b)$, is persistent. That is, it exists for any choice of positive parameters. Moreover, the positive steady states corresponding to $X \in]0, \frac{6a+1}{2}[$ are always at positive distance from those corresponding to $X \in]\frac{6a+1}{2}, 1[$ for every choice of parameters. Hence, each positive steady state joins a single positive steady state undergoing a fold bifurcation. This rules out the hysteresis phenomenon, which always accompanies cusp bifurcation. Hence, it also precludes cusp bifurcation. In (II)(c) seen as the continuous generic extension of its boundary the sub-case (II)(b), we are keeping $\frac{(6a+1)}{2} < 1$ and sharpening the equality into the inequality $b > \frac{(6a+1)^2}{12a}$. Thus letting $R(X)$ be negative through the whole positive X-axis and forcing the still existing three positive roots of $P(X)$ to occur before $X = 1$. There are no well-defined intervals of the parameters for which three positive roots of $P(X)$ exist. At least for $\frac{(6a+1)}{2} < 1$ and $\frac{(6a+1)^2}{12a} + \varepsilon > b > \frac{(6a+1)^2}{12a}$ for some suitable $\varepsilon > 0$, there is a numerical evidence that these roots exist and are bounded from above by $X = 1$. At this point, this will be sufficient since once $P(X)$ loses two of its three positive roots, we are then back to the same scenario encountered in case (I) and sub-case (II)(a). Thus, the richest of dynamical behavior is given by case (II)(c).
Actually, an explicit study of the number of roots of $P(X)$ was not needed throughout the discussion since their existence was directly implied by the interval sections according to the poles of function $\frac{de}{dX}$. It is only in the latter sub-case (II)(c), where only two poles exist at $X = 0$ and $X = 1$, that we could not decide about the number of positive roots of $P(X)$ and thus about the number of extrema of e. However, by continuity of the function, it is safely known that three positive roots of $P(X)$ keep existing in some interval of parameters upon choosing $b > \frac{(6a+1)^2}{12a}$ and letting $\frac{(6a+1)}{2} < 1$. We can see that two positive stationary solutions will first be born upon varying e in (II)(c). Then upon elevating e, two other positive stationary solutions will be born in a seemingly fold bifurcation scheme. If we further elevate e, two positive stationary solutions will eventually be lost and we end up with only two positive stationary solutions. If the positive stationary solutions are ordered alternately as stable and then unstable or vice versa, one stable positive stationary solution is lost once by elevating e and, otherwise, another stable positive stationary solution is lost when lowering e. This is the generic case. The two fold bifurcations might be realized for the same value of e. This is not generic, which means it happens for a zero measure set of values of e compared to the generic case.

Proposition 56 *Solutions of System (5.26-5.28) exist globally over a two-dimensional manifold given by $b = 2X + \frac{Z}{a} + W$ and only fold-type bifurcation is possible for System (5.26-5.28). In other words, it undergoes either a simple fold bifurcation or a cusp bifurcation if it does bifurcate. Moreover, periodic orbits are ruled out.*

Proof: Since solutions of System (5.26-5.28) are constrained by the following conserved quantity $b = 2X + \frac{Z}{a} + W$, they exist for all $t \geq 0$ once they start on the two-dimensional manifold given by the same aforementioned quantity. Moreover, all initial points starting on this manifold within the non-negative orthant $\mathbb{R}^3_{\geq 0}$ remain on it in $\mathbb{R}^3_{\geq 0}$. For instance, suppose $X = 0$, it follows from Equation (5.26) that $\dot{X} = 3eZ^5(ab - Z) \geq 0$. If $\dot{X} = 0$, we pass to the second time derivative $\ddot{X}$, which is positive for $Z = ab$. For $Z = 0$, we get the stable trivial steady state $(0,0,b)$. Analogously, a solution starting at $Z = 0$ have by Equation (5.27), $\dot{Z} = 2aX + 3aX^2 \geq 0$. Again, for $X = 0$, the trivial steady state $(0,0,b)$ is generated. Hence, all solutions starting in $\mathbb{R}^3_{\geq 0}$ at the two-dimensional manifold

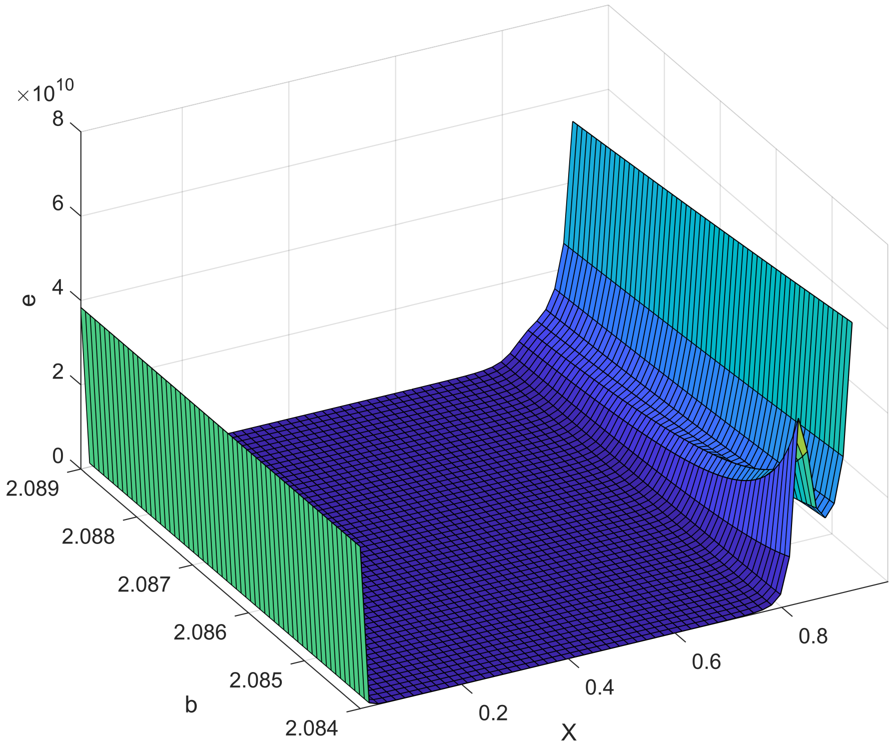


Figure 5.7: The values of e for $a = \frac{1}{9}$ and b as in (II)(c). Cusp point is encountered exactly where the peak in the middle is flattened

$b = 2X + \frac{Z}{a} + W$ remain there for all $t \geq 0$ and any solution starting at its boundary leaves it toward the interior of the manifold except for the trivial steady state $(0, 0, b)$.
There are few types of bifurcation possible for two-dimensional systems, as is the case of our System (5.26-5.28). Either or both of the eigenvalues might approach the imaginary axis and pass through it as some parameters change or one or both of the eigenvalues approach zero. In the former case, it is a Hopf bifurcation or generalized-Hopf bifurcation, depending on the degree of degeneracy. In the latter case, Bogdanov-Takens bifurcation happens when both eigenvalues are zero while fold bifurcation happens when only one eigenvalue is zero. Simple fold bifurcation is when the equilibrium has a single zero eigenvalue and a non-zero second-order term of the suspension to the differential equation governing the centre manifold dynamics (see [65]). Cusp bifurcation occurs when, in addition to the single zero eigenvalue, the second-order term is also zero. In order to unravel the bifurcations possible for System (5.26-5.28), we utilize the following linear transformation: $(X, Z) \to (U = \frac{5a}{3}X + Z, V = Z)$. We study then the new system by restricting ourselves to $\dot{U}$ and $\dot{V}$ since W keeps up with X and Z satisfying the equation $b = 2X + \frac{Z}{a} + W$.

$$\dot{U} = \frac{1}{5}U - \frac{25a^2 + 5a}{25a}V - \frac{3}{25a}U^2 + \frac{6}{25a}UV - \frac{3}{25a}V^2 \tag{5.34}$$

$$\dot{V} = \frac{6}{5}U - \frac{25a^2 + 30a}{25a}V + \frac{27}{25a}U^2 - \frac{54}{25a}UV + \frac{27}{25a}V^2 - 5a^2beV^5 + 6aeuV^5 - aeV^6 \tag{5.35}$$

The Jacobian matrix of System (5.34-5.35) is:

$$J = \begin{pmatrix} -6U+6V+5a & -5a-25a^2+6U-6V \\ 30a+54U-54V+150a^2eV^5 & -30a-25a^2-54U+54V-625a^3beV^4+750a^2euV^4-150a^2eV^5 \end{pmatrix} \tag{5.36}$$

Computing the trace of J :

$$\text{Trace}(J) = -5\left(5a^2 + 5a + 12U - 12V\right) - 25a^2eV^4\left(6V - 30U + 25ab\right)$$

We make use of the following conservation value:

$$\begin{aligned} b &= 2X + \frac{Z}{a} + W \\ &= \frac{6}{5a}U - \frac{1}{5a}V + W \end{aligned} \tag{5.37}$$

for (U, V) of a stationary solution, we have:

$$U = \frac{5a}{3}X + V > V \Rightarrow \left(5a^2 + 5a + 12U - 12V\right) > 0$$

$$(6V - 30U + 25ab) > 0 \;\text{ via (5.37)}$$

There is no Hopf-bifurcation type allowed since Trace$(J) = \lambda_1 + \lambda_2 < 0$ for every choice of positive parameters. For the same reason, Bogdanov-Takens bifurcation is ruled out. The two remaining possibilities are cusp bifurcation and fold bifurcation.
Notice that Trace$(J) = \frac{d\dot{X}}{dX} + \frac{d\dot{Z}}{dZ} < 0$ for all choices of positive parameters and for X and Z satisfying $b = 2X + \frac{Z}{a} + W$, a two-dimensional simply connected compact manifold in $\mathbb{R}^3_{\geq 0}$. Trace(J) is nothing but the divergence of the vector field. It is negative throughout the mentioned two-dimensional manifold. Hence, by Bendixson's criterion (sometimes called Bendixson-Dulac Theorem), no periodic orbit lies entirely in this manifold and then no periodic orbit exists for System (5.26-5.28). □

Cusp Bifurcation in the Singularly Perturbed New Model

We will proceed in this section with the analysis of the singularly perturbed model of the new model in (5.26-5.28). We will focus here on the sub-case(II)(c) for the purpose of proving that the witnessed bifurcation in the schematic graph of this sub-case refers in its most complex form to a cusp bifurcation. This means that there are parameters for which three equilibria come together forming a single equilibrium with one zero eigenvalue and whose stability follows the sign of the coefficient of a third-order term. We translate a stationary solution (X_0, Z_0) to $(0, 0)$ by the following linear transformation $(X, Z) \to (\tilde{X} = X - X_0, \tilde{Z} = Z - Z_0)$, then we recover the same variables' naming. We reuse X and Z instead of $\tilde{X}$ and $\tilde{Z}$. Note that it is not necessary to consider $\dot{W}$ since a change in W is implied by the conserved quantity $b = 2X + \frac{Z}{a} + W$. The transformed singularly perturbed System (5.26-5.28) reads now:

$$\dot{X} = (-6aeZ_0^5 - 4X_0 - 1)X + (15Z_0^4abe - 30X_0Z_0^4ae - 18Z_0^5e)Z - 2X^2$$
$$+(-30Z_0^4ae)XZ + (30Z_0^3abe - 60X_0Z_0^3ae - 45Z_0^4e)Z^2 + (-60Z_0^3ae)XZ^2$$
$$+(30Z_0^2abe - 60X_0Z_0^2ae - 60Z_0^3e)Z^3 + (-60Z_0^2ae)XZ^3 + (15Z_0abe - 30X_0Z_0ae - 45Z_0^2e)Z^4$$
$$+(-30Z_0ae)XZ^4 + (3abe - 18Z_0e - 6X_0ae)Z^5 + (-6ae)XZ^5 + (-3e)Z^6 \tag{5.38}$$

$$\dot{Z} = (2a + 6X_0a + 10Z_0^5a^2e)X + (30Z_0^5ae - a + 50X_0Z_0^4a^2e - 25Z_0^4a^2be)Z + (3a)X^2$$
$$+(50Z_0^4a^2e)XZ + (75Z_0^4ae + 100X_0Z_0^3a^2e - 50Z_0^3a^2be)Z^2 + (100Z_0^3a^2e)XZ^2$$
$$+(100Z_0^3ae + 100X_0Z_0^2a^2e - 50Z_0^2a^2be)Z^3 + (100Z_0^2a^2e)XZ^3$$
$$+(75Z_0^2ae + 50X_0Z_0a^2e - 25Z_0a^2be)Z^4 + (50Z_0a^2e)XZ^4$$
$$+(10X_0a^2e - 5a^2be + 30Z_0ae)Z^5 + (10a^2e)XZ^5 + (5ae)Z^6 \tag{5.39}$$

We denote by:

$$f(X,Z) = \begin{pmatrix} f_1(X,Z) \\ f_2(X,Z) \end{pmatrix} \tag{5.40}$$

the subsequent right-hand sides of $\dot{X}$ and $\dot{Z}$ of System (5.38-5.39). We let $(X,Z) = u$ and then we write the Taylor expansion of f near $u = (0,0)$ in the following way:

$$f(u) = Au + \frac{1}{2}B(u,u) + \frac{1}{6}C(u,u,u) + \mathcal{O}(\|u\|^4) \tag{5.41}$$

where $B(u,v)|$ and $C(u,v,w)|$ are the multilinear functions with components

$$B_j(u,v) = \sum_{k,l=1}^{n} \frac{\partial^2 f_j(\xi,0)}{\partial\xi_k\partial\xi_l}|_{\xi=0}u_kv_l \tag{5.42}$$

$$C_j(u,v,w) = \sum_{k,l,m=1}^{n} \frac{\partial^3 f_j(\xi,0)}{\partial\xi_k\partial\xi_l\partial\xi_m}|_{\xi=0}u_kv_lw_m \tag{5.43}$$

for $j = 1,2$.

Definition 5.3.1 *Consider the continuous-time system depending on one parameter*

$$\dot{x} = f(x,\alpha), \quad x \in \mathbb{R}^n, \alpha \in \mathbb{R}$$

where f is smooth. Let $x = x_0$ be an equilibrium of the system at $\alpha = \alpha_0$. Further assume that the Jacobian of f admits exactly one zero eigenvalue. Then the system is said to have undergone a fold bifurcation (also called saddle-node bifurcation).

Recall that in the sense of Definition 5.3.1, both fold bifurcation and cusp bifurcation are called fold bifurcation. The difference between the two bifurcations is clarified in the following theorems. The first theorem defines the generic-fold bifurcation by defining a non-degeneracy condition and a transversality condition.

Theorem 10 *Suppose that a one-dimensional system*

$$\dot{x} = f(x, \alpha), \;\; x \in \mathbb{R}, \alpha \in \mathbb{R}$$

where f is smooth and has at $\alpha = 0$ the equilibrium $x = 0$ and let $\lambda = f_x(0,0) = 0$. Assume that the following conditions are satisfied:
(A.1) $f_{xx}(0,0) \neq 0$ (Non-degeneracy Condition).
(A.2) $f_\alpha(0,0) \neq 0$ (Transversality Condition).
Then there are smooth invertible parameter and coordinate changes transforming the system into

$$\dot{\xi} = \mu + a(\mu)\xi^2 + \mathcal{O}(\xi^3).$$

where $\mu = \mu(\alpha)$ is a function of α and $\mu(0) = 0$.

The non-degeneracy condition differentiates fold bifurcation from cusp bifurcation since its violation opens the door for defining the latter. The transversality condition is a technical condition necessary for transforming the system into the theorem's generic system (see [75]). Let us assume that condition $(A.1)$ is violated upon the variation of one parameter. This necessitates the dependence of the one-dimensional system on two parameters. Compared with the cusp bifurcation, the fold bifurcation is a codim-1 bifurcation since it occurs upon changing only one parameter. The following theorem describes the generic cusp bifurcation with respect to a one-dimensional system. This will suffice since the suspension to the one-dimensional centre manifold in both bifurcations generates a one-dimensional system.

Theorem 11 *Suppose that a one-dimensional system*

$$\dot{x} = f(x, \beta), \;\; x \in \mathbb{R}, \beta \in \mathbb{R}^2$$

where f is smooth has at $\beta = (\beta_1, \beta_2) = (0,0)$ the equilibrium $x = 0$ and let the following cusp bifurcations hold:
$\lambda = f_x(0,0) = 0, \qquad f_{xx}(0,0) = 0$
If also the following conditions are satisfied:
(C.1) $f_{xxx}(0,0) \neq 0$ (Non-degeneracy Condition)
(C.2) $(f_{\beta_1} f_{x\beta_2} - f_{\beta_2} f_{x\beta_1}) \neq 0$ (Transversality Condition)
then there are smooth invertible parameter and coordinate changes transforming the system into:

$$\dot{\xi} = \mu_1 + \mu_2\xi + c(\mu)\xi^3 + \mathcal{O}(\xi^4).$$

with $\mu_1 = \mu_1(\beta)$ and $\mu_2 = \mu_2(\beta)$ are functions of β and $\mu_1(0,0) = \mu_2(0,0) = 0$.

The core of the bifurcations is manifested in the conditions $(A.1)$ and $(C.1)$. The transversality conditions are necessary as much as transforming the studied system into the generic form system is necessary. It is easy to check for both types of conditions if the system is scalar. However, the computation gets subsequently complicated as the dimension of the system increases if the system is not given in its eigenbasis form. System (5.38-5.39) is not given in the eigenbasis form. Thus, we need to use a known projection method to compute $a(\mu)$ and $c(\mu)$ and thus track the cusp when the former is zero and the latter is non-zero. The idea is to split the vector variable $x \in \mathbb{R}^n$ of the continuous system $\dot{x} = Ax + F(x)$ into two components, the first belonging to the one-dimensional eigenspace T^c of $\lambda = 0$ and the other component to the $(n-1)$-dimensional eigenspace T^{su} referring to all the other eigenvalues. This is done in the following way:

$$x = \underbrace{uq}_{\in T^c} + \underbrace{y}_{\in T^{su}}, \quad u \in \mathbb{R}, q, y \in \mathbb{R}^n. \tag{5.44}$$

$$Aq = 0, \quad \langle q, q \rangle = 1. \tag{5.45}$$

The system is then transformed into the $(n+1)$-dimensional system

$$\dot{u} = a(\mu)u^2 + c(\mu)u^3 + \mathcal{O}(u^4) \tag{5.46}$$

$$\dot{y} = Ay + \frac{1}{2}\left(\frac{\partial^2 F(uq)}{\partial u^2}|_{u=0} - \frac{\partial^2}{\partial u^2}\langle p, F(uq)\rangle|_{u=0} q\right) u^2 + \cdots \tag{5.47}$$

The restriction to the centre manifold takes the form of Equation (5.46), with the following coefficients at the bifurcation moment $\mu = 0$:

$$a(0) = \frac{1}{2}\langle p, B(q,q)\rangle, \quad A^T p = 0, \langle p, q \rangle = 1. \tag{5.48}$$

$$c(0) = \frac{1}{6}\langle p, C(q,q,q) + 3B(q,h)\rangle, \tag{5.49}$$

$$\begin{pmatrix} A & q \\ p^T & 0 \end{pmatrix}\begin{pmatrix} h \\ s \end{pmatrix} = \begin{pmatrix} -B(q,q) \\ 0 \end{pmatrix} \tag{5.50}$$

$C(u,v,w)$ and $B(u,v)$ are given in Equations (5.42) and (5.43). It turns out that tracking fold and cusp bifurcations is essentially a question of computing the coefficients $a(\mu)$ and $c(\mu)$. The next propositions will show some identities that facilitate the computation while profiting from the Resultant (5.29).

Proposition 57 *Let* $F(X,Z,\lambda) = \sum_{i=1}^{n} f_i(X,\lambda)Z^i = 0$ *and* $G(X,Z,\lambda) = \sum_{j=1}^{m} g_j(X,\lambda)Z^j = 0$ *with* F *and* G *smooth enough. If we assume that* $\frac{\partial F}{\partial Z}|_{(X_0, Z_1^{i_0})} \neq 0$ *and* $\frac{\partial G}{\partial Z}|_{(X_0, Z_1^{j_0})} \neq 0$ *and if* $\mathrm{Res}_Z(F,G)$ *admits a root at* X_0 *up to its third derivative with respect to* X*, then* Z *can be written as a function of* X *in a neighborhood of* X_0 *and the system of polynomials*

$$\begin{cases} F(X,Z,\lambda) \\ G(X,Z,\lambda) \end{cases}$$

admits the following identities at solution (X_0, Z_0) *where* $Z(X_0) = Z_0$

$$\frac{dF}{dX} = \frac{\partial F}{\partial X} + \frac{\partial F}{\partial Z}\frac{dZ}{dX} = 0. \tag{5.51}$$
$$\frac{d^2F}{dXdZ} = \frac{\partial^2 F}{\partial X\partial Z} + \frac{\partial^2 F}{\partial Z^2}\frac{dZ}{dX} = 0. \tag{5.52}$$
$$\frac{d^2F}{dX^2} = \frac{\partial^2 F}{\partial X^2} + 2\frac{\partial^2 F}{\partial X\partial Z}\frac{dZ}{dX} + \frac{\partial^2 F}{\partial Z^2}\left(\frac{dZ}{dX}\right)^2 + \frac{\partial F}{\partial Z}\frac{d^2Z}{dX^2} = 0. \tag{5.53}$$
$$\frac{d^3F}{dXdZ^2} = \frac{\partial^3 F}{\partial X\partial Z^2} + \frac{\partial^3 F}{\partial Z^3}\frac{dZ}{dX} = 0. \tag{5.54}$$
$$\frac{d^3F}{dX^2dZ} = \frac{\partial^3 F}{\partial^2 X\partial Z} + 2\frac{\partial^3 F}{\partial X\partial Z^2}\frac{dZ}{dX} + \frac{\partial^3 F}{\partial Z^3}\frac{dZ}{dX} + \frac{\partial^2 F}{\partial Z^2}\frac{d^2Z}{dX^2} = 0. \tag{5.55}$$
$$\frac{d^3F}{dX^3} = \frac{\partial^3 F}{\partial X^3} + 3\frac{\partial^3 F}{\partial X^2\partial Z}\frac{dZ}{dX} + 3\frac{\partial^3 F}{\partial X\partial Z^2}\left(\frac{dZ}{dX}\right)^2 + 3\frac{\partial^2 F}{\partial X\partial Z}\frac{d^2Z}{dX^2}$$
$$+\frac{\partial^3 F}{\partial Z^3}\left(\frac{dZ}{dX}\right)^3 + 3\frac{\partial^2 F}{\partial Z^2}\frac{dZ}{dX}\frac{d^2Z}{dX^2} + \frac{\partial F}{\partial Z}\frac{d^3Z}{dX^3} = 0. \tag{5.56}$$

Same identities hold by replacing F *with* G*. The converse is true.*

Proof: As in Definition 4.2.1, the resultant of F and G with respect to Z and then its derivatives up to third order with respect to X are given by

$$\mathrm{Res}_Z(F,G) = f_n^m g_m^n \prod_{i,j}(Z_1^i - Z_2^j) \tag{5.57}$$
$$\frac{d\,\mathrm{Res}_Z(F,G)}{dX} = m f_n^{m-1} g_m^n f_n' \prod_{i,j}(Z_1^i - Z_2^j) + n f_n^m g_m^{n-1} g_n' \prod_{i,j}(Z_1^i - Z_2^j)$$
$$+f_n^m g_m^n \left(\sum_{i_0,j_0}\left(\frac{dZ_1^{i_0}}{dX} - \frac{dZ_2^{j_0}}{dX}\right)\prod_{i\neq i_0, j\neq j_0}(Z_1^i - Z_2^j)\right) \tag{5.58}$$
$$\frac{d^2\,\mathrm{Res}_Z(F,G)}{dX^2} = \frac{d^2 f_n^m g_m^n}{dX^2}\prod_{i,j}(Z_1^i - Z_2^j)$$
$$+f_n^m g_m^n \left(\sum_{i_0,j_0}\left(\frac{d^2Z_1^{i_0}}{dX^2} - \frac{d^2Z_2^{j_0}}{dX^2}\right)\prod_{i\neq i_0, j\neq j_0}(Z_1^i - Z_2^j)\right) \tag{5.59}$$
$$\frac{d^3\,\mathrm{Res}_Z(F,G)}{dX^3} = \frac{d^3 f_n^m g_m^n}{dX^3}\prod_{i,j}(Z_1^i - Z_2^j)$$
$$+f_n^m g_m^n \left(\sum_{i_0,j_0}\left(\frac{d^3Z_1^{i_0}}{dX^3} - \frac{d^3Z_2^{j_0}}{dX^3}\right)\prod_{i\neq i_0, j\neq j_0}(Z_1^i - Z_2^j)\right) \tag{5.60}$$

Having $\frac{\partial F}{\partial Z}|_{(X_0, Z_1^{i_0})} \neq 0$ and $\frac{\partial G}{\partial Z}|_{(X_0, Z_1^{j_0})} \neq 0$ contributes then to the existence of two functions $Z_1(X)$ and $Z_2(X)$ in a neighborhood of X_0. Following the notation in Proposition 19, these functions equates at X_0 i.e. $Z_1(X_0) = Z_2(X_0) = Z_1^{i_0} = Z_2^{j_0} = Z_0$. The identities above are then the outcome of differentiating F and G along the roots curves $Z_1(X)$

and $Z_2(X)$ in a neighborhood of X_0 at the point (X_0, Z_0). Therefore, the right-hand sides of the identities are set to zero. It remains to argue that a unified notation resembled by $\frac{d^kZ}{dX^k},\ k = 0,1,2$ is legitimate for both identities of F and G. This is profited from setting the polynomials in (5.57), (5.58), (5.59) and (5.60) to zero. We notice that $\frac{d^k \operatorname{Res}_Z(F,G)}{dX^k}|_{X_0} = 0 \implies \frac{d^kZ_1^{i0}}{dX^k} = \frac{d^kZ_2^{j0}}{dX^k}$, where, by $\frac{d^kZ_1^{i0}}{dX^k}$, we mean $\frac{d^kZ_1}{dX^k}|_{(X_0,Z_1^{i_0})}$ and similarly, $\frac{d^kZ_2^{j0}}{dX^k}$ is the notation for $\frac{d^kZ_2}{dX^k}|_{(X_0,Z_2^{j_0})}$. Therefore, let us denote with $\frac{d^kZ}{dX^k}$ simply both $\frac{d^kZ_1}{dX^k}$ and $\frac{d^kZ_2}{dX^k}$. The identities are then mere calculation.

Let us now investigate the converse of the statement. The first derivative $\frac{d \operatorname{Res}_Z(F,G)}{dX}|_{X_0} = 0$ implies that the following matrix

$$\begin{pmatrix} \frac{\partial F}{\partial X} & \frac{\partial F}{\partial Z} \\ \\ \frac{\partial G}{\partial X} & \frac{\partial G}{\partial Z} \end{pmatrix}|_{(X_0,Z_0)} \tag{5.61}$$

has a zero determinant which is equivalent to the identity (5.51) for both F and G. Proving the forward and backward directions was done in Proposition 19. We consider the second-order case when $\frac{d^2 \operatorname{Res}_Z(F,G)}{dX^2}|_{X_0} = 0$. This generates the following equations at (X_0, Z_0) after simplifying (5.53) by using (5.51) and (5.52):

$$\frac{\partial^2 F}{\partial X^2} - \frac{\partial^2 F}{\partial Z^2}\left(\frac{dZ}{dX}\right)^2 + \frac{\partial F}{\partial Z}\frac{d^2Z}{dX^2} = 0 \tag{5.62}$$

$$\frac{\partial^2 G}{\partial X^2} - \frac{\partial^2 G}{\partial Z^2}\left(\frac{dZ}{dX}\right)^2 + \frac{\partial G}{\partial Z}\frac{d^2Z}{dX^2} = 0 \tag{5.63}$$

which is equivalent to the matrix equation:

$$\begin{pmatrix} \frac{\partial^2 F}{\partial X^2} & \frac{\partial^2 F}{\partial Z^2} & \frac{\partial F}{\partial Z} \\ \\ \frac{\partial^2 G}{\partial X^2} & \frac{\partial^2 G}{\partial Z^2} & \frac{\partial G}{\partial Z} \end{pmatrix}|_{(X_0,Z_0)} \begin{pmatrix} 1 \\ \\ -\left(\frac{dZ}{dX}\right)^2 \\ \\ \frac{d^2Z}{dX^2} \end{pmatrix}|_{X_0} = \begin{pmatrix} 0 \\ \\ 0 \end{pmatrix} \tag{5.64}$$

which means that

$$\begin{pmatrix} \frac{\partial^2 F}{\partial X^2} & \frac{\partial^2 F}{\partial Z^2} & \frac{\partial F}{\partial Z} \\ \\ \frac{\partial^2 G}{\partial X^2} & \frac{\partial^2 G}{\partial Z^2} & \frac{\partial G}{\partial Z} \end{pmatrix}|_{(X_0,Z_0)} \tag{5.65}$$

has a rank one. Without loss of generality, this means that its rows are multiple of each other. Now proving the converse, suppose that Matrix 5.65 is a rank one matrix and thus its rows are multiple of each other. Now differentiating over the solution functions Z_1 and Z_2 for F and G respectively, the following identities do hold at (X_0, Z_0):

$$\frac{\partial^2 F}{\partial X^2} - \frac{\partial^2 F}{\partial Z_1^2}\left(\frac{dZ_1}{dX}\right)^2 + \frac{\partial F}{\partial Z_1}\frac{d^2Z_1}{dX^2} = 0 \tag{5.66}$$

$$\frac{\partial^2 G}{\partial X^2} - \frac{\partial^2 G}{\partial Z_2^2}\left(\frac{dZ_2}{dX}\right)^2 + \frac{\partial G}{\partial Z_2}\frac{d^2Z_2}{dX^2} = 0 \tag{5.67}$$

Knowing that $\frac{dZ_1}{dX}|_{X_0} = \frac{dZ_2}{dX}|_{X_0}$, it is easy then to check that $\frac{d^2Z_1}{dX^2}|_{X_0} = \frac{d^2Z_2}{dX^2}|_{X_0}$ upon using the Identities (5.66),(5.67) and the rank one property of the Matrix 5.65. They imply that $\frac{d^2 \operatorname{Res}_Z(F,G)}{dX^2}|_{X_0} = 0$. Same analysis can be done for proving the converse of $\frac{d^3 \operatorname{Res}_Z(F,G)}{dX^3}|_{X_0} = 0 \implies$ Identities 5.56 for both F and G. $\square$

Proposition 58 *Consider System (5.38-5.39) and its resultant* $\operatorname{Res}_Z(\dot{X}, \dot{Z})$ *same as in (5.29). We embrace the same notation as in (5.40) for the right-hand sides of* $\dot{X}$ *and* $\dot{Z}$. *Suppose that* $\frac{d^k \operatorname{Res}_Z(f_1,f_2)}{dX^k}|_{X_0} = 0, \ \ k = 0, 1, 2$ *where* (X_0, Z_0) *is a solution of System* $(5.38 - 5.39)$. *We let* $\frac{\partial f_1}{\partial Z}|_{(X_0,Z_0)}, \frac{\partial f_2}{\partial Z}|_{(X_0,Z_0)} \neq 0$. *Then the linearization of System (5.38-5.39) admits a zero eigenvalue at* (X_0, Z_0). *Moreover, the restriction to the centre manifold as in (5.46) upon transforming the system admits the coefficient* $a(0) = 0$ *for the given parameters* (a, b, e). *The converse is true.*

Proof: The proof of the equivalence for which a zero eigenvalue of f at $(X_0, Z_0) \iff \frac{d \operatorname{Res}_Z(f_1,f_2)}{dX}|_{X_0} = 0$ was done in Proposition 19. From now on we use alternatively the notation f_{iX} instead of $\frac{\partial f_i}{\partial X}$ and $Z_X^{(k)}$ instead of $\frac{d^k Z}{dX^k}$. Solving for q and p as in (5.44) and (5.48) respectively, let $f_{1X} \neq 0$. The other case is trivial.

$$q = \frac{1}{\sqrt{(-\frac{f_{1Z}}{f_{1X}})^2 + 1}} \begin{pmatrix} -\frac{f_{1Z}}{f_{1X}} \\ \\ 1 \end{pmatrix}|_{(X_0,Z_0)} \tag{5.68}$$

$$p = \frac{1}{\sqrt{(-\frac{f_{2X} f_{1Z}}{f_{1X}^2})^2 + 1}} \begin{pmatrix} -\frac{f_{2X}}{f_{1X}} \\ \\ 1 \end{pmatrix}|_{(X_0,Z_0)} \tag{5.69}$$

We have the following identities after simplifying those in Proposition 57:

$$f_{1X} = -f_{1Z} Z'_X. \tag{5.70}$$
$$f_{1XZ} = -f_{1ZZ} Z'_X. \tag{5.71}$$
$$f_{1XX} = f_{1ZZ} Z'^2_X - f_{1Z} Z''_X. \tag{5.72}$$
$$f_{1XZZ} = -f_{1ZZZ} Z'_X. \tag{5.73}$$
$$f_{1XXZ} = 2f_{1ZZZ} Z'^2_X - f_{1ZZZ} Z'_X - f_{1ZZ} Z''_X. \tag{5.74}$$
$$f_{1XXX} = -4f_{1ZZZ} Z'^3_X + 3f_{1ZZZ} Z'^2_X + 3f_{1ZZ} Z'_X Z''_X - f_{1Z} Z'''_X. \tag{5.75}$$

Similar identities hold by replacing f_1 by f_2. According to the assumption, it is possible to use any of the simplified identities except (5.75) since it contains a third derivative $Z'''_X|_{X_0}$ which is not necessarily common between Z_1 and Z_2 of f_1 and f_2 respectively. Using these identities and substituting in $B(q, q)$, we compute the following matrix:

$$B(q,q) = \frac{1}{(-\frac{f_{1Z}}{f_{1X}})^2 + 1} \begin{pmatrix} -f_{1Z} \frac{Z''_X}{Z'^2_X} \\ \\ -f_{2Z} \frac{Z''_X}{Z'^2_X} \end{pmatrix}|_{(X_0,Z_0)} \tag{5.76}$$

Now computing $a(0)$ and making use of the simplified identities

$$\begin{aligned}a(0) &= \frac{1}{2}\langle p, B(q,q)\rangle|_{(X_0,Z_0)}\\ &= \frac{1}{2\sqrt{(-\frac{f_{2X}f_{1Z}}{f_{1X}^2})^2+1}}\frac{1}{(-\frac{f_{1Z}}{f_{1X}})^2+1}\left[\left(-\frac{f_{2X}}{f_{1X}}\right)\left(-f_{1Z}\frac{Z''_X}{Z'^2_X}\right)\right.\\ &\left.+\left(-f_{2Z}\frac{Z''_X}{Z'^2_X}\right)\right] = 0. \end{aligned} \tag{5.77}$$

We prove now the other direction, that $a(0) = 0 \implies \frac{d^2\,\mathrm{Res}_Z(f_1,f_2)}{dX^2}|_{X_0} = 0$. Following the assumption, we notice that $\langle p, B(q,q)\rangle = 0$ is equivalent up to a scalar factor to having the following matrix system zero at (X_0, Z_0)

$$\begin{pmatrix} -\frac{f_{2X}}{f_{1X}} \\ 1 \end{pmatrix} \begin{pmatrix} \begin{pmatrix} -\frac{f_{1Z}}{f_{1X}} & 1 \end{pmatrix}\begin{pmatrix} f_{1XX} & f_{1XZ} \\ f_{1XZ} & f_{1ZZ}\end{pmatrix}\begin{pmatrix} -\frac{f_{1Z}}{f_{1X}} \\ 1\end{pmatrix} \\ \begin{pmatrix} -\frac{f_{1Z}}{f_{1X}} & 1 \end{pmatrix}\begin{pmatrix} f_{2XX} & f_{2XZ} \\ f_{2XZ} & f_{2ZZ}\end{pmatrix}\begin{pmatrix} -\frac{f_{1Z}}{f_{1X}} \\ 1\end{pmatrix}\end{pmatrix} = 0 \tag{5.78}$$

Profiting from the already done proof of the converse implication of the zero eigenvalue, we know that Identity (5.70) still holds for f_1 evidently and for f_2 by replacing f_1 with f_2 in (5.70). System (5.78) can then be simplified into

$$\begin{pmatrix} -\frac{f_{2Z}}{f_{1Z}} \\ 1 \end{pmatrix}|_{(X_0,Z_0)} \begin{pmatrix} \frac{f_{1XX}}{Z'^2_X} + 2\frac{f_{1XZ}}{Z'_X} + f_{1ZZ} \\ \frac{f_{2XX}}{Z'^2_X} + 2\frac{f_{2XZ}}{Z'_X} + f_{2ZZ} \end{pmatrix}|_{(X_0,Z_0)} = 0 \tag{5.79}$$

which implies that

$$\left(\frac{f_{1XX}}{Z'^2_X} + 2\frac{f_{1XZ}}{Z'_X} + f_{1ZZ}\right)|_{(X_0,Z_0)} = \frac{f_{1Z}}{f_{2Z}}\left(\frac{f_{2XX}}{Z'^2_X} + 2\frac{f_{2XZ}}{Z'_X} + f_{2ZZ}\right)|_{(X_0,Z_0)}. \tag{5.80}$$

Now computing $\frac{d^2 f_1}{dX^2}$ and $\frac{d^2 f_2}{dX^2}$ along Z_1 and Z_2, we get the identities as in (5.53) at (X_0, Z_0):

$$\frac{d^2 f_1}{dX^2} = \frac{\partial^2 f_1}{\partial X^2} + 2\frac{\partial^2 f_1}{\partial X \partial Z_1}\frac{dZ_1}{dX} + \frac{\partial^2 f_1}{\partial Z_1^2}\left(\frac{dZ_1}{dX}\right)^2 + \frac{\partial f_1}{\partial Z_2}\frac{d^2 Z_1}{dX^2} = 0. \tag{5.81}$$

$$\frac{d^2 f_2}{dX^2} = \frac{\partial^2 f_2}{\partial X^2} + 2\frac{\partial^2 f_2}{\partial X \partial Z_2}\frac{dZ_2}{dX} + \frac{\partial^2 f_2}{\partial Z_2^2}\left(\frac{dZ_2}{dX}\right)^2 + \frac{\partial f_2}{\partial Z_2}\frac{d^2 Z_2}{dX^2} = 0. \tag{5.82}$$

Knowing that $\frac{dZ_1}{dX}|_{X_0} = \frac{dZ_2}{dX}|_{X_0}$ and substituting (5.80) in (5.81), we easily obtain $\frac{d^2 Z_1}{dX^2}|_{X_0} = \frac{d^2 Z_2}{dX^2}|_{X_0}$ and thus $\frac{d^2\,\mathrm{Res}_Z(f_1,f_2)}{dX^2}|_{X_0} = 0$ is established. □

Proposition 59 *Under the same settings of Proposition 58, if in addition* $\frac{d^3\,\mathrm{Res}_Z(f_1,f_2)}{dX^3}|_{X_0} = 0$*, then the restriction to the centre manifold as in (5.46) upon transforming the system admits the coefficients* $a(0) = 0$ *and* $c(0) = 0$ *for the given parameters* (a, b, e) *and the converse is true.*

Proof: We need to compute the coefficient $c(0)$ of the restriction to the centre manifold as in (5.46). It was proven in Proposition 58 that $a(0) = 0$, it is enough then to show that $c(0) = 0$. We start by computing h as in (5.50), we have upon using the simplified identities of the previous proposition

$$h = \begin{pmatrix} h_1 \\ \\ h_2 \end{pmatrix} = \begin{pmatrix} \frac{f_{1Z}}{f_{2Z} - f_{1Z} Z'_X} \frac{Z''_X}{Z'^2_X} \\ \\ \frac{f_{2Z}}{f_{1Z}} h_1 \end{pmatrix} |_{(X_0, Z_0)} \tag{5.83}$$

Now computing $B(q, h)$, we get the following matrix:

$$B(q, h) = \begin{pmatrix} -f_{1Z} \frac{Z''_X}{Z'_X} h_1 \\ \\ -f_{2Z} \frac{Z''_X}{Z'_X} h_1 \end{pmatrix} |_{(X_0, Z_0)} \tag{5.84}$$

It follows that

$$\begin{aligned} \langle p, B(q, h) \rangle |_{(X_0, Z_0)} &= h_1 \left(-\frac{f_{2X}}{f_{1X}} \left(-f_{1Z} \frac{Z''_X}{Z'_X} \right) + \left(-f_{2Z} \frac{Z''_X}{Z'_X} \right) \right) \\ &= h_1 \left(f_{2Z} \frac{Z''_X}{Z'_X} - f_{2Z} \frac{Z''_X}{Z'_X} \right) = 0. \end{aligned} \tag{5.85}$$

Now computing $C(q, q, q)$, we get the following matrix:

$$C(q, q, q) = \frac{1}{((-\frac{f_{1Z}}{f_{1X}})^2 + 1)^{\frac{3}{2}}} \begin{pmatrix} -f_{1Z} \frac{Z'''_X}{Z'^3_X} \\ \\ -f_{2Z} \frac{Z'''_X}{Z'^3_X} \end{pmatrix} |_{(X_0, Z_0)} \tag{5.86}$$

and it follows that

$$\begin{aligned} \langle p, C(q, q, q) \rangle |_{(X_0, Z_0)} &= \frac{1}{((-\frac{f_{1Z}}{f_{1X}})^2 + 1)^{\frac{3}{2}}} \frac{1}{2\sqrt{(-\frac{f_{2X} f_{1Z}}{f_{1X}^2})^2 + 1}} \left[-\frac{f_{2X}}{f_{1X}} \left(-f_{1Z} \frac{Z'''_X}{Z'^3_X} \right) \right. \\ &\left. + \left(-f_{2Z} \frac{Z'''_X}{Z'^3_X} \right) \right] \\ &= f_{2Z} \frac{Z'''_X}{Z'^3_X} - f_{2Z} \frac{Z'''_X}{Z'^3_X} = 0. \end{aligned} \tag{5.87}$$

Therefore,

$$c(0) = \frac{1}{6} \langle p, C(q, q, q) + 3B(q, h) \rangle = 0.$$

as required.

Now proving the converse of the statement, we assume that $c(0) = 0$ in addition to $a(0) = 0$ and the zero eigenvalue case discussed before. It is therefore

$$c(0) = \frac{1}{6} \langle p, C(q, q, q) \rangle + \frac{1}{6} \langle p, B(q, h) \rangle = \frac{1}{6} \langle p, C(q, q, q) \rangle + 0 \tag{5.88}$$

since $\langle p, B(q,h)\rangle = 0$ follows from (5.85) where only second-order in X identities were used. It was proven in Proposition 58 that these identities hold if $a(0) = 0$. The assumption is then that $\langle p, C(q,q,q)\rangle = 0$. This can be written up to a scalar factor and upon using the first and second-order identities in the following matrix form:

$$\begin{pmatrix} -\frac{f_{2X}}{f_{1X}} & 1 \end{pmatrix}|_{(X_0,Z_0)} \begin{pmatrix} \frac{f_{1XXX}}{Z_X'^3} + 3\frac{f_{1XXZ}}{Z_X'^2} + 3\frac{f_{1XZZ}}{Z_X'} + f_{1ZZZ} \\ \frac{f_{2XXX}}{Z_X'^3} + 3\frac{f_{2XXZ}}{Z_X'^2} + 3\frac{f_{2XZZ}}{Z_X'} + f_{2ZZZ} \end{pmatrix}|_{(X_0,Z_0)} = 0 \quad (5.89)$$

which implies that

$$\left(\frac{f_{1XXX}}{Z_X'^3} + 3\frac{f_{1XXZ}}{Z_X'^2} + 3\frac{f_{1XZZ}}{Z_X'} + f_{1ZZZ}\right)|_{(X_0,Z_0)} = \frac{f_{1Z}}{f_{2Z}}\left(\frac{f_{2XXX}}{Z_X'^3} + 3\frac{f_{2XXZ}}{Z_X'^2} + 3\frac{f_{2XZZ}}{Z_X'} + f_{2ZZZ}\right)|_{(X_0,Z_0)} \quad (5.90)$$

We substitute this quantity in $\frac{d^3 f_1}{dX^3}$ and $\frac{d^3 f_2}{dX^3}$ given by the following expressions at Z_1 and Z_2 given by (5.56):

$$\begin{aligned} \frac{d^3 f_1}{dX^3} &= \frac{\partial^3 f_1}{\partial X^3} + 3\frac{\partial^3 f_1}{\partial X^2 \partial Z_1}\frac{dZ_1}{dX} + 3\frac{\partial^3 f_1}{\partial X \partial Z_1^2}\left(\frac{dZ_1}{dX}\right)^2 + 3\frac{\partial^2 f_1}{\partial X \partial Z_1}\frac{d^2 Z_1}{dX^2} \\ &+ \frac{\partial^3 f_1}{\partial Z_1^3}\left(\frac{dZ_1}{dX}\right)^3 + 3\frac{\partial^2 f_1}{\partial Z_1^2}\frac{dZ_1}{dX}\frac{d^2 Z_1}{dX^2} + \frac{\partial f_1}{\partial Z_1}\frac{d^3 Z_1}{dX^3} = 0. \end{aligned} \quad (5.91)$$

$$\begin{aligned} \frac{d^3 f_2}{dX^3} &= \frac{\partial^3 f_2}{\partial X^3} + 3\frac{\partial^3 f_2}{\partial X^2 \partial Z_2}\frac{dZ_2}{dX} + 3\frac{\partial^3 f_2}{\partial X \partial Z_2^2}\left(\frac{dZ_2}{dX}\right)^2 + 3\frac{\partial^2 f_2}{\partial X \partial Z_2}\frac{d^2 Z_2}{dX^2} \\ &+ \frac{\partial^3 f_2}{\partial Z_2^3}\left(\frac{dZ_2}{dX}\right)^3 + 3\frac{\partial^2 f_2}{\partial Z_2^2}\frac{dZ_2}{dX}\frac{d^2 Z_2}{dX^2} + \frac{\partial f_2}{\partial Z_2}\frac{d^3 Z_2}{dX^3} = 0. \end{aligned} \quad (5.92)$$

It is then easy to check that $\frac{d^3 Z_1}{dX^3}|_{X_0} = \frac{d^3 Z_2}{dX^3}|_{X_0}$, knowing that $f_{1XZ} = \frac{f_{1Z}}{f_{2Z}} f_{2XZ}$ and $f_{1ZZ} = \frac{f_{1Z}}{f_{2Z}} f_{2ZZ}$ are a direct outcome of $a(0) = 0$. Consequently, $\frac{d^3\,\mathrm{Res}_Z(f_1,f_2)}{dX^3}|_{X_0} = 0$. □

In order to prove the occurrence of cusp bifurcation for System (5.26-5.28), three characteristics must hold at an equilibrium (X_0, Z_0, W_0): First, the Jacobian matrix must admit a zero eigenvalue at the equilibrium. Second, $a(0) = 0$. Third, $c(0) \neq 0$. Evidently, if (X_0, Z_0, W_0) is an equilibrium then $\mathrm{Res}_Z(\dot{X}, \dot{Z})|_{(X_0,Z_0)} = 0$. We conclude from Propositions 57, 58 and 59 that the three characteristics are equivalent to having $\frac{d\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{dX}|_{(X_0,Z_0)} = 0$, $\frac{d^2\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{d^2X}|_{(X_0,Z_0)} = 0$ and $\frac{d^3\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{d^3X}|_{(X_0,Z_0)} \neq 0$ respectively. To make things easier, we simplify the resultant in (5.29) in the following manner: $\frac{\mathrm{Res}_Z(\dot{X},\dot{Z})}{a^6 e^5}$ and then we consider this simplified resultant with its derivatives.

$$\mathrm{Res}_Z(\dot{X},\dot{Z}) = X^5 e(X-1)^5\left[X^2+(-1-6a)X+3ab\right]+486X^2+243X \tag{5.93}$$

$$\frac{d\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{dX} = 3X^4 e(X-1)^4\left[4X^3+(-22a-6)X^2+(12a+10ab+2)X-5ab\right] \\ +972X+243 \tag{5.94}$$

$$\frac{d^2\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{dX^2} = 6X^3 e(X-1)^3\left[22X^4+(-110a-44)X^3+(120a+45ab+27)X^2\right. \\ \left.+(-30a-45ab-5)X+10ab\right]+972 \tag{5.95}$$

$$\frac{d^3\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{dX^3} = 60X^2 e(X-1)^2\left[22X^5+(-99a-55)X^4+(162a+36ab+48)X^3\right. \\ \left.+(-81a-54ab-17)X^2+(12a+24ab+2)X-3ab\right] \tag{5.96}$$

Setting (5.93), (5.94) and (5.95) to zero and solving for e gives rise to e_0, e_1 and e_2 respectively. These are rational functions depending on X, a and b. Now setting $e_0 = e_1$ and $e_1 = e_2$ at X_0 suffices to having the first and second characteristic satisfied. $e_0 = e_1$ is equivalent to the following identity at X_0:

$$20X^4+(-108a-17)X^3+(48ab-12a-8)X^2+(30a+9ab+5)X-12ab=0 \tag{5.97}$$

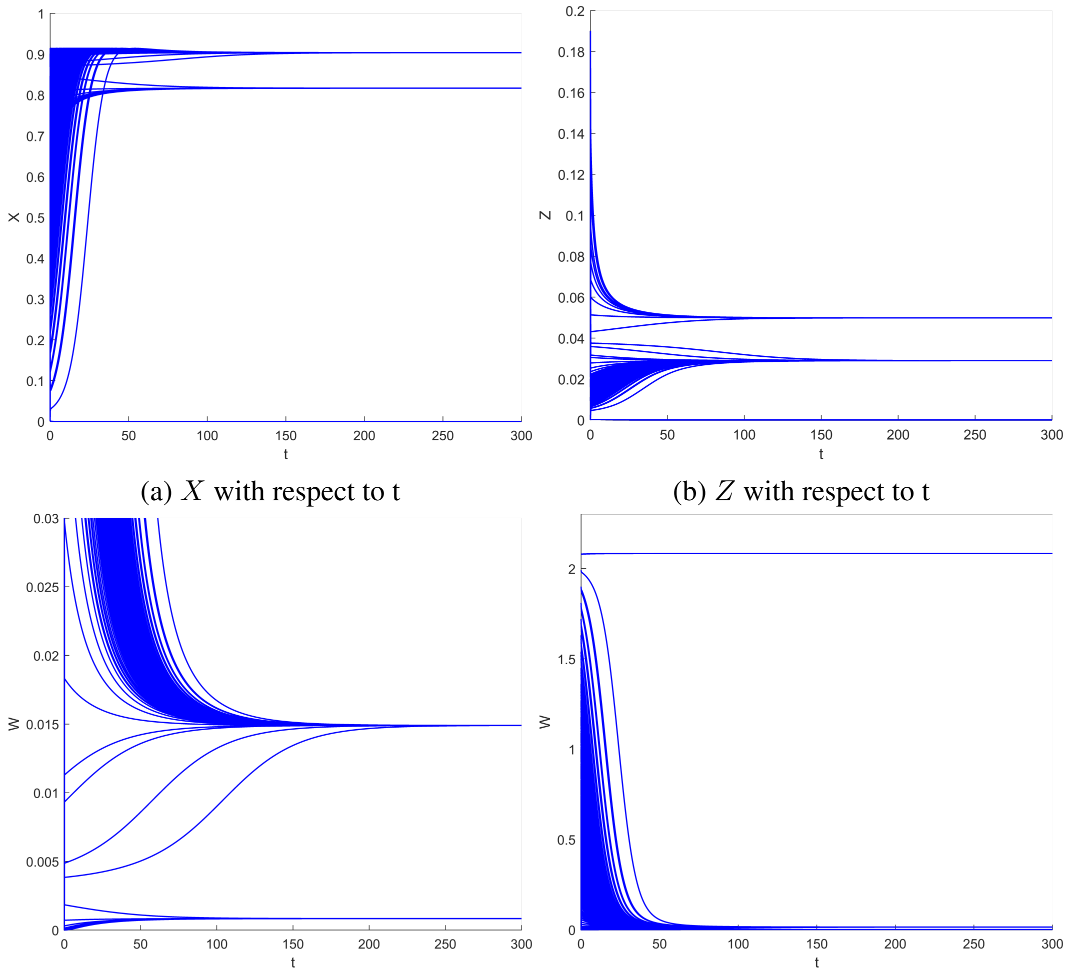
$e_1 = e_2$ generates the following identity at X_0

$$80X^5+(-396a-134)X^4+(302a+160ab+48)X^3+(24a-105ab+11)X^2 \\ +(-30a-15ab-5)X+10ab=0 \tag{5.98}$$

while the third characteristic is equivalent to having $\frac{d^3\,\mathrm{Res}_Z(\dot{X},\dot{Z})}{dX^3}|_{X_0} \neq 0$ and then it is equivalent to the following non-equality:

$$60X^2 e(X-1)^2\left[22X^5+(-99a-55)X^4+(162a+36ab+48)X^3\right. \\ \left.+(-81a-54ab-17)X^2+(12a+24ab+2)X-3ab\right]|_{X_0} \neq 0 \tag{5.99}$$

As an example, we fix a value for parameter a. Then we substitute this value in the resultant of the Polynomials (5.97) and (5.98) and then we solve for b. We can then solve for X and subsequently for e. Having all the data at hand, we can then compute $a(0)$ and $c(0)$ in an interval of confidence. For instance, for $a = \frac{1}{9}$, we obtain $b \approx 2.086240313$ and the equilibrium, for which the cusp occurs, is approximately at $(0.8586160316, 0.040464847293, 0.004824624163)$. Then $e \approx 1.337192592 \times 10^{10}$ and $c(0) \approx -9716317.38$. All the conditions for cusp bifurcation are satisfied. Moreover, it is guaranteed that no degenerate cusp will be encountered for all parameter domain, where a cusp occurs. Taking the resultant of (5.99) and (5.98) and that of (5.97) and (5.98), we notice that there are no relevant parameters a and b, for which both are zero. In nearby region, the cusp point bifurcates into three equilibria, two of them are stable. In this case, the model admits three stable equilibria, two positive ones besides the trivial equilibrium $(0, 0, b)$. This is illustrated in Figure 5.8 when taking the following choice of parameters $(a, b, e) = \left(\frac{1}{9}, \frac{(6a+1)^2}{12a}, 3 \times 10^{10}\right)$. Upon starting



(a) X with respect to t
(b) Z with respect to t
(c) W with respect to t
(d) W with respect to t (different range)

Figure 5.8: Three stable steady states exist for $(a, b, e) = \left(\frac{1}{9}, \frac{(6a+1)^2}{12a}, 3 \times 10^{10}\right)$. The higher stable equilibrium for W is at b and it corresponds to the trivial steady state $(0, 0, b)$ for the model

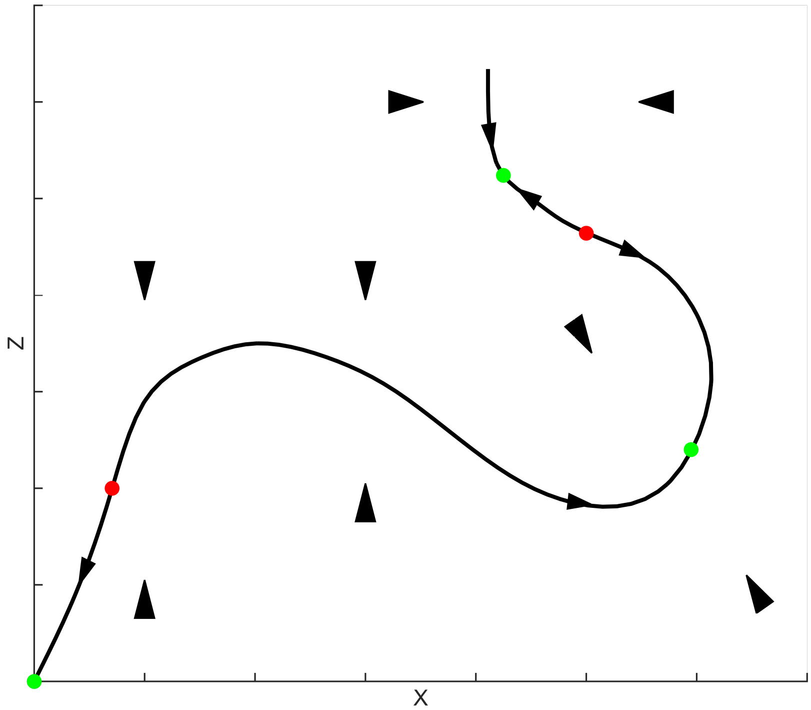


Figure 5.9: Dynamics near the one-dimensional manifold where equilibria are located rush toward it. The essential dynamics then take place over this manifold. Green points represent stable equilibria while red ones represent unstable equilibria

from different initial states, solutions converge to one of the three stable equilibria. Figure 5.9 is a schematic but realistic figure of the one-dimensional manifold, where all equilibria are located. At least three of the equilibria are not related to each other by partial order in the non-negative orthant $\mathbb{R}^3_{\geq 0}$. In contrary to Hahn's model studied in the last chapters, this un-order limits the application of the huge literature of results in monotone systems, especially those satisfying the strongly order preserving property.

Proposition 60 *System (5.38-5.39) undergoes simple fold bifurcation in Case (I)(a),(b) and (c) and in Case (II)(a). In Case (II)(b), it undergoes generically two successive simple fold bifurcations and in Case (II)(c), it undergoes generically three successive simple fold bifurcations. Hysteresis phenomenon is witnessed in Case (II)(c). Moreover, if System (5.38-5.39) admits unique steady state (i.e., at the trivial steady state $(0, 0, b)$), all solutions converge to this steady state later in time.*

Proof: In Cases (I)(a), (b), (c) and in the Case (II)(a), a change in the phase portrait of System (5.38-5.39) happens based on the schematic Figures 5.2, 5.3 and 5.4. These figures are u-shaped and in each there is $e_0 > 0$ such that for $e < e_0$ no non-trivial positive steady states exists for the system. For $e = e_0$, there exists exactly one non-trivial positive steady state and for $e > e_0$, there are two non-trivial positive steady states. This change in the number of non-trivial positive states must correspond to simple fold bifurcation. Based on Proposition 56, a change in the phase portrait is due to simple fold bifurcation or cusp bifurcation. In the mentioned cases, the trivial positive steady state $(0, 0, b)$ is a persistent

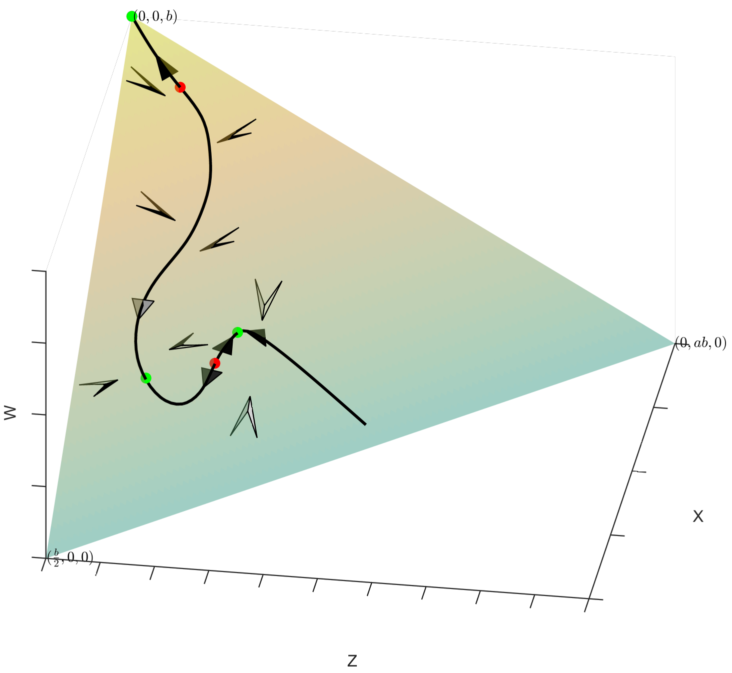


Figure 5.10: The dynamics of the singularly perturbed model take place over a two-dimensional manifold in $\mathbb{R}^3_{\geq 0}$. The figure shows the dynamics rushing toward a one-dimensional manifold where three stable equilibria are present

stable steady state that does not change with a change in parameters. Hence, it does not unite with any of the two non-trivial steady states. Notice that if this happens, one of the non-trivial steady states will unite alternatively with two steady states each time in a simple fold bifurcation. Hysteresis means this, the phenomenon implying cusp bifurcation for some choice of parameters.

In Case (II)(b), Figure 5.5 shows that there is $e_0, e_1 > 0$ such that for $e < \min\{e_0, e_1\}$ no non-trivial steady states exist. Suppose $e_0 < e_1$, then for $e = e_0$, e is at its minimum in one of the curves existing in one of the intervals $]0, \frac{6a+1}{2}[$ or $]\frac{6a+1}{2}, 1[$ and a single non-trivial steady state is born. For $e_1 > e > e_0$, two non-trivial steady states exist. For $e = e_1$, e is at the other minimum on the other curve in one of the intervals $]0, \frac{6a+1}{2}[$ or $]\frac{6a+1}{2}, 1[$ and there are three non-trivial positive steady states. For $e > e_1$, there are four non-trivial positive steady states. None of the steady states encountered in the interval $]0, \frac{6a+1}{2}[$ or $]\frac{6a+1}{2}, 1[$ undergo more than a single simple fold bifurcation. Hence, there is no hysteresis. If $e_0 = e_1$, then at $e = e_0 = e_1$, two non-trivial steady states exist and for $e > e_0 = e_1$, four non-trivial steady states exist. In all these, simple fold bifurcation occurs since all correspond to exactly two steady states uniting at $e = e_0$ and at $e = e_1$. Notice that when $e = e_0 = e_1$, two simultaneous simple fold bifurcations occur. However, this is not generic. In the last case, Case (II)(c) shown in Figure 5.6, it is numerically evident that there exist $\varepsilon > 0$ such that for $b \in]\frac{(6a+1)^2}{12a}, \frac{(6a+1)^2}{12a} + \varepsilon[$, there exist $0 < e_0 < e_1 < e_2$ with the following properties: For $e < e_0$, the unique positive steady state is the trivial steady state $(0, 0, b)$. For $e = e_0$, there is exactly a single non-trivial steady state and e is at its minimum value in the interval of relevance $]0, 1[$. For $e_1 > e > e_0$, there are two non-trivial steady states. For $e = e_1$, e hits a local minimum and there are three non-trivial steady states. For $e_2 > e > e_1$, there

exist four non-trivial steady states. For $e = e_2$, e is at its local maximum and two of the non-trivial positive steady states unite in a simple fold bifurcation. For $e > e_2$, a non-trivial positive steady state is lost and we are left with two non-trivial positive steady states.
Case (II)(c) corresponds then to the hysteresis phenomenon since there exist two non-trivial positive steady states undergoing with another non-trivial positive steady state two simple fold bifurcations alternatively. Once for $e = e_1$ and otherwise for $e = e_2$.
For all cases, whenever $(0, 0, b)$ is the single positive steady state, all solutions converge to it later. By applying the generalized Poincaré-Bendixson Theorem on the sufficiently smooth two-dimensional manifold (plane in $\mathbb{R}^3_{\geq 0}$) defined by $b = 2X + \frac{Z}{a} + W$, a solution converges either to a periodic orbit, a homoclinic or a heteroclinic connection between equilibria or to an equilibrium. However, $(0, 0, b)$ is then the unique equilibrium and it is asymptotically stable for every choice of positive parameters. Hence, all solutions must converge to $(0, 0, b)$ in future time. In the other cases, a solution converge into a heteroclinic connection (see Figure 5.10) of equilibria since periodic orbits are precluded for System (5.38-5.39) (Proposition 56). □

Conclusion

On Hysteresis in Photosynthesis

Hysteresis encountered in this chapter shows that photosynthesis can work in two different positive stable equilibria that do not lie on the boundary of the space of concentrations. It does not correspond to the exhaustion of some or many species, which is usually an extreme scenario (e.g., collapse of the cycle). When choosing a suitable set of parameters, a change in the parameter e causes a loss of one of these positive stable equilibria when it crosses a certain threshold upwards or downwards. In future modeling, it is reasonable to introduce some control function, which lets solutions switch between these two positive stable equilibria by leaving a neighborhood of one positive stable steady state into a neighborhood of the other positive steady state. The system would then behave like a toggle switch interchanging between two stable states. A good candidate for this feedback is the inhibition played by inorganic phosphate on the carboxylation/oxygenation reactions. It could then be interesting to implement a term like $\frac{1}{k+x_n^m}$ with x_n representing the concentration of inorganic phosphate P_i in the equations of System (5.38-5.39) (see the Example System 2.3 in Chapter 3). Although System (5.38-5.39) is monotone in nature, introducing such a term might lead to a new behavior provided that the negative feedback mechanism is powerful enough (see [81]). The robustness of monotonicity in System (5.38-5.39) will guarantee that this term will not destroy stable equilibria. However, it might introduce sustained oscillations (*relaxation oscillation*) having stable equilibria at their peaks and troughs and with a fast switch from a neighborhood of one into the neighborhood of the other. It is beyond this thesis's scope to assess hysteresis *in vitro*. It could be interesting to test this result experimentally. This is usually done once by adding a variant of inorganic phosphate into the chloroplast and checking the concentration of a traced species and otherwise by depleting inorganic phosphate into the cytosol. The experiment copes with the anticipated hysteresis if, upon adding inorganic phosphate, a steady state is reached, different from the stable steady state reached upon depleting it.

On RuBisCO

It is unusual that an enzyme is equally abundant as its substrates in nature. This is the case with RuBisCO, at the same time, a sluggish enzyme. It is reported that RuBisCO in the chloroplast is 1000 times as big as CO_2 and is comparable with RuBP. It was later discovered, after the revelation of the Calvin cycle, that RuBisCO is involved in a competitive inhibitor reaction of CO_2 fixation (see [77], [78]). Oxygen as an alternative substrate leads to photorespiration. The efforts to patch the sluggishness and promiscuity of this enzyme have not yet been successful [99]. However, once RuBisCO assimilates carbon, the reaction occurs irreversibly [105]. This confirms a long-standing belief that a trade-off exists in nature: High-rates enzymes are low-substrate-specific and vice versa [106]. Hence, oxygenation which pursues its activity at night (thus the naming "dark" respiration, see [37], [38]) is an essential process during photosynthesis and it should be explicitly recognized upon any modeling, which we have done.

On All Reactions Involved in Photosynthesis

Triose phosphate produced during the Calvin cycle is used for recovery of the cycle by regenerating RuBP. It is also partly used for starch synthesis in the chloroplast and partly depleted into the cytoplasm for a phosphate group entering through the entering inorganic phosphate from the cytosol. An elevated PGA concentration and reduced P_i one activates starch synthesis by activating ADP-glucose pyrophosphorylase [9]. In this case, or when too much TP is depleted toward the cytoplasm, the Calvin cycle is stressed at one of its substrates and will drastically collapse. The Calvin cycle's three key regulating processes are photorespiration, starch, sucrose synthesis, inorganic phosphate P_i translocation and the Calvin cycle functioning. These have been explicitly modeled in our model for photosynthesis. A more detailed model might include the regulating role of energy compounds ATP and NADPH, which we did not elaborate on since we assumed based on previous models that oscillations in ATP are temporary. The stability of ATP production during sunlight and the homogeneity of light intensity projecting the leaf (C_3 leaf) are customary assumptions. However, they are worth studying since it is well-known that RuBisCO activity changes with light intensity so that carboxylation's rate is coordinated with electron transport activity. In reality, RuBisCO activase, the enzyme-activator of RuBisCO, requires ATP to work. Additionally, it is shown in [66], [68] and [88] how ATP, NADPH and photosynthetic rates oscillate because of different sudden changes either in the pressure of CO_2 and O_2 in the light intensity or because of sudden darkness. The common conclusion of all this is that only damped oscillations are exhibited [25]. Moreover, oscillations are rapidly stabilized. Therefore, this backs our assumption of not including the light-phase ATP and NADPH production by the seemingly robust stable behavior. Photosynthesis modeled remains reluctant to sustained oscillations.

*

Appendix A

Computing $a(0)$ for Hahn's Three-Dimensional Model

Notice that it was unnecessary to prove that the second-order coefficient term $a(0) \neq 0$ for System (4.1-4.3) in the light of reduction to the one-dimensional centre manifold dynamics as in (5.46). The reason is that only simple fold bifurcation or cusp bifurcation are plausible bifurcation scenarios. However, cusp bifurcation is accompanied by hysteresis, which requires three equilibria, with two of them being stable. An interchangeable fold bifurcation occurs between the unstable equilibrium and one of the stable equilibria each time. Both stable equilibria must disappear in an alternative fashion for certain parameters' choice. However, $O(0,0,0)$, a stable equilibrium, is persistent. It is always there for all choices of non-negative parameters, which are eventually the relevant parameters. This excludes then hysteresis together with cusp bifurcation. There remains only the possibility of simple fold bifurcation, which was adequately illustrated in Chapter 4. Another reason cusp bifurcation is not plausible for (4.1-4.3) is learned from the non-dimensionalization carried out in (5.3-5.5). γ and δ are nothing but a scale for $\frac{dY}{d\tau}$ and $\frac{dZ}{d\tau}$. A simple calculation shows then that the only decisive parameter concerning the number and nature of stationary solutions is e. Knowing that cusp bifurcation is a codim-2 bifurcation, it depends then on the variation of two independent parameters and since System (5.3-5.5) depends only on e, cusp bifurcation is then ruled out.
For the sake of completion, we will compute $a(0)$ for System (4.1-4.3). This can be done by setting $\dot{y} = 0$ and substituting $y = 2ax + 3bx^2$ in $\dot{z}$, we have then after the translation $(x, y, z) \rightarrow (X := x - x_0, Y := y - y_0, Z := z - z_0)$:

$$\dot{X} = -aX - 4bx_0X - 2bX^2 + 15z_0^4Z + 30z_0^3Z^2 + 30z_0^2Z^3 + 15z_0Z^4 + 3Z^5 \tag{A.1}$$

$$\dot{Z} = 2aX + 6bx_0X + 3bx^2 - 25z_0^4Z - 50z_0^3Z^2 - 50z_0^2Z^3 - 25z_0Z^4 - 5Z^5 - cZ \tag{A.2}$$

Calling the right-hand sides of $\dot{X}$ and $\dot{Z}$ by f_1 and f_2 respectively, we proceed according to the given formulas in the last chapter. It remains to compute the fold equilibrium (x_0, y_0, z_0). This can be done by considering both $q(z)$ and $q'(z)$ from Chapter 4 and making the ansatz $z = \mu c^{\frac{1}{4}} = \frac{m}{k} c^{\frac{1}{4}}$ as in (4.41), we end up with the following equations:

$$q(\mu c^{\frac{1}{4}}) = bc^{\frac{9}{4}}\mu \left(\mu^8 + (4-k)\mu^4 + (4+k)\right) = 0 \tag{A.3}$$

$$q'(\mu c^{\frac{1}{4}}) = bc^2 \left(9\mu^8 + (20-4k)\mu^4 + 4\right) = 0 \tag{A.4}$$

With two equations with two unknowns, we solve for k and μ and we have $k_0 = \frac{19\sqrt{5}\sqrt{53}}{40} + \frac{37}{8}$ and $\mu_0 = \frac{k_0^4(32+9k_0)}{5k_0-16}$. The fold equilibrium is then at

$$(x_0, y_0, z_0) = \left(\frac{z_0^5 - 2cz_0}{a}, 5z_0 + cz_0, \frac{m_0}{k_0}c^{\frac{1}{4}}\right) \tag{A.5}$$

with m_0 given in (4.38). Notice that we have the freedom to choose b and c as arbitrary positive numbers, we have then to choose $a = \sqrt{m_0 b}c^{\frac{5}{8}}$. It suffices then to compute $a(0)$ for any choice of positive b and c. Upon changing the values of b and c, neither the sign of $a(0)$ will change nor will it become zero. This is because there is a single bifurcation parameter, which is m in this case since fold bifurcation is essentially a codim-1 bifurcation. At $m = m_0$ this bifurcation occurs. Now taking $b = c = 1$, we compute $a(0) \approx -0.0667637 \neq 0$. For other values of b and c, the value of $a(0)$ changes, but it cannot become zero. A zero $a(0)$ for some parameters' choice implies a cusp bifurcation, which is impossible for System (4.1-4.3).

Appendix B

Dynamics of Hahn's Three-Dimensional Model at Fold Equilibrium

We didn't study the dynamics of Hahn's three-dimensional model at the parameters' values, for which a fold equilibrium exists. Fold equilibrium happens exactly when $m = m_0$. The dynamics arising at this particular value are not significant to investigate since they happen for a zero measure set of parameters' values. Nevertheless, for the sake of completeness, we consider this case here.
Hahn's model admits at $m = m_0$ two steady states: The trivial steady state $O(0,0,0)$ and a positive steady state with one zero eigenvalue and two eigenvalues with negative real part. Let us call this fold equilibrium F. It possesses a two-dimensional stable manifold and a one-dimensional centre manifold. We can argue that the set $\tilde{W}^s(F) := \left(\overline{B(F)} \cap \overline{B(O)}\right) \cup W^s(F)$, the extension of the stable manifold of F, is a Lipschitz balanced, compact manifold as we had proven for $\tilde{W}^s(A)$ in Propositions 26, 33 and 34. $\tilde{W}^s(F)$ constitutes the set of all solutions that do not converge into F or O on the boundary of their basins of attraction. As shown in Proposition 35, all non-trivial $\omega-$limit sets above or below $\tilde{W}^s(F)$ implies non-trivial $\omega-$limit sets of the same quality on $\tilde{W}^s(F)$. Particularly, non-trivial $\omega-$limit sets are periodic orbits for Hahn's model. It is sufficient then to study the dynamics on $\tilde{W}^s(F)$. We illustrate this in the following proposition.

Proposition 61 *For $m = m_0$, a solution of System (4.1-4.3) starting in $\mathbb{R}^3_{\geq 0}$ converges either into the fold equilibrium F or into the origin O.*

Proof: Suppose there lies a periodic orbit P on $\tilde{W}^s(F)$ and let $p \in P$. Since $B(F)$ is an unbounded set including $[F, +\infty[$, there is $q \in B(F)$ such that $p \ll q$. By strong monotonicity of the system, $\omega(p) \leq \omega(q) = F$. We assume that $\omega(p) < F$. Then there is $t_0 > 0$ such that $\phi_t(p) \in [O, F]$ for all $t > t_0$ and $\omega(p) = O$ since all solutions starting in $[O, F[$ converge to O as $t \to \infty$. Hence, p is not on a periodic orbit, which contradicts our assumption. The other possibility would be that $\omega(p) = F$, which also contradicts our assumption. Hence, no periodic orbit exists on $\tilde{W}^s(F)$. By the generalized Poincaré-Bendixson Theorem, all solutions starting on $\tilde{W}^s(F)$ must eventually converge into F and no periodic orbits exist in $\mathbb{R}^3_{\geq 0}$. Therefore, any solution starting in $\mathbb{R}^3_{\geq 0}$ converges either to O or to F. $\square$

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