OPTIMALITY AND RESILIENCE IN PATTERNS OF CARBON ALLOCATION AND GROWTH IN VEGETATION UNDER ACCLIMATION RESPONSE TO CLIMATE CHANGE

BY
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DISSERTATION
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The earth’s climate has changed significantly in the last 250 years due to activities arising from a rapidly growing human population such as, agriculture, industrialization, deforestation, pollution etc. While the pre-industrial atmospheric concentration of the greenhouse gas carbon dioxide was 280 ppm, it is currently at 400 ppm and is expected to reach 550 ppm by 2050. Under such a changing environmental condition plants undergo acclimation, by which they adjust to the altered environment and in doing so enhance their probability of survival. The acclimation response of plants significantly alters the land surface fluxes of water, carbon and energy thereby impacting the hydrologic cycle. Furthermore, the consequences of this acclimation on agricultural ecosystems is critical in tackling future food security issues. In this study we investigate the acclimation response of an agricultural ecosystem and its impact on the hydrologic cycle. We further explore the effects of plant acclimation on optimizing seed yield under climate change.

In this study we consider 4 types of plant acclimation to one aspect of climate change, which is the elevated atmospheric carbon dioxide concentration. These are: a) eco-physiological, b) allocation c) biochemical and d) structural acclimation. We employ a multi-layer canopy, soil, and root system vegetation model to capture the effects of plant acclimation. This vegetation model is coupled with a teleonomic carbon allocation and growth model that we develop in this study to specifically capture the acclimation of carbon allocation. Our modeling results are tested using field experiments performed in a soybean agricultural system at the SoyFACE research facility in Illinois.

Our modeling results indicate that the acclimation response of plants significantly alters the land surface fluxes of water, carbon and energy thereby impacting the hydrologic cycle. They confirm the widely observed effects of decreased transpiration (latent heat) fluxes, increased sensible heat fluxes, and increased plant carbon uptake. More interestingly, our results illustrate that each of the four acclimation responses cause a decrease in plant carbon uptake. Furthermore, under acclimation to elevated carbon dioxide, the increased carbon uptake is not proportionally allocated to different plant parts according to prior carbon
allocation patterns, that is allometry. Compared to the vegetative parts, a significantly lower proportion of carbon is allocated to the reproductive parts of the plant. This result has significant consequences in obtaining projections of future crop yield under a changing climate, where we now project lower than expected yield increases for our crops.

Further optimality analysis indicates that while plants are sub-optimal in terms of maximizing seed yield under current climate conditions, the extent of sub-optimality increases under future climate scenarios. This is because plants allocate more carbon to vegetative parts compared to reproductive parts. We test this result through a set of canopy thinning field experiments, and the results illustrate that plants which are artificially modified to have fewer leaves have a higher seed yield compared to plants growing under control conditions under both ambient and elevated carbon dioxide conditions. These results indicate the existence of a potential to increase seed yield by upto 23% through canopy modification alone.

We hypothesize that the reason for this observed sub-optimality is a resilience trade off, whereby plants need to maintain resilience against extreme disturbance events such as drought, hail, herbivory and diseases. Through the help of simple non-linear systems, we illustrate how different attributes of resilience can be investigated and quantified. Finally, we propose a combined optimality versus resilience trade off framework which can be used to manage risk and optimize productivity in agricultural ecosystems.
I dedicate this dissertation to my parents.
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LIST OF ABBREVIATIONS

DOA: Domain of Attraction
GPP: Gross Primary Productivity
LAI: Leaf Area Index
NPP: Net Primary Productivity
PDF: Probability Density Function
Anthropogenic climate change is one of the most serious challenges that mankind faces in this century. Since the advent of the industrial revolution towards the end of the 18th century, human population growth and economic development have contributed to climate change through fossil fuel burning, deforestation and large scale agriculture, population explosion and aerosol pollution [Field et al., 2012, Solomon et al., 2007]. The increase in atmospheric concentrations of greenhouse gasses such as CO$_2$ has contributed to a rise in global mean temperatures and increased occurrence of extreme events such heat and cold waves [Schar et al., 2004, Stott et al., 2004]. Climate change has also impacted the global precipitation regimes and this has led to increased occurrences of droughts and floods [Pall et al., 2011, Timmermann et al., 2011]. The presence of industrial pollutants such as oxides of nitrogen and other volatile organic compounds has caused an increase in tropospheric ozone pollution resulting in harm to human health and terrestrial vegetation [Betzelberger, 2012, Morgan et al., 2003]. Furthermore, CO$_2$ induced global warming has contributed to rise in mean sea levels, and endangering coastal cities [Field et al., 2012, Solomon et al., 2007], and acidification of the oceans damaging marine life [Cote and Darling, 2010]. Finally, recent studies have indicated that the effects of anthropogenic climate change are largely irreversible for the next 1000 years [Solomon et al., 2009]. Hence the need to develop mitigation strategies to combat climate change becomes essential [Perrings, 2006].

Terrestrial vegetation plays an important role in the earth’s climate by influencing the water, energy, and nutrient cycles that occur at the land surface [Drewry et al., 2010a, Quijano et al., 2012]. Under changing climatic conditions, vegetation undergoes acclimation by modifying its properties to suit the altered environmental conditions [Ainsworth and Long, 2005]. Predicting this vegetation acclimation under altered environmental conditions is an extremely important and challenging task especially in the context of developing strategies to mitigate climate change [Arora and Boer, 2005, Givnish, 2002]. The processes that occur at the vegetated land surface boundary layer can be best described using a complex adaptive systems approach [Moorcroft, 2006]. There exists distinct cycles of carbon, water,
energy, and nutrients that are strongly coupled through a series of feedbacks [Drewry et al., 2010a, Kumar, 2007] encompassing processes related to ecology, hydrology, climatology and bio-geochemistry [Pitman, 2003, Quijano et al., 2012]. Figure 1.1 describes this complex coupling. It must be noted that while external climate forcing affects the vegetated land surface boundary layer, the surface fluxes in turn are the boundary drivers of the climate system and hence the feedbacks are mutual. When vegetation acclimates to an altered climatic condition, it creates a hydrological impact on land surface fluxes such as sensible heat, latent heat, infiltration, runoff, CO$_2$, and nutrients etc. These fluxes in turn serve as the boundary conditions for climate systems and act as important drivers which shape the climate of the earth system [Rodriguez-Iturbe, 2000].

Predicting one aspect of the processes involved in a vegetated land surface, for example the hydrologic processes which deal with infiltration, runoff, soil moisture, evapo-transpiration, stream flow [Drewry et al., 2010a] requires the consideration of the other aspects such as the ecological and bio-geochemical processes [Moorcroft, 2006]. This is because ecology and bio-geochemistry affect hydrology through the interception of precipitation by leaves thereby affecting the water flux that reaches the ground thus decreasing infiltration [Drewry et al., 2010a]; the litter layer acts as a buffer zone for moisture storage increasing infiltration and hence decreasing runoff [Quijano et al., 2012]; plant roots and leaf litter enhance microbial activity and hence change the soil structure enabling it to store more water [Saxton and Rawls, 2006]; and roots also act as passive pumps which uptake soil moisture and transpire it through the leaves [Amenu and Kumar, 2008].

The ecological processes are in turn coupled with the climatological processes such as radiation, boundary layer atmospheric stability, wind profile, etc. [Baudena et al., 2008, Dominguez et al., 2006]. Vegetation influences the surface albedo which determines the net energy absorbed by the land surface; transpiration by plants affect the partitioning of the sensible, latent, and ground heat fluxes which influences the stability and mixing of the boundary layer atmosphere; the canopy roughness affects how the wind profile and hence the momentum is transferred across the land surface boundary etc. [Drewry et al., 2010a, Moorcroft et al., 2001].

Researchers have built several models that capture the processes occurring at the vegetated land surface with varying degrees of success [Friend et al., 1997, Iwasa, 2000, Pitman, 2003]. While atmospheric and boundary layer scientists have focused on the climatological aspects [Baudena et al., 2008, Schaefl et al., 2011], hydrologists have focused on the hydrological aspects [Rodriguez-Iturbe, 2000], ecologists on the ecological processes [Arora and Boer,
Figure 1.1: Illustration of the feedback mechanisms present while modeling vegetation dynamics. The normal environmental conditions are represented by the inner loop while the climate change induced altered environmental conditions are represented by the outer loop. Notice that an impact on any one of the processes (represented by the boxes) cascades into all the other processes due to the presence of connected feedback loops.
2005, Parton et al., 1987, S. W. Humphries, 1995] and bio-geochemists on the process in the soil [Quijano et al., 2012]. More recently there have been a number of attempts to couple these different fields and present a unified framework that better captures the processes occurring at the land surface boundary layer [Drewry et al., 2010a,b, Friend et al., 1997, Moorcroft et al., 2001, Quijano et al., 2012]. It is these kinds of holistic models that enhance our understanding and provide a higher predictive capability of the processes at the vegetated land surface.

While holistic models provide a better predictive capability of the processes in the vegetated land surface boundary layer under current climatic conditions, the performance of these models under future climatic scenarios needs to be investigated. In this regard, it is important to distinguish between models that are process based from those that are empirically based. From a complex adaptive systems perspective of vegetated land surface, it is essential to realize that vegetated land surfaces constantly evolve and acclimate to ever changing climatic conditions [Kumar, 2007, Moorcroft, 2006]. Hence, empirical models that are calibrated for current climate scenarios are not able to capture acclimation aspects of vegetation under future climate [Drewry et al., 2010b]. Process based models which possess the required degrees of freedom provide the system with predictive capability under future environmental conditions. Hence, in order for holistic land surface models to be able to characterize the response to different climatic conditions, they must be process based models. In the absence of such a process based model, a teleonomic approach provides a strong alternative compared to calibrated empirical models.

One of the key aspects of complex adaptive systems is the ability of the system to adapt to changes [Brand and Jax, 2007, Carpenter et al., 2001, Cote and Darling, 2010, Folke et al., 2004]. Ecological processes and vegetation acclimate in the short term and adapt in the long term to changes in environmental conditions [Givnish, 2002]. Several holistic process based models capture the non-biological processes with a very high degree of success and to a great extent the biological processes at the biochemical level which are short term (days) [Drewry et al., 2010a, Moorcroft et al., 2001, S. W. Humphries, 1995]. However, very few models [Arora and Boer, 2005, Iwasa, 2000] that capture the biological processes involving acclimation behavior at medium to longer (weeks and months) temporal scales and adaptation behavior over evolutionary times scales.

In this context, acclimation is defined as “phenomenon whereby living organisms adjust to the present environmental conditions and in doing so enhance their probability of survival” [Calow, 1998]. Acclimation occurs in time scales larger than the immediate response to its
environmental changes and within its life span [Ainsworth et al., 2002b]. It must be noted that acclimation is different from adaptation which represents changes across several life spans [Morgan-Kiss et al., 2006].

Acclimation and adaptation of vegetation are one of the essential features of the vegetated land surface that need to be incorporated in process based models in order to make accurate predictions for future climate scenarios, and to date there has been limited success in this aspect of vegetation modeling. In this work, we address this problem and develop a framework to include the phenomenon of acclimation of vegetation to climate change. This coupled model would provide a robust complex adaptive system based land surface model which can better predict land surface fluxes due to environmental change.

There exists a multitude of overlapping attributes of climate change that can induce an acclimation response in vegetation. For example, changes in the precipitation regime such as changes in mean precipitation or frequency of droughts and floods can induce acclimations in the root systems of vegetation [Pall et al., 2011, Timmermann et al., 2011]. Similarly, increased average temperature, extremes such as heat and cold waves, decreased snow cover, and increased growing season length can induce acclimation behavior in plants [Schar et al., 2004, Stott et al., 2004]. Oxides of nitrogen and other volatile organic compounds which cause an increase in concentrations of tropospheric ozone can also induce acclimation of vegetation [Betzelberger, 2012]. More recently, it has been shown that climate change induced plant acclimation causes changes in patterns of herbivory [Hamilton et al., 2005]. On larger spatial scales, climate change can cause vegetation acclimations by changing patterns of growth, mortality, and composition through changes in the frequency and magnitude of fires [Hirota et al., 2012], hail [Mahoney et al., 2012], and other climate extremes etc.

In this study we focus on the acclimation aspects of vegetation due to increases in concentrations of atmospheric CO$_2$ alone. In particular, we consider four different plant acclimations occurring at increasing but overlapping time scales, namely a) eco-physiological, b) biochemical, c) allocation, and d) structural. These are discussed in detail in the following section. At the shortest time scales (instantaneous) we have the eco-physiological acclimation which represents the stomatal closure response [Drewry et al., 2010a, Leakey et al., 2006a]; and at the intermediate time scale (day), we have allocation based acclimation where plants alter their relative proportion of carbon allocation to the different parts [Arora and Boer, 2005]. At larger time scales (week), we have biochemical acclimation which represents photosynthetic down regulation due to decreased rubisco concentrations and an increase in the electron transport chain processing rate [Bernacchi et al., 2005]. Over an even longer time
period (weeks), we have changes in plant structural characteristics such as canopy height, stem diameter, Leaf Area Index (LAI), rooting depth, etc. resulting from acclimation and this is captured through the structural acclimation [Ainsworth and Long, 2005, Dermody et al., 2006, Drewry et al., 2010b].

While the effect of eco-physiological and biochemical and some aspects of structural acclimation have been previously studied through a process based models [Drewry et al., 2010a,b], the effects of allocation acclimation have not been explored from a complex systems perspective. In this work, we develop a framework to capture the acclimation aspects of carbon allocation in vegetation. This is overlaid with other acclimations to model the ecological response and its associated hydrologic impact due to environmental change. It must be noted that this carbon allocation and growth model is coupled with an existing eco-hydrological model [Drewry et al., 2010a,b, Quijano et al., 2012] to develop a complex adaptive land surface model that is then used to predict the effect of climate change on vegetated land surfaces. Note that, while the allocation of other resources such as nutrients (nitrogen, phosphorous etc.) among plant parts can play a significant role in plant growth and development, in this work, these effects are not included.

1.1 Challenges in modeling carbon allocation in plants

Plants allocate assimilated carbon to different plant parts such as the leaves, roots, stem, flowers, seeds and fruit [Arora and Boer, 2005]. Some of the assimilated carbon is also used to produce chemical compounds for defense, maintain symbiotic relationships, produce hormones, repair damaged tissue, etc. [Lacointe, 2000]. Under normal growing conditions, plants try to maintain a fixed allometry at different growth stages, which corresponds to a particular relationship between the different parts [Friend et al., 1997, Warren-Wilson, 1972]. However, plants have the ability to modify their allometric relationships and exhibit some degree of plasticity by varying the relative proportions of biomass contained in each of the tissue [Arora and Boer, 2005]. The ability of plants to be plastic provides them with the potential to acclimate to changing environmental conditions in order to enhance their probability of survival. The fundamental process that enables plant acclimation and its associated plasticity is the ability of plants to modify the allocation of the assimilated carbon to the different parts [Arora and Boer, 2005].

Hence, in order to have a vegetation land surface model which is capable of capturing plant acclimation due to environmental change, we need to incorporate a plant carbon allocation
and growth model that has sufficient degrees of freedom to capture plant plasticity. Several allocation models have been proposed in the literature and these are reviewed below.

Empirical models are usually based on allometric relationships [Rouxa et al., 2001]. These allometric relationships are usually fixed and hence do not allow for the possibility of plant plasticity. Other empirical models that depend on derived environmental variables such as growing degree days [Arora and Boer, 2005] are calibrated to current climate and hence cannot be extrapolated to model future climate scenarios [Castro et al., 2009]. Hence empirical models are not suited to capture plant acclimation aspects.

Transport resistance models are process based models that simulate the transport of assimilated plant carbon in the form of sugars through the vascular bundle [Thornley, 1998], based on differences in concentration gradients. Different resistances caused in the flow path of the photoassimilate through the phloem bundle sheath fibers cause differences in the allocation to each plant part. This spatially explicit model and requires estimates of transport resistance measures to accurately capture the allocation patterns. These resistances are conceptual estimates which cannot be directly measured and are usually computed based on calibration with observed data [Lacointe, 2000]. However, data is often not available at this fine process scale, and hence transport resistance models have mostly been restricted to theoretical studies.

Source-sink models are similar to transport resistance models in that they attempt to model plant carbon allocation through a process based model [Allen et al., 2005]. According to this model, assimilated carbon in the form of sugars are transported in the vascular bundle due to differences in osmotic pressure from a carbon source to a carbon sink through the well known Munch hypothesis [Rouxa et al., 2001]. However, the boundary conditions which represent the source and sink strengths used to maintain the osmotically driven flow cannot be measured easily and are usually empirically calibrated based on sparsely available observed data. Furthermore, the transport resistance and the source-sink models are not capable of accurately capturing the phloem loading and unloading strategies and also assimilated carbon storage within the cells in the vacuole in the form of immobilizeable starch [Rennie and Turgeon, 2009]. Hence, similar to the transport resistance model, the source-sink models cannot be used across a wide range of vegetation types.

In the absence of a sound process based understanding of transport of assimilated carbon within plants, the best available alternative is to use teleonomic or goal seeking models [Lacointe, 2000]. These models assume that plants allocate carbon among the different parts in order to satisfy a overarching goal [Arora and Boer, 2005]. Examples of such goals can
be to maintain a specific allometric relationship [Friend et al., 1997, Moorcroft et al., 2001], minimize stress, maximize productivity [Schymanski et al., 2008], maximize seed biomass [Iwasa, 2000] etc. As we discuss in the next section, among the different teleonomic functions, the one that maximizes end of season seed biomass for annual plants, and the end of life span seed biomass for perennial vegetation provides an attractive and evolutionarily consistent model for plant carbon allocation and growth. In this work, we use a teleonomic framework employing maximizing seed biomass to model the acclimation of plant carbon allocation under changing climatic conditions.

1.2 Optimality and resilience in patterns of vegetation growth under acclimation

The origins of the concepts of optimality in vegetation has its roots in the theory of evolution by natural selection [Darwin, 1859]. Fisher [1930], later introduced the concept of fitness in an evolutionary perspective, which has been advantageously used in developing the concepts for a mathematically quantifiable approach to vegetation optimality [Parker and Smith, 1990]. Fitness is a measure of the ability of organisms to survive and reproduce in a given environment [Fisher, 1930, Orr, 2006]. Hence, it has been suggested that vegetation acclimates and adapts under a changing climate forcing in order to maximize its fitness [Makela et al., 2002, Orr, 2006, Parker and Smith, 1990]. Parker and Smith [1990] lay out the different steps involved in the formulation of an optimality model. These are summarized below:

1. Construct a model about adaptation by asking an explicit question.

2. Identity the range of strategies related to the question.

3. Make an assumption about what is being maximized. The optimization criterion is often an indirect measure of Darwinian fitness.

4. Make assumptions about the fitness consequence or payoffs of the different strategies. Payoffs are expressed in units of the criterion to be maximized and are thus an indirect measure of fitness. This involves the construction of mathematical models.

5. Test the predictions against observations.
Several criticisms have been presented in employing the optimality approach to model vegetation acclimation and adaptation [Makela et al., 2002, Orr, 2006, Parker and Smith, 1990]. One of the most important is that heterogeneity and changing environmental conditions would prevent populations from reaching optimum strategies [Makela et al., 2002, Parker and Smith, 1990]. Even under stable conditions, selection becomes progressively weaker towards the peak of the fitness function. This means that infinite time and infinite populations would be required to achieve the peak itself.

Some of the other criticisms involved in using the optimality approach stem from the recognition of physical and biological constraints on optimization [Makela et al., 2002]. Moreover, the nature of genetic variation available within a population and constraints imposed by the rates of mutation, recombination and migration might not allow a global optimal trait to evolve. Furthermore, there can be fundamental physical or chemical constraints on metabolic processes that can prevent the optimum regulation of the biochemical process.

In the context of optimizing fitness, distinction must be made between two types of optimum, frequency independent and frequency dependent. While frequency dependent optimum includes the effects of competitive effects of other individuals, frequency independent is simpler and ignores this effect. The strategy followed by individuals resulting in a competitive equilibrium under a frequency dependent optimum is termed as the evolutionary stable strategy [Smith and Price, 1973]. It is important to note that the evolutionary stable strategy maximizes individual fitness and not population fitness.

Another set of challenges that arise in implementing the optimality approach is in determining the degrees of freedom employed in the optimization. The degrees of freedom for optimization in models are often minor compared with reality since the ultimate adaptive response might be a function of a large number of variables, and there could be no limit to the complexity of the adaptive response surface. Complications also arise due to equifinality of solutions when the degrees of freedom are large [Freer and Beven, 2001, Parker and Smith, 1990]. Furthermore, formulating a precise fitness function can be challenging and oftentimes one might have to test different fitness functions with observations [Orr, 2006, Parker and Smith, 1990].

Despite these difficulties, it has been suggested that optimization approaches help us to test insights into the biological constraints that influence the outcome of evolution or acclimation and can be used as a powerful and elegant tools for understanding vegetation acclimation and adaptation [Makela et al., 2002, Parker and Smith, 1990]. Hence it is useful to adopt the approach that optimization models improve our understanding about
adaptations rather than demonstrate that natural selection produces optimal solutions. For example, Makela et al. [2002] point out that the solutions of the optimization problems do not yield any information about the actual development of the mechanisms we are trying to model. Instead they produce a functional relationship between the driving variables, and between functional relationships and the control variables yielding an optimal behavior. In this regard, Makela et al. [2002] suggest that qualitative optimization models are better than quantitative models.

In the absence of a detailed understanding of the various biophysical and biochemical process that we are trying to capture, we can use optimality theory to analyze how allocation to different plant parts should maximize fitness under a given environmental condition. While it is acknowledged that this does not guarantee an accurate answer, it provides us with an attractive alternative approach for developing a series of workable hypothesis. The use of optimality models is not aimed at proving that a trait is adaptive, but rather, given a domain of possible solutions and their functional significance, what should the trait be if it were optimal [Makela et al., 2002]. This leads to a testable optimality hypothesis about the trait. If this trait can be shown to represent reality, it can be used to make predictions and analyze what would happen if selective pressures were modified as a result of environmental change, at least in the short term. While challenges exist in applying optimality principles to model vegetation acclimation, it has been suggested that optimality models give a predictive knowledge of the direction in which the mean behavior of the trait would move under altered environmental conditions, rather than the present value of the trait [Makela et al., 2002].

Another criticism against optimality approaches is the lack of survivability or resilience constraints to optimality. Recent studies have put forth the concept of most probable (likely) fitness rather than most optimal fitness [Whitfield, 2007] to model ecological systems. The concept of ecological resilience which is defined as the amount of disturbance that a system can withstand without a change in the dynamic regime has been widely investigated [Brand and Jax, 2007, Folke et al., 2004, Gunderson, 2009, Holling, 1973, 1996, Tilman and Downing, 1994, Walker et al., 2004]. In this study we propose that resilience can be viewed as an additional optimality constraint, whereby vegetation is sub-optimal with respect to a given fitness function because it has to survive and be resilient against a particular set of disturbance events. For example, while maximizing seed yield at the end of the growing season (in annual plants) might be optimal, plants have to invest in more roots than optimal to manage drought stress and reduce susceptibility to wilting due to lack of moisture.
A quantitative measure of resilience is required to develop a resilience constrained optimization framework. However, there have been few quantitative studies on resilience [Brand and Jax, 2007]. In order to develop quantitative measure of resilience we need to have a well posed question for measuring resilience. This is accomplished by asking these four questions:

1. Resilience of what aspect of the ecosystem dynamics;
2. Resilience to what disturbance;
3. Resilience in what attribute of ecosystem behavior;
4. Resilience under what spatial and temporal scales;

“Resilience of what” refers to, resilience of ecosystem state to changing its present dynamics, feedbacks, and processes which can be characterized by the concept of a ecological regime. The magnitude and type of disturbances such as floods, droughts, hail, herbivory, heat stress etc. can affect resilience and this answers the “resilience to what disturbance” question. The different attributes of resilience can refer to its ability to resist regime change, speed of recovery following a disturbance, the amount of energy required to return to the original regime, etc. Finally, the spatial and temporal scales at which resilience is measured can vary from point or aggregate to global spatial scales, and transient time scales which are shorter than the response time of the ecosystem dynamics to stationary time scales which results in an overall aggregate level steady state. A stochastic non-linear mathematical framework is best suited to describe resilience and is used in this study to quantify resilience.

We hypothesize that incorporating resilience constraints in an optimality framework would result in observations being closer to modeling results. It must be noted that while resilience is viewed as a constraint on optimization, it is also the ability of vegetation to be resilient that makes it acclimate and adapt to changing environmental conditions.

A popular fitness function that has been successfully used in several optimization models is net energy gain per unit energy expended [Schmidhempel et al., 1985]. Applications of these in the field of vegetation optimality have been explored by several researchers [Arora and Boer, 2005, Eagleson, 2010, Iwasa, 2000, Lacointe, 2000, Schymanski et al., 2008]. These come in the form of maximizing Net Primary Productivity (NPP), net carbon profit, seed production, water use efficiency, etc. For example, Osone and Tateno [2003] illustrate the use of optimality approach in demonstrating the effect of stem fraction on maximum photosynthetic capacity of the leaves in herbaceous species. Schymanski et al. [2008] optimized net carbon profit as a measure of fitness and applied it to predict vegetation growth at
decadal time scales. Iwasa [2000] optimized the seed production of vegetation and used it as a fitness measure to predict vegetation growth of annual as well as perennial plants. For the case of annual plants, the end of growing season seed yield was optimized, and for the case of perennial plants, the total seed yield throughout the entire life span of the plant was optimized.

Based on this review, we conclude that among the different fitness functions, the one that is most attractive from an evolutionary perspective is the one that maximizes seed yield, proposed by Iwasa [2000]. We employ this in our study to test the hypothesis that an optimality based teleonomic approach with suitable resilience constraints offers the best approach for predicting vegetation acclimation due to climate change.

1.3 Research contribution

Most vegetation models do not adequately represent the acclimation aspects of vegetation under changing environmental conditions. Furthermore, very few studies combine modeling and experimental approaches towards understanding the controls, feedbacks and processes involved in vegetation acclimation at field scale. While optimality principles have been widely used in vegetation modeling studies, there has been little testing or validation performed on these models especially under climate change scenarios. Furthermore, most optimality models ignore key constraints such as survivability and resilience in their approaches. The problem is further compounded by the lack of quantifiable measures of resilience to be used as mathematical constraints and the lack of clarity in the choice of fitness to be used in the optimization models.

In this study we aim to address these major issues by providing quantitative measures of resilience to be used as optimality constraints, and using evolutionarily agreeable and quantifiable fitness function to analyze and infer the characteristics of vegetation acclimation under climate change due to growth under elevated CO\textsubscript{2}. These results can then be used to provide insights into how the vegetated land surface fluxes respond to climate change, and in turn how it feeds back into the environmental forcing itself. The key contributions of this study are:

1. The modeling framework developed by Drewry et al. [2010a] is extended and employed to quantify the detrimental effects of the different acclimatory effects of soybean towards increasing NPP and finally seed yield when grown under elevated CO\textsubscript{2}. The
reasons for decline in stimulation of NPP are investigated using concepts of light attenuation through photosynthetic down regulation, canopy structure etc. These are used to obtain quantitative insights into the acclimation response of vegetation. The observed growth, structure and functioning of plants are tested against a model derived optimal vegetation and the differences between observed and optimal characteristics are quantified. The insights from the modeling exercise are used to design experimental studies to test and validate the model results.

2. Canopy thinning experiments are used to quantify the extent of sub-optimality when plants are subject to growth under both current and elevated CO$_2$ concentrations. This allows us to test the optimal strategies of plant carbon allocation at the field scale under current and future climate scenarios. We use soybean agricultural ecosystems for this study and the end of season seed biomass which is related to NPP is used to test for the presence of sub-optimality. The insights from this study can be used to develop crops that have the potential to increase yield significantly.

3. A carbon allocation and growth model is coupled with an existing dynamic vegetation model [Drewry et al., 2010a], to develop a combined modeling tool that is used to quantify the degree of sub-optimality with respect to carbon allocation under acclimation. Combining data and modeling results, the temporal patterns of carbon allocation are obtained and they are used to infer the changes in carbon allocation under acclimation. An optimality framework is superimposed on this coupled model for obtaining insights into the behavior of carbon allocation under acclimation. These results can potentially be used by seed developers to increase yield of current and future crops. These results are then used to provide insights into how the vegetated land surface fluxes of water, carbon and energy respond to changes in the environmental forcing.

4. A stochastic non-linear dynamical systems approach is adopted to develop a mathematical framework that is used to obtain quantitative resilience measures and identify different attributes of resilience. This allows us to discover emergent characteristics of resilience as the properties of the system and disturbance change. Some of the interesting emergent phenomenon such as catastrophic shifts, hysteresis, stabilization or destabilization of regimes, detecting trap and escape regions etc. have been shown to play a critical role in influencing the behavior of ecosystems. The framework also enabled us to develop the concept of iso-resilience curves which are contour lines connecting regions in the parameter space having identical resilience values. These iso-resilience
curves are a useful tool for scientists interested in managing and controlling ecosystems by enabling them to design travel paths in the resilience landscape.

5. A conceptual framework of resilience constrained optimality is proposed to address the observed sub-optimality. This resilience versus optimality trade off concept can be employed under current and future climate scenarios. This framework is proposed as a starting point for future work on developing teleonomic models to predict plant acclimation under climate change scenarios.

The modeling studies used in this work build and expand on the MLCan model [Drewry et al., 2010a,b] to include plant carbon allocation and growth. Simulations are performed for the soybean agricultural system at the Ameriflux site at Bondville, IL and the SoyFACE research facility at the University of Illinois. The research is detailed in five chapters. The main objectives of each of these chapter are described below:

**Effects of the different plant acclimations on carbon and energy fluxes when subject to growth under elevated CO$_2$**

In this chapter, we use the existing modeling framework of MLCan [Drewry et al., 2010a,b] to investigate the details of three of the four different acclimations (excluding allocation acclimation) that soybean plants undergo when subjected to growth under elevated CO$_2$. The contribution of different acclimations are isolated artificially through the help of model switches. Detailed analysis of the optimal aspects of the canopy are investigated through modeling studies where it is demonstrated that soybean canopies produce almost twice as much leaves than what would be required to maximize seed yield. The model is run using the environmental data from the Ameriflux site at Bondville, IL and the NOAA weather station at the Willard Airport in Savoy, IL for the years 2002, 2004 and 2006. The main objectives of this chapter are:

- Analyze the effects of different acclimations on NPP for plants grown under elevated CO$_2$ conditions.

- Investigate light attenuation through the canopy and estimate the changes in the contribution of sunlit and shaded leaves in the canopy to NPP when subject to growth under ambient and elevated CO$_2$ conditions.

- Investigate canopy net carbon assimilation through the day and illustrate a competitive effect between gross carbon assimilation and canopy respiration.
• Obtain the optimal leaf area index for maximizing canopy net carbon assimilation under current and elevated CO₂ conditions.

• Analyze and quantify the effects of different acclimations on the carbon and energy and fluxes.

Field scale canopy thinning experiments to test sub-optimality in leaf area index to maximize seed yield

Canopy manipulation experiments were conducted at the SoyFACE research facility at the University of Illinois during the summer of 2010. Young emerging leaf trifoliates were removed through a series of leaf cutting experiments to artificially reduce the leaf area index. The field scale experiment was designed to bring down the leaf area index closer to the optimum value. End of season seed yield was used as an indicator of NPP. The main objectives of this chapter are:

• Develop an experimental plan to test the sub-optimality in the canopy structure as indicated by the modeling studies.

• Perform canopy thinning experiments, measuring the leaf area indices and obtain end of season seed yield.

• Perform statistical analysis on the experimental results to establish significant differences between control and treatment plots.

• Analyze the experimental results and compare it with expected modeling studies.

Plant carbon allocation acclimation and sub-optimality when subject to growth under elevated CO₂ conditions

The effects of allocation acclimation are tested using a carbon allocation and growth model. The results of this study are combined with the results of the previous chapter to analyze the effects of the different acclimation responses in decreasing yield stimulation of soybean plants when subject to growth under elevated CO₂. Results of the modeling exercise indicate that soybean carbon allocation is sub optimal under current and future climate scenarios. Furthermore, the extent of sub-optimality is more severe under future climatic conditions. The model is run using the environmental data from the Ameriflux site at Bondville, IL and the biomass data for the experiments were obtained from the SoyFACE research facility at the University of Illinois Urbana Champaign. The simulations were performed for the year 2002. The main objectives of this chapter are:
• Develop a carbon allocation and growth model and apply it analyze the temporal carbon allocation patterns.

• Analyze the effect of allocation acclimation due to growth under elevated CO$_2$.

• Obtain optimal estimates of plant carbon allocation through model simulations.

• Establish that plants exhibit a sub-optimal carbon allocation behavior and that the degree of sub-optimality is more severe under future climate scenarios.

A framework to quantify resilience in non-linear dynamical systems when subject to disturbance

Resilience constraints are hypothesized as one of the key reasons for the observed sub-optimality in soybean canopies. A stochastic non-linear dynamical approach is developed to quantify resilience in a complex adaptive systems framework. The quantification of resilience will provide important tools to formulate a constrained optimization framework to model the behavior of ecosystems under climate change. The main objectives of this chapter are:

• Develop a well posed mathematical framework to quantify resilience of non-linear dynamical systems when subject to disturbance.

• Demonstrate that resilience is a property of system dynamics, disturbance characteristics and the particular attribute of interest.

• Illustrate that different resilience attributes can capture diverging aspects of resilience.

• Examine the impact of noise induced bifurcation and emergent phenomenon on resilience.

• Demonstrate the use of iso-resilience curves to design travel paths in resilience landscapes for managing resilience under parameter change.

Conclusions

In this chapter we provide an exploratory framework for a resilience constrained optimality model that captures the effects of acclimation of vegetation due to climate change. The main objectives of this chapter are:

• Examine the conceptual framework for resilience constraints on optimality and establish a resilience versus optimality trade off.

• Examine limitations of current approach and explore alternative hypothesis to resilience.
CHAPTER 2

EFFECTS OF THE DIFFERENT PLANT ACCLIMATIONS ON CARBON AND ENERGY FLUXES WHEN SUBJECT TO GROWTH UNDER ELEVATED CARBON DIOXIDE

2.1 Introduction

In this chapter we will investigate the effects of vegetation acclimation on ecosystem carbon and energy fluxes due to growth under elevated carbon dioxide conditions. C3 plants exhibit different kinds of acclimation response when subject to growth under elevated CO$_2$ conditions [Ainsworth and Long, 2005, Drewry et al., 2010a,b]. The different kinds of acclimations which we consider for this study occurring at increasing but overlapping time scales are: a) eco-physiological b) allocation c) biochemical and d) structural. In this chapter we will not consider the allocation acclimation effects, this is discussed in detail in Chapter 4. The details of the modeling methods used in this work are provided in Drewry et al. [2010a,b].

2.1.1 Eco-physiological acclimation

At the shortest time scales (instantaneous) C3 plants experience eco-physiological acclimation which represents the stomatal closure response [Bernacchi et al., 2005, Drewry et al., 2010a, Leakey et al., 2006a]. According to the Ball and Berry model [Ball et al., 1987], the stomatal conductance of the leaf is inversely proportional to the leaf internal concentration of CO$_2$ [Collatz et al., 2001]. Since, CO$_2$ enters the leaf via diffusion processes driven by concentration gradients, a higher atmospheric CO$_2$ concentration results in faster rates of diffusion through the stomates increasing the leaf internal CO$_2$ concentrations. This causes the stomates to close, creating an eco-physiological acclimation response. These processes occur at very short times scales and hence eco-physiological acclimation is the first acclimation response that plants exhibit when subject to growth under elevated CO$_2$. It is important to note that this response of stomates does not change due to long term exposure to elevated CO$_2$ [Leakey et al., 2006a].

While the effect of elevated CO$_2$ is to cause an increased GPP, it also results in decreased
transpiration losses on a unit leaf area basis. Furthermore, due to the partitioning of energy into sensible and latent heat fluxes, a decreased leaf level transpiration results in an increase in leaf temperatures resulting in higher sensible heat from the leaves [Drewry et al., 2010a,b].

2.1.2 Allocation acclimation

At intermediate time scales (day), we have allocation based acclimation where plants alter their relative proportion of carbon allocation to its different parts [Arora and Boer, 2005]. As mentioned earlier, this aspect is explored in detail in Chapter 4.

2.1.3 Biochemical acclimation

At larger time scales (week), C3 plants down-regulate their photosynthetic capacity by decreasing leaf rubisco content while simultaneously increasing their electron transport chain rates [Ainsworth et al., 2002a, Bernacchi et al., 2005]. These acclimations have been termed as biochemical acclimation [Drewry et al., 2010a]. Unlike eco-physiological acclimation which occurs instantaneously, these acclimations can take place over a period of several days.

Photosynthetic down-regulation occurs by lowering of rubisco concentrations in the leaf [Ainsworth et al., 2002a] and this effect is captured by decreasing $V_{c_{\text{max}}}$ in the Farquhar et al. [1980] model for photosynthesis [Collatz et al., 2001, Drewry et al., 2010a]. Several studies have shown that photosynthetic down-regulation as experienced by a decrease in $V_{c_{\text{max}}}$ causes a lowering of GPP and NPP [Ainsworth et al., 2002a]. When soybean plants are exposed to elevated CO$_2$ at 550 ppm they typically experience a 5% decline in $V_{c_{\text{max}}}$ [Bernacchi et al., 2005].

Experimental studies have shown that plants increase their electron transport chain rate when subject to growth under elevated CO$_2$ [Ainsworth et al., 2002a, Ainsworth and Long, 2005, Bernacchi et al., 2005]. Up-regulation of electron transport chain is captured by $J_{\text{max}}$ in the Farquhar et al. [1980] model for photosynthesis [Drewry et al., 2010a]. While the extent of $J_{\text{max}}$ up-regulation is less strong (only 2%) compared to $V_{c_{\text{max}}}$ down-regulation, as we show in this work, this is the only acclimation that increases net photosynthetic assimilation. All the other plant acclimations cause a decrease in NPP when subject to growth under elevated CO$_2$. 
2.1.4 Structural acclimation

Over a longer time period (weeks), we have changes in plant structural characteristics such as canopy height, stem diameter, LAI, rooting depth, etc. resulting from the acclimation and this is captured through the structural acclimation portion [Ainsworth and Long, 2005, Dermody et al., 2006, Drewry et al., 2010b]. C3 plants exhibit an increase in LAI when subject to growth under elevated CO$_2$ [Ainsworth et al., 2002a, Dermody et al., 2006]. Soybean plants when subject to growth at 550 ppm of CO$_2$ typically experience a 10% increase in LAI [Dermody et al., 2006]. Furthermore, experimental studies have indicated increased root biomass for soybean plants grown under elevated CO$_2$ conditions [Rodriguez, 2004].

It is important to note that while soybean plants experience an increase in its different biomass components, the increase is not proportional across all plant parts [Morgan et al., 2005]. C3 plants such as soybean experience significant plasticity whereby they change their allometric relationships under acclimation [Arora and Boer, 2005, Morgan et al., 2005]. Typically these acclimation effects occur at time scales of a week and are the longest time scales of acclimation considered in this study.

While, C3 plants exhibit acclimations in other aspects such as changes in leaf area distribution through the canopy, leaf thickness, rooting depth and distribution, changes in densities of root nodules etc. in this work we do not consider these effects due to lack of experimental data. However the model that we use is capable of incorporating some of these aspects based on available data. In the following sections we investigate the effect of three of these acclimations on water, carbon and energy fluxes on soybean canopies.

2.2 Acclimation effects on plant net primary productivity

In order to test the effect that each of the acclimation has on NPP, modeling simulations were performed where each of the individual acclimation was analyzed independently and in combination. Figure 2.1 illustrates of the effect of eco-physiological, structural (increased LAI) and biochemical (decreased $V_{\text{cmax}}$ and $J_{\text{max}}$) acclimation on above-ground NPP for soybean canopies when subject to growth under elevated CO$_2$. It can be observed from the figure that eco-physiological acclimation results in a 40% stimulation of NPP for plants grown under elevated CO$_2$ conditions. As discussed earlier, under elevated CO$_2$ conditions, plants close their stomates, and thereby decrease the fluxes of carbon and water between the
leaf and its surrounding micro-climate. Excluding this acclimation would result in a greater stimulation of NPP for plants grown under elevated CO$_2$ conditions.

Adding the effects of biochemical acclimation on soybean canopies results in a 3% decline on the stimulation of NPP (Figure 2.1). The effects of biochemical acclimation are two fold and are in opposing directions. While the 5% decline in $V_{c,max}$ causes a significant decline in NPP stimulation, the 2% increase in $J_{max}$ causes a mild improvement in the NPP stimulation. The combined effect of both of these biochemical acclimations is to cause a net decline in NPP stimulation. It is interesting to note that among all the different plant acclimations to elevated CO$_2$, only the stimulation of $J_{max}$ causes an improvement in the NPP stimulation. All the other acclimation responses causes a decline in NPP stimulation. This aspect presents an interesting topic for further study.

The coupled effect of eco-physiological and structural acclimation results in a NPP stimulation of 35% for growth under elevated CO$_2$ conditions. This represents a 5% decline in stimulation compared to that of including the effects of eco-physiological acclimation alone. This result is counter intuitive, since the effect of structural acclimation is to create an increase in LAI, and higher LAI is generally associated with increased photosynthetic assimilation which could potentially translate to increased NPP. However, as we demonstrate in the next section, this is not necessarily true since there exists trade offs between gains in photosynthesis and losses in respiration as the LAI is increased. This aspect is investigated in detail in the reminder of this chapter.

The combined effects of eco-physiological, biochemical and structural acclimation results in 32% stimulation of NPP (Figure 2.1). Comparing this result with the effects of individual acclimations, it can be inferred that the effects of biochemical and structural acclimations on NPP stimulation due to growth under elevated CO$_2$ are roughly additive. Based on these analyses it can be concluded that the individual and combined effects of each of the acclimations is to decrease the NPP stimulation caused by growth under elevated CO$_2$ conditions.

### 2.3 Canopy light interception and self-shading

The analysis performed in the previous section illustrated that structural acclimation under elevated CO$_2$ conditions, expressed as increased LAI, causes a decline in NPP stimulation. This counter intuitive result can be explained using the concept of light interception induced shading resulting in trade offs in NPP caused by diminishing gains in GPP and increasing losses in maintenance respiration. Several studies have indicated that maximal light inter-
Figure 2.1: Illustration of the effect of eco-physiological, biochemical (decreased $V_{\text{cmax}}$ and $J_{\text{max}}$) and structural (increased LAI) acclimation on above-ground NPP for soybean canopies when subject to growth under elevated CO$_2$. Biochemical acclimation also causes a reduction in the stimulation above-ground NPP due to decrease in leaf level photosynthesis. Structural acclimation causes a reduction in the stimulation of above-ground NPP due to increased respiration caused by self-shading of the canopy leaves. The combined effect of structural and biochemical acclimation is roughly additive. Results are for soybean canopies under closed canopy assumption (LAI greater than 3.5) averaged over the growing seasons 2002, 2004 and 2006.
ception efficiencies are obtained at LAI values around 3.5 [Hipps et al., 1983, Peltonen-Sainio et al., 1997, Thorne et al., 1988]. Higher LAI values causes self-shading of plant canopies resulting in declining light intensities in the lower portions of the canopy.

Figure 2.2 illustrates the variation of the minimum and mean fraction of shaded soybean canopy leaves as a function of LAI. This result is based on the canopy light interception model employed in Drewry et al. [2010a]. It can be observed from the figure that, as the LAI is increased, a greater proportion of the canopy is shaded. Applying this to soybean canopies grown at SoyFACE, we find the LAI that maximizes above-ground NPP are 3.5 and 3.8 for ambient and elevated CO\textsubscript{2} conditions, whereas the observed peak LAI for years 2002, 2004 and 2006 are between 6.5 and 8.0. From Figure 2.2, it is interesting to note that, for a closed canopy (LAI > 3.5), at least 50% of the canopy is shaded even under peak sun conditions, and across a daily average at least 80% of the canopy is shaded.

Figure 2.3 illustrates the effect that shading has on NPP under both ambient and elevated CO\textsubscript{2} conditions. It can be observed from the figure that the maximum PAR absorbed for shaded leaves is around 100 \( \mu \) moles m\(^{-2}\) s\(^{-1}\), whereas the maximum PAR absorbed for sunlit leaves is around 350 \( \mu \) moles m\(^{-2}\) s\(^{-1}\) under both ambient and elevated CO\textsubscript{2} conditions. It must be noted that for a given LAI value, the PAR absorbed remains the same under both ambient and elevated CO\textsubscript{2} conditions. This is because in our model we assume that the optical properties of the leaf do not change with atmospheric CO\textsubscript{2} concentrations. However, it must be noted that under elevated CO\textsubscript{2} conditions plants undergo structural acclimation resulting in increased LAI values and this can cause an increase in PAR absorption.

Combining the results from Figures 2.2 and 2.3, we can infer that on an average about 80% of the canopy is shaded and it absorbs less than 100 \( \mu \) moles m\(^{-2}\) s\(^{-1}\) producing an NPP of less than 3 \( \mu \) moles m\(^{-2}\) s\(^{-1}\). Under observed peak LAI values, we can infer that on an average about 90% of the canopy is shaded. This means that under peak LAI conditions, only 10% of the canopy experiences direct sunlight absorbing 350 \( \mu \) moles m\(^{-2}\) s\(^{-1}\) of PAR, which is more than three times the PAR absorbed by the shaded leaves and producing NPP fluxes up to 7 \( \mu \) moles m\(^{-2}\) s\(^{-1}\). Hence, 10% of the canopy produces three times as much NPP compared to the remaining 90% on a per unit area basis. These results point to significant inefficiencies in canopy LAI with respect to maximizing NPP.

Figure 2.4 illustrates the differences in PAR absorbed and NPP between ambient and elevated CO\textsubscript{2} for soybean plants. It can be observed from the figure that under low values of PAR absorbed, the absolute differences in NPP between ambient and elevated CO\textsubscript{2} become very small and the relative differences drop by more than 10%.
Figure 2.2: The variation of the minimum and mean fraction of soybean canopy leaves shaded as a function of LAI. The LAI that maximizes above-ground NPP under ambient and elevated CO\textsubscript{2} conditions is represented by the black vertical lines. The observed peak LAI for years 2002, 2004 and 2006 are represented by grey vertical lines. Solid lines represent growth ambient CO\textsubscript{2} and dashed lines represents growth under elevated CO\textsubscript{2} conditions. Note that, for a close canopy (LAI >3.5), greater than 50\% of the canopy is shaded even under peak sun conditions and on a daily average greater then 80\% of the canopy is shaded.
Figure 2.3: Illustration of the differences between PAR absorbed and NPP for sunlit and shaded leaves under both ambient and elevated CO$_2$ conditions. Note that the maximum PAR absorbed by shaded leaves is less than 100 $\mu$ moles m$^{-2}$ s$^{-1}$. Simulations were performed on soybean canopies grown at SoyFACE for years 2002, 2004 and 2006 under a closed canopy assumption.
Figure 2.4: Comparison of the differences in PAR absorbed and NPP between ambient (blue) and elevated (red) CO$_2$ for soybean plants. Simulations were performed at Bondville, IL, for a total of 156 days during the growing season in years 2002, 2004 and 2006 when canopy closure was achieved (LAI >3.5). The solid lines represent average NPP for a given value of PAR absorbed. The relative difference between ambient and elevated CO$_2$ is indicated by the green line.
Since we know that more than 80% of the canopy is shaded (Figure 2.2) and that the maximum PAR absorbed by shaded leaves is less than 100 $\mu$ moles $m^{-2} s^{-1}$ (Figure 2.2), we infer that absolute differences in NPP between ambient and elevated CO$_2$ for shaded leaves are less than 2 $\mu$ moles $m^{-2} s^{-1}$ and the corresponding relative differences are less than 15% (Figure 2.4). These conditions are expected to occur at the lower portions of the canopy. On the other hand less than 20% of the canopy experiences sunlit conditions where the absolute difference in NPP between ambient and elevated CO$_2$ conditions can be up to 7 $\mu$ moles $m^{-2} s^{-1}$ with the corresponding relative difference at 30%. These conditions occur at the top canopy leaves where most of the measurements are performed. Averaging out the different behaviors between the top and bottom of the canopy would result in lower average relative differences between ambient and elevated CO$_2$ conditions.

The above simulations illustrate the effect that canopy light interception and shading result in the lowering of NPP production in the lower canopy leaves. This results in the trade off in NPP caused by diminishing gains in GPP and increasing losses in maintenance respiration. These trade offs are explored in the following section.

2.4 Optimal leaf area index resulting from gross primary productivity and respiration trade off

Figure 2.5a illustrates the competition between gains in GPP and losses in respiration at the diurnal time scale as LAI is increased, resulting in the NPP maximization at intermediate LAI values. Doubling the LAI from 3.5 to 7.0, causes significant daytime gains in GPP. However, as expected there are no increases in nighttime GPP uptake. In contrast, the respiration fluxes increase as the LAI is increased, and more importantly the increase is present throughout the day (Figure 2.5a).

Combining the GPP gains and the respiration losses we obtain the NPP. As LAI is increased, the daytime increases in NPP are marginal due to the cancellation effect between gains in GPP and losses in respiration (Figure 2.5a). However, during nighttime there is a significant decrease in NPP as the LAI is increased. This results in daily NPP being lower at higher LAI compared to a lower LAI (Figure 2.5b). These proof of concept simulations were performed assuming constant LAI throughout the 156 days of simulation over three growing seasons.

As the LAI is increased, we see that the average daily respiration increases in an almost
Figure 2.5: a) Illustration of the competition between gains in average GPP and losses in average respiration at diurnal time scales as LAI is increased. Solid lines represent simulations with LAI of 3.5 and boxed lines represent simulations with LAI of 7.0. b) Variation of the different components of carbon fluxes as a function of LAI. Solid lines represent ambient CO$_2$ conditions and dashed lines represent elevated CO$_2$ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO$_2$ conditions.
linear fashion (Figure 2.5b). However, increases in GPP with LAI show diminishing returns (Figure 2.5b) due to the effect of self-shading as discussed in the previous section. The combined effect of these on NPP results in a nonlinear behavior whereas LAI is increased from a low value, NPP peaks at intermediate LAI values and then drops at higher LAI values (Figure 2.5b). Similar behavior is observed under elevated CO\textsubscript{2} conditions as well. However, the LAI that maximizes NPP is slightly higher. This is attributed to the fact that while GPP gains due to elevated CO\textsubscript{2} are higher compared to ambient conditions, respiration losses do not change in a significant manner.

Figure 2.6 illustrates the effect of the observed NPP trade off in the light of optimal canopy LAI for the maximization of NPP. Similar to the results produced in Figure 2.5, LAI was fixed at a constant value during the model simulation. The optimum LAI for maximizing daily averaged above-ground NPP under ambient and elevated CO\textsubscript{2} conditions are 3.5 and 3.8 (Figure 2.6a). Comparing this with observed peak LAI we infer that soybean canopies are significantly sub-optimal with respect to their LAI.

The trade offs between increased nighttime respiration and increased daytime assimilation under ambient and elevated CO\textsubscript{2} conditions is highlighted through the use of diurnal plots in Figures 2.6 b and c. As can be observed from the figure, with increasing LAI, daytime increases in NPP get smaller, whereas nighttime decreases in NPP get larger. Based on these simulations we can infer that soybean plants have more leaves than what would lead to optimum NPP and hence a higher yield. Note that the above simulations do not include the cost of building leaf tissue, including these costs would push the optimal values towards even lower LAI values.

### 2.5 Acclimation impacts on water and energy fluxes

In this section we investigate the effects of acclimation on surface energy fluxes. Figure 2.7 presents the average difference in ecosystem energy fluxes with different acclimations when subjected to ambient and elevated CO\textsubscript{2} conditions at diurnal time scales. The energy fluxes include net radiation, latent heat, sensible heat and ground heat.

It can be observed from Figure 2.7a that eco-physiological acclimation causes a mild decrease in daytime ecosystem net radiation because of relatively larger decreases in soil net radiation compared with smaller increases in canopy net radiation, however this effect is not significant. Similarly, eco-physiological acclimation does not contribute to any changes in the ground heat fluxes either (Figure 2.7d). However, the effect of eco-physiological acclimation
Figure 2.6: Illustration of the effect of trade-offs between GPP and leaf respiration as a function of LAI resulting in a maximization curve for above-ground NPP in soybean at intermediate LAI values. Solid lines represent ambient CO\(_2\) conditions and dashed lines represent elevated CO\(_2\) conditions. (a) The optimum LAI for maximizing daily averaged above-ground NPP under ambient (3.5) and elevated (3.8) CO\(_2\) conditions are highlighted by black circles. Also shown are the observed peak LAIs for growth under ambient (solid) and elevated (dashed) CO\(_2\) conditions for the years 2002, 2004 and 2006. (b) The trade-offs between increased nighttime respiration and increased daytime assimilation under ambient and elevated CO\(_2\) conditions is highlighted. It can be observed that beyond the optimal LAI values, there is a diminishing return on daytime assimilation, whereas nighttime respiration continues to increase resulting in a net loss of total daily averaged above-ground NPP.
Figure 2.7: Average difference in ecosystem energy fluxes between growth with different acclimations when subjected to elevated CO$_2$ and ambient conditions at diurnal time scales. (a) Net radiation, (b) Latent heat, (c) Sensible heat and (d) Ground heat. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO$_2$ conditions.
is to cause a decrease in daytime latent heat flux and a corresponding increase in sensible heat fluxes (Figure 2.7 b and c). This is attributed to the closure of stomates when plant leaves are exposed to elevated CO$_2$ conditions which results in decreased latent heat and compensatory increase in sensible heat.

Including the effect of biochemical acclimation on eco-physiological acclimation does not significantly alter the behavior of net radiation or ground heat flux. However, biochemical acclimation tends to enhance the effects of eco-physiological acclimation on latent and sensible heat fluxes. This is because $V_{c_{max}}$ has a stronger control biochemical acclimatory response, and a lower $V_{c_{max}}$ results in lower rates of photosynthesis and higher leaf internal CO$_2$ concentrations. This effect causes the stomates to close further, decreasing the latent heat and correspondingly increasing the sensible heat.

Structural acclimation produces the strongest response to net radiation and ground heat fluxes. Structural acclimation which is represented by a 10% increase in LAI, causes significant decreases in daytime fluxes of net radiation and ground heat (Figure 2.7 a and d). While decreased daytime ground heat fluxes can be explained by increased shading due to the presence of more leaves, applying a similar concept on net radiation fluxes should result in increase in net radiation. This is because, thicker canopies can intercept and absorb more light compared to thinner canopies and this should translate to higher net radiation fluxes. However, this is not the case as observed from Figure 2.7a. This anomalous behavior is explored in greater detail in the following section.

The addition of structural acclimation on eco-physiological acclimation is to increase daytime latent heat fluxes (Figure 2.7) because a higher LAI results in greater transpiration. However, the daytime sensible heat fluxes increases further with the addition of structural acclimation (Figure 2.7c). This is attributed to the compensation effect of energy balance with respect to significant decreases in net radiation and ground heat flux. i.e. decreases in net radiation and ground heat flux are higher than increases in latent heat flux causing an increase in sensible heat to close the energy balance.

The effect of including all acclimations is approximately additive and we do not observe significant non-linearities for the combination effect. Over all, it is interesting to note that excluding sensible heat flux, the effect of acclimation is to cause a decrease in daytime fluxes for all other components of energy balance (Figure 2.7). This indicates that acclimation due to elevated CO$_2$ causes a general heating of the canopy during the daytime. This is attributed to the lack of evaporative cooling caused by the closing of stomates. Except for structural acclimation which causes an increase in net radiation and ground heat flux during
nighttime, the effect of the different acclimations on nighttime fluxes are negligible.

2.6 Trade off in energy fluxes between canopy and ecosystem

In this section, we investigate the effects of structural acclimation on energy fluxes and explain some apparent anomalous behaviors associated with changes in ecosystem net radiation fluxes as a function of LAI.

Figure 2.8a presents the variation of different components of the radiative energy balance. Note that the energy balance formulation for the canopy applies only to the above-ground canopy and does not include the soil. It can be observed from Figure 2.8 that as the LAI is increased, the canopy net radiation increases as expected, and the soil net radiation decreases. However, the gains in canopy net radiation are smaller than the corresponding losses in soil net radiation and since the ecosystem net radiation is a sum of these two components, it decreases with increasing LAI (Figure 2.8). This explains the apparent anomalous effect observed on ecosystem net radiation when subject to structural acclimation in Figure 2.7. It must be noted that the eco-physiological acclimation effect of elevated CO$_2$ has no noticeable effect on the average net radiation fluxes (Figure 2.8).

Investigating the effects of structural acclimation on daytime ecosystem level energy fluxes, we see that with increasing LAI, both latent and sensible heat fluxes increase, whereas net radiation and ground heat flux decrease (Figure 2.9). Increased LAI causes shading of the soil which results in decreased soil net radiation fluxes thereby decreasing ground heat fluxes. Hence soil temperatures under thicker canopies will be cooler leading to lesser evaporation. This cooling effect is illustrated in Figure 2.10.

Increases in latent heat fluxes due to increased LAI (Figure 2.9) results from increased canopy transpiration. However, higher shading under a thicker canopy can lead to less soil evaporation (Figure 2.11). Furthermore, higher water loss through the leaves can result in decreased soil moisture resulting in lower soil evaporation. The two competing latent heat fluxes interact such that gains in canopy latent heat are higher than losses in soil evaporation resulting in a net increase in latent heat with increasing LAI (Figure 2.11b). Hence, under higher LAI conditions, a greater portion of the latent heat fluxes are through the plants compared to the soil. Note that while canopy transpiration potentially translates to direct carbon gain, soil evaporation does not have a significant direct effect on plant carbon uptake.

The effect of eco-physiological acclimation to elevated CO$_2$ causes a decrease in canopy latent heat fluxes resulting in the lowering of ecosystem latent heat fluxes (Figure 2.11b).
Figure 2.8: a) Illustration of the competition between gains in average canopy net radiation and losses in soil net radiation at diurnal time scales as LAI is increased under ambient CO₂ conditions. Solid lines represent simulations with LAI of 3.5 and boxed lines represent simulations with LAI of 7.0. b) Variation of the different components of net radiation energy fluxes as a function of LAI. Solid lines represent ambient CO₂ conditions and dashed lines represent elevated CO₂ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO₂ conditions.
Figure 2.9: a) Illustration of the diurnal variation of different energy fluxes as LAI is increased under ambient CO₂ conditions. Solid lines represent simulations with LAI of 3.5 and boxed lines represent simulations with LAI of 7.0. b) Variation of the different ecosystem energy fluxes as a function of LAI. Solid lines represent ambient CO₂ conditions and dashed lines represent elevated CO₂ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO₂ conditions.
Figure 2.10: Illustration of the variation of mean canopy temperature and soil moisture as LAI is increased under ambient and elevated CO$_2$ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO$_2$ conditions.

Eco-physiological acclimation does not affect soil latent fluxes in a significant manner (Figure 2.11b).

Sensible heat fluxes increase with increasing LAI since canopy level net radiation is higher at higher LAI values (Figure 2.9). A higher LAI causes lesser soil sensible heat loss during the daytime due to increased shading (Figure 2.12). Furthermore, with plant water stress causing closure of stomates, latent heat fluxes per leaf area can be lower resulting in a higher proportion of net radiation partitioned as sensible heat. It must be noted that with increasing LAI, average plant canopy temperatures decrease due to self-shading and hence the increase in canopy sensible heat fluxes are contributed by sensible heat loss over a larger amount of leaf area rather than higher rates of sensible heat flux per unit area. The effect of eco-physiological acclimation on sensible heat fluxes is to increase ecosystem sensible heat through increased canopy sensible heat loss (Figure 2.12). It must be noted that eco-physiological acclimation has negligible effect on soil sensible heat fluxes (Figure 2.12b).
Figure 2.11: a) Illustration of the competition between gains in average canopy latent heat fluxes and losses in soil evaporation at diurnal time scales as LAI is increased under ambient CO₂ conditions. Solid lines represent simulations with LAI of 3.5 and boxed lines represent simulations with LAI of 7.0. b) Variation of the different components of latent heat fluxes as a function of LAI. Solid lines represent ambient CO₂ conditions and dashed lines represent elevated CO₂ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO₂ conditions.
Figure 2.12: a) Illustration of the competition between gains in average canopy sensible heat fluxes and losses in soil sensible heat fluxes at diurnal time scales as LAI is increased under ambient CO$_2$ conditions. Solid lines represent simulations with LAI of 3.5 and boxed lines represent simulations with LAI of 7.0. b) Variation of the different components of sensible heat fluxes as a function of LAI. Solid lines represent ambient CO$_2$ conditions and dashed lines represent elevated CO$_2$ conditions. Simulations were performed in soybean canopies using a model simulation for a total of 156 days during canopy closure (LAI >3.5) for the growing season in years 2002, 2004 and 2006 at Bondville, IL, under ambient and elevated CO$_2$ conditions.
2.7 Conclusions

Soybean canopies exhibit an acclimation response to growth under elevated CO$_2$. These include eco-physiological, allocation, biochemical, and structural acclimation. Investigating the impact of these acclimations on NPP, we see that all the acclimations cause a decrease in average NPP values. For example, the impacts of biochemical and structural acclimations cause a 3% and 5% decrease in NPP, respectively. The combined impact of both these acclimations is roughly additive at 8% (Figure 2.1).

Since structural acclimation causes an increase in LAI, the counter intuitive behavior of higher LAI resulting in lower NPP is investigated. Two key reasons were attributed for this behavior:

1. Self-shading: Our results demonstrate that increased LAI results in increased self-shading resulting in diminishing returns in NPP. We observe that on an average 90% of the canopy is shaded under peak LAI while 80% of the canopy is shaded under optimal LAI (Figure 2.2). Furthermore, the maximum par absorbed by these shaded canopies is less than 100 µ moles m$^{-2}$ s$^{-1}$ whereas for the sunlit canopies, the maximum PAR absorbed can reach 350 µ moles m$^{-2}$ s$^{-1}$ (Figure 2.3). These correspond to a NPP gain of about 2 µ moles m$^{-2}$ s$^{-1}$ and 7 µ moles m$^{-2}$ s$^{-1}$ respectively (Figure 2.3).

Comparing the effects of self-shading on NPP between ambient and elevated CO$_2$, we see that the relative differences in NPP for sunlit leaves (at the top of the canopy) is at 30% and this drops to about 15% for shaded leaves (Figure 2.4). Since on an average 80% of the canopy is shaded, the relative differences between ambient and elevated CO$_2$ conditions are weighted down. These results demonstrate that at higher LAI values self-shading causes decreases in PAR absorption and hence lowering of NPP.

2. GPP versus respiration trade offs: Our modeling results illustrate the trade off between GPP and respiration as the LAI is increased, resulting in NPP maximization at intermediate levels of LAI between 3.5-4.0 (Figure 2.5b). While GPP increases with increasing LAI, the rates of increase gets smaller and asymptotically approaches a peak value at very large LAI values (Figure 2.5b). On the other hand, respiration increases nearly linearly as a function of LAI (Figure 2.5b). Furthermore, it must be noted that as LAI increases GPP increases only during the daytime, whereas respiration increases during both day and night times (Figure 2.5a). These two carbon fluxes counter each other and result in NPP peaking at intermediate LAI values (Figure 2.6a).
Our results demonstrate that optimal LAI which occurs between 3.5 and 4.0 is half that of observed peak LAI which occurs between 6.5 and 8.0 under both ambient and elevated CO\textsubscript{2} conditions (Figure 2.6). Due to the photosynthetic stimulation caused by elevated CO\textsubscript{2}, for the same LAI, GPP is higher under elevated CO\textsubscript{2} compared to ambient conditions, however there is little change in respiration caused by elevated CO\textsubscript{2} (Figure 2.5b). This causes the maximum NPP to occur at a higher LAI under elevated CO\textsubscript{2} conditions (Figure 2.5b).

The optimality results indicate that soybean canopies are severely sub optimal in maximizing their NPP with respect to their LAI. Since NPP can translate to end of season seed yield, this means that soybean canopies are sub-optimal in maximizing their yield. In the following chapter we test this model observed sub-optimal behavior in seed yield through the use of LAI reduction experiments.

The effects of acclimation on ecosystem energy fluxes is an overall decreased net radiation, latent heat and ground heat fluxes and increased sensible heat fluxes. While structural acclimation exhibits a strong influence on all the fluxes, eco-physiological and biochemical acclimations only influence the sensible heat and latent heat fluxes. The combined effects of all these fluxes is additive without any observable non-linear interaction effects (Figure 2.7).

The effects of structural acclimation on ecosystem energy and water fluxes indicate the presence of competition between canopy and soil fluxes (Figures 2.8, 2.11 and 2.12). Our results explain the apparent anomalous effect of structural acclimation on ecosystem net radiation (Figures 2.7 and 2.8). While higher LAI increases canopy level net radiation, it decreases overall ecosystem net radiation by decreasing soil net radiation.

Our results also illustrate the competition between soil and vegetation for transpiration or evaporative water loss. While higher LAI causes an increase in canopy transpiration, it also causes a decrease in soil evaporation. Hence as LAI increases, a greater fraction of water loss is accomplished through canopy transpiration compared to soil evaporation. Another reason for lower soil evaporation is the lowering of soil moisture under increasing LAI values (Figure 2.10). Since, canopy transpiration can potentially translate to direct carbon uptake, a higher LAI would result in scenario with a better water use efficiency.

The effect of structural acclimation to sensible heat flux is to increase overall canopy and ecosystem sensible heat flux, even though soil heat flux is reduced due to shading. It must be noted that average canopy temperatures are cooler at higher LAI (Figure 2.10a) and the increased canopy sensible heat is accomplished not by higher sensible heat fluxes per unit area, but rather by a larger leaf area contribution to the loss of sensible heat.

Finally it is interesting to note that the variation of water and energy fluxes with LAI are
strictly monotonic for the range of LAI considered. In most cases the trends are asymptotic. However, the variation of NPP as a function of LAI exhibits a non-linear behavior peaking at intermediate values of LAI. In the following chapter we test this model observed non-linear behavior by conducting field experiments.
CHAPTER 3

FIELD SCALE CANOPY THINNING EXPERIMENTS TO TEST SUB-OPTIMALITY IN LEAF AREA INDEX TO MAXIMIZE SEED YIELD

3.1 Introduction

The modeling analysis presented in the previous chapter demonstrates that plant canopies have a higher than optimal LAI and this causes a decrease in the overall NPP of the plant. In this chapter, we will discuss the design, analysis and results of the experimental procedure that we adopt to corroborate this sub-optimal behavior.

Past studies have shown that reduction of LAI has considerable desirable effects on plants resulting in improved crop yields [Huxley and Summerfield, 1976, Peltonen-Sainio et al., 1997, Richards, 1983]. The age old concept of pruning of trees and plants to increase yields is still widely used by horticultural scientists. There are a multitude of reasons as to why pruning of leaves can result in an increase in yield, some of which are discussed below.

1. Self shading: Several studies have demonstrated that optimal photynthetic absorption of radiation occurs at LAI values around 3.5 [Hipps et al., 1983, Peltonen-Sainio et al., 1997, Thorne et al., 1988]. At higher LAI values, self shading results in diminishing gains in photosynthetic uptake and increasing losses in leaf respiration. This photosynthesis versus respiration trade off is illustrated in our modeling study in Figures 2.5 and 2.6 in Chapter 2. It is argued that higher rates of carbon assimilation and storage enables the plant to make greater the investments in reproductive parts thereby increasing yield.

2. Carbon savings: Plants invest significant amount of energy in the form of photoas-similates to build tissue, most of which cannot be remobilized [Skinner et al., 1999, Whitfield, 2007]. There are additional costs associated with repair and maintenance, developing chemicals defenses against herbivory and diseases etc. that have to be incurred throughout the life span of the plant [Whitfield, 2007]. Photosynthesizing leaves have a higher nitrogen content compared to other vegetative plant parts, and the car-
bon costs of building tissue richer in nitrogen increases with nitrogen content [Bunce and Ziska, 1996]. Furthermore, since the newest leaves typically have the highest nitrogen content [Drewry et al., 2010a, Field, 1983, Wilson et al., 2000], production of fewer new leaves results in significant carbon savings which can be utilized towards investment in the seeds and fruits.

3. Removal of competing sinks: According to the source-sink and transport resistance hypothesis of photoassimilate translocation within plants, the meristematic tissues of leaves, stem, roots, and the fruit/seeds act as competing sinks for photoassimilates [Allen et al., 2005]. While the strength of the sinks can influence the relative allocation of photoassimilates [Allen et al., 2005], the resistance to transport can play a significant role in the allocation process as well [Thornley, 1998]. Typically transport resistances increase with increasing distances between sources and sinks [Thornley, 1998]. Since most leaf meristematic tissues are located physically close to fruits and seeds, they have smaller transport resistance costs compared to roots and act as significant competitors. Eliminating or reducing such competing sinks through LAI reduction will allow a greater portion of photoassimilates to be allocated to the seeds and fruits resulting in increased yield.

4. Drought mitigation: Stomates in the leaves act as a sinks of water in plants where they uptake CO$_2$ and release water vapor [Bernacchi et al., 2005]. Hence having a fewer number of leaves results in lower water requirements for the plants and this can potentially result in drought stress mitigation [Leakey et al., 2006b, Richards, 1983]. However, it must be noted that higher LAI results in greater ground shading and hence lesser soil evaporation loss.

3.2 Experimental method

Based on the above introduction we employ the following experimental methods to test the sub-optimal nature of soybean canopies. We prescribe a LAI reduction experiment by removing leaves throughout the entire depth of the canopy. This would result in canopies with a lower LAI and hence lesser self shading thereby increasing NPP. Leaf thinning is carried out on young and emerging leaves so as to prevent carbon investment into building leaf tissue. Furthermore, thinning is performed after pod onset so as to remove competing
sinks and enable a higher carbon allocation to the seeds. The details of the methods are described below.

3.2.1 Site description

Experiments were performed at the 32 hectare SoyFACE (Soybean Free Air Concentration Enrichment) research facility in South Farms, University of Illinois Urbana Champaign, IL in the year 2010. The site is located at 40.0559 N, 88.2009 W, 230 m elevation with a Drummer-Flanagan series (ne-silty, mixed, mesic Typic Endoa-quoll) soil [Morgan et al., 2005]. Tile drains are present at a depth of about 1 to 2 m below the ground surface and hence the water table is always below this level. The average ground surface slope in this site is less than 1%. The site has been subjected to a crop rotation practice of alternating annual soybean and maize and the crop residue of the previous season was retained in the field.

For the year 2010, the precipitation, wind speed, temperature, radiation, and humidity during the growing season is obtained using the weather station at the Ameriflux tower site located in Bondville, Illinois (40.0062 N, 88.2904 W, 219 m above sea level). Continuous measurements were collected at half hourly intervals from an instrument located 10 m above-ground.

The FACE experiment for elevated CO$_2$ is performed using 8 octagonal rings of 20 m diameter, four of which were control plots at ambient CO$_2$ concentration of 390 ppm and 4 other treatment plots were at an elevated CO$_2$ concentrations of 550 ppm which is expected to occur in the year 2050 [Morgan et al., 2005]. No fertilizer, pesticide or insecticide was applied within the ring. However, there can be some residual fertilizer in the soil from the previous year’s maize crop [Leakey et al., 2004]. The site is not irrigated and crops are rainfed. A more detailed site description is provided in Leakey et al. [2004], Rogers et al. [2004].

3.2.2 Planting

Indeterminate soybean (Glycine max (L.) Merr.) cultivar Pioneer 93B15 of maturity group type 3 were used in this study. The seeds were planted on the 26th of May 2010 using a mechanical seed planter with an approximate density of 200,000 plants per hectare with a row spacing of 0.38 m with a plant density of approximately 17 plants m$^{-1}$ along each row.
In order to achieve a plant density of 20 plants m$^{-1}$ [Morgan et al., 2005], plants were overseeded on the 3rd and 4th of June 2010. Over seeding was performed by hand by making a 2-3 inch groove on the soil using a small hand held row right next to the existing row. Care was taken to avoid any damage to the existing seedlings that had already emerged. Seeds were placed inside the groove and then the groove was covered up by hand. Overall there was above 95% success of germination of the seeds.

The plants were then thinned down to a density of 20 plants m$^{-1}$ between the 17th and 26th of June. Preference was given to retain the biggest plants and most healthy looking plants, with the spacing between plants maintained approximately even along the row. Thinning was achieved using a razor blade by cutting the plant at the base of the stem. Manual weeding was performed on all the plots between the 13th and 15th of July 2010. Weeding was achieved by cutting the base of the stem using a razor blade. Although one weeding treatment was sufficient, there were occasional weeds later in the season and these were periodically removed as and when observed using the same method.

### 3.2.3 LAI reduction

The LAI reduction experiments were conducted in a 6 m by 4 m plot within each ring. The plot was divided into two subplots of 2 m by 6 m with one sub-plot being a LAI reduction treatment termed as the treatment subplot and the other subplot being the control subplot. This resulted in both the treatment and control subplots having 5 rows of plants each with length of 6 m. Since the plant density along the the row was 20 plants m$^{-1}$, each subplot had a total of 600 plants. Figure 3.1 presents the layout of the experiment.

Two sets of LAI reduction exercises were performed to artificially reduce the carbon allocation to the leaves. The first LAI reduction was performed between the 17th and 26th of July, 2010 and the second was performed between the 4th and 6th of August, 2010. This was accomplished by manually removing young and emerging leaf trifoliates less than 2 cm in length throughout the entire plant. For both sets of LAI reductions, an average of 3 to 4 leaf trifoliates were removed per plant. Hence we estimate that a total of about 20 leaves per plant was removed by our treatment. The LAI reduction was performed across the entire length of the 6 m row for all the 5 rows in the treatment block in all the 8 rings. The leaf cuttings were bagged, oven dried for a period of 70 days and weighed. Care was taken to avoid damage to the young and emerging pods during this LAI reduction. We were able to observe that the removal of leaves did not affect the pod formation at the nodes where the
Figure 3.1: Illustration of the layout for the LAI reduction experiment. Each subplot consists of a 6 m by 2 m rectangle. The row spacing is 0.38 m and this results in 5 rows of plants per subplot. The density of plants along the row is 20 plants m\(^{-1}\) and hence we have 120 plants along each row. For the measurement of LAI and biomass a 1 m boundary buffer on either sides along the length of the sub-plot was used.
leaf trifoliates were removed. However, differences in the size and number of pods formed between control and treatment nodes were not measured.

3.2.4 LAI measurement

LAI was measured using a LAI-2000 plant canopy analyzer, which calculates LAI using a fisheye optical sensor that measures radiation attenuation through the canopy [Welles and Norman, 1991]. Measurements were performed in conditions where the solar radiation regime was predominantly diffuse, such as early mornings just after sunrise, and late evenings just before sunset. Each LAI measurement was performed along a diagonal transect between rows using a 45 degree view cap. Every measurement consisted of 1 above canopy reading followed by 3 below canopy readings, 2 of which were in row and 1 between rows. The consecutive below canopy measurements were spaced at 1 m each and the consecutive measurements were performed in the direction away from the sun. LAI measurements were conducted at the center row of each treatment subplot on an approximate weekly basis from the beginning of July to the end of August. The standard error (SEL) was maintained below 0.3 when LAI was less than 3.5 (before canopy closure) and below 0.15, when LAI was greater than 3.5 (after canopy closure). The LAI value with the lowest standard error was used in this study. The plants achieved complete leaf senescence between September 13 and 17.

3.2.5 Harvest

The final harvest was performed between 27th September and 2nd October, 2010. Harvest was performed manually by cutting the base of the stem using a razor blade and collecting the entire above-ground biomass. This was conducted for the innermost 2 rows, for a length of 4 m, with a 1 m buffer on either side. A mechanical portable belt thresher BT-14, which was designed specifically for threshing single plants of soybeans, was used to remove the seeds from the stem and pods. The entire above-ground portion of the plant was fed into the thresher and the seeds that were output from the thresher were collected, bagged and tagged according to their treatments. Subsequently, the bags were then oven dried for a period of 73 days and weighed using a digital scale. The biomass data is then converted to the units of g m$^{-2}$. Figure 3.2 presents a collage of the different processes involved in performing the experimental procedure.
Figure 3.2: Collage of the different processes involved in performing the LAI reduction experiment. Clockwise from top left, using a mechanical seeder to over seed to the required plant density, plant thinning to thin down to the required plant density, manual weeding, sample trifoliates of leaf cutting, feeding into the mechanical thresher, bagging and labeling seeds obtained from the thresher.
3.2.6 Timeline

The time line of the experimental procedure is summarized in Figure 3.3.

![Timeline of Experimental Procedure](image)

Figure 3.3: Illustration of the time line of the experimental procedure performed to test the sub-optimality in end of season seed biomass caused by increased canopy LAI.

3.2.7 Other considerations

In this section we list some of the other considerations that might potentially influence our results that we currently ignore to include in our experimental as well as modeling efforts.

1. Herbivory: Towards the later part of the growing season (late July to August), the plants were attacked by Japanese beetles which caused significant damage to leaves. Based on visual inspection we infer that the loss in LAI associated with herbivory due to Japanese beetles can be significant enough to affect our results. Furthermore, several studies have suggested differences in herbivory patterns of insects between plants grown under ambient and elevated CO$_2$ conditions [Hamilton et al., 2005, Nabity et al., 2009]. These results can further influence the interpretation of our experimental outcome.

2. Windfall: On a couple of occasions after severe storm events, significant disturbance to the canopies were observed due to windfall. While, none of the main stems of the plants were severed, several side branches were broken on each plant in areas of significant
windfall damage. Furthermore, the damage due to windfall was not uniform across all plots or treatment blocks.

3. Brown leaves: Leaf senescence is a continuous process that occurs in a soybean plant. With an average leaf life span of 80 days, by the middle of the growing season (late July), leaves of the early season trifoliate begin to turn brown and senesce. Brown leaves have different optical properties and absorb, reflect, and transmit light differently compared to green leaves. The LAI-2000 plant canopy analyzer which uses a light attenuation based computation of LAI cannot distinguish between brown and green leaves and this results in erroneous results. The severity of the errors caused by brown leaves get further exacerbated towards the later part of the growing season when more leaves begin to senesce. The problem gets further complicated due to structural and phenological differences between plants growing under ambient and elevated CO$_2$ [Castro et al., 2009].

3.3 Statistical analysis

As mentioned in Section 3.2, the experimental layout employed in this study yields 2 sets of end of season biomass data, one for ambient and one for elevated CO$_2$ conditions. Each set contains 8 different data points representing 4 samples each of LAI control and LAI treatment subplots. This represents a nested design structure which requires a split plot statistical analysis using analysis of variance (ANOVA). Furthermore, since it is expected that the LAI treatment sub-plots will yield a higher end of season seed biomass compared to the control sub-plots, we perform a one sided test. The summary of this statistical analysis is presented in Table 3.1.

Similar analysis is also performed on the LAI values at each time point. The one sided test is still valid for the LAI analysis, however, here the LAI treatment sub-plots will yield a lower LAI value than the control plots.

3.4 Results

The summary of our experimental results for the LAI and biomass are presented in Figure 3.4. These results represent the average across four replicates. From Figure 3.4a one can observe the seasonality in variation of LAI. Note that LAI was linearly interpolated between
Table 3.1: Summary of the LAI reduction experiment results performed at SoyFACE research facility, University of Illinois, for year 2010 illustrating the effect of increased seed yield under both ambient and elevated CO$_2$ conditions due to a decrease in LAI through artificial experimental reduction. Both elevated CO$_2$ and LAI reduction treatments resulted in a significant increase in end of season seed yield. Reported p-values are computed using the one sided F-test in ANOVA using the split plot design.

<table>
<thead>
<tr>
<th>Treatment effect</th>
<th>Mean difference g m$^{-2}$</th>
<th>% difference</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevated CO$_2$</td>
<td>93.4</td>
<td>24.8</td>
<td>0.013</td>
</tr>
<tr>
<td>LAI reduction</td>
<td>33.0</td>
<td>8.1</td>
<td>0.041</td>
</tr>
<tr>
<td>Interaction: Elevated CO$_2$ × LAI reduction</td>
<td></td>
<td></td>
<td>0.427</td>
</tr>
</tbody>
</table>

observation points. The effect of CO$_2$ on LAI can be realized throughout the duration of LAI measurement. This is an indication of the structural acclimation that plants undergo when subject to growth under elevated CO$_2$ conditions [Drewry et al., 2010a]. These results are in accordance with past experimental results of Dermody et al. [2006]. It must be noted that maximal differences in LAI between the ambient and elevated CO$_2$ are observed after peak LAI is achieved (day of year >210). As observed from Figure 3.4a, statistical analysis reveals that the differences between ambient and elevated CO$_2$ are significant at all time points.

Since the LAI treatments did not commence until the later part of July (day of year >195), no differences in LAI for the LAI reduction control and treatment plots are observed for a given CO$_2$ concentration. However, after the onset of leaf cutting, we can observe significant differences between LAI in control and treatment plots. Maximal differences between LAI control and treatment are observed after the second LAI treatment (day of year between 216 and 218). It must be noted that the typical time taken for a soybean leaf trifoliate to fully flush is about 15 days. Hence, we can expect a similar delay in time to notice a corresponding decrease in LAI. The timing and locations of peak differences in LAI between LAI control and treatment sub-plots are in accordance with expected values.

As mentioned in Section 3.2, the number of trifoliates removed from each plant was between 3 and 4 per treatment which resulted in an average of 7 trifoliates removed per plant for both the treatments. The leaf area of each trifoliate is approximately 0.012 m$^2$ Chung et al. [1998] and we have a plant density of 52 plants m$^{-2}$. From this we can expect an LAI reduction of approximately 4.3. However, from Figure 3.4a we only observe a peak LAI reduction of
Figure 3.4: Summary of the results of the LAI reduction experiment illustrating the sub-optimal nature of soybean canopies where a lower LAI results in a higher end of season seed biomass. Experiments were conducted at the SoyFACE research facility, University of Illinois, during the growing season of 2010. a) Variation of leaf area index (LAI) in soybean through the growing season of 2010 under elevated CO$_2$ and LAI reduction treatments illustrating that LAI is higher under elevated CO$_2$ and lower under LAI reduction treatment. Each point represents the average across 4 replicates ± standard error. Significance using one way ANOVA is highlighted; red represents CO$_2$ effect and blue represents LAI reduction effect. Significance of 0.1, 0.05 and 0.01 are represented by ‘∗’, ‘∗∗’, and ‘∗∗∗’. Note that the combination effect was not significant. b) Variation of end of season seed biomass values under ambient and elevated CO$_2$ and LAI treatment and control conditions indicating that while elevated CO$_2$ causes a 24% increase end of season pod biomass, LAI reduction causes a 8% increase in end of season pod biomass. Each bar represents the average across 4 replicates ± standard error.
0.5 after the completion of both LAI treatments. This is attributed to the fact that plants whose leaves have been removed (LAI treatment) put out more leaves from other leaf nodes to compensate for the loss. This is accomplished through internal regulatory mechanisms using chemical and hormonal metabolic pathways [Hopkins and Huner, 2004]. Examples of similar behavior have been observed in pruning studies [Hopkins and Huner, 2004, Richards, 1983]. The tendency for soybean plants to maintain a higher LAI after the application of LAI treatment that push the plant canopies towards optimal LAI values can potentially indicate inherent inefficiencies in the plant yield maximization strategy.

The biomass results presented in Figure 3.4b illustrate that the elevated CO$_2$ treatment results in a higher end of season seed biomass as expected [Morgan et al., 2005]. This is attributed to the photosynthetic stimulation of growth under elevated CO$_2$ conditions. As summarized in Table 3.1, the mean difference in seed biomass between ambient and elevated CO$_2$ was recorded at 93.4 g m$^{-2}$ with a p-value of 0.013 and the relative difference was observed to be 24%. It must be noted that this stimulation in yield due to elevated CO$_2$ is significantly higher than what was observed in prior studies, which have indicated a difference of about 15% [Morgan et al., 2005].

Comparing the seed biomass between LAI control and treatment effects from Figure 3.4b we see that LAI reduction treatment results in a higher end of season biomass under both ambient and elevated CO$_2$ conditions, in agreement with our modeling result. This is attributed to the LAI treatment canopies being closer to the optimum LAI values compared to the control. The mean difference in seed biomass between LAI treatment and control was recorded at 33.0 g m$^{-2}$ with a p-value of 0.041 and the relative difference was observed to be 8.1%. Based on the modeling studies performed in Chapter 2, a reduction in LAI of 0.5 results in an approximately 12% increase in NPP (Figure 2.6). It is important to recognize that the optimality studies considers changes in NPP while the experimental results deal with seed biomass resulting in the model yielding a non-conservative estimate. Furthermore, the modeling studies do not include the cost of leafing, and including these costs which further decrease the gains in NPP. Finally, it must be noted that the interaction effect of CO$_2$ and LAI reduction was not significant (p-value of 0.427).

### 3.5 Conclusions

In this chapter we describe canopy manipulation experiments to test the sub-optimal nature of soybean canopies with respect to maximizing the end of season seed output. This
experiment was motivated on the model results of the optimality studies described in Chapter 2. The model results indicated that optimum LAI values for soybean canopies grown under ambient and elevated CO\textsubscript{2} were 3.5 and 3.8 respectively, whereas, observed peak LAI values for ambient and elevated CO\textsubscript{2} were in the range of 6.5 and 8.0 respectively (Figure 2.6). Further modeling analysis revealed that trade offs between decreasing gains in daytime photosynthetic assimilation and increasing losses due to leaf respiration caused by increased shelf shading of leaves occurred as LAI was increased.

In order to test this modeling result, canopy manipulation experiments were performed on soybean plants at the SoyFACE research facility at the University of Illinois during the year 2010. A LAI reduction technique was developed whereby, young and emerging soybean leaf trifoliates were removed from the plants through a series of two leaf cutting experiments. By removing young and emerging trifoliates, we do not cause a significant loss to the investment made by plants in their leaves. LAI treatments were performed on both ambient and elevated CO\textsubscript{2} canopies and the end of season pod biomass was obtained. The end of season pod biomass was used as an indicator of NPP. As discussed earlier, seed biomass is a more conservative estimate as compared to NPP.

An average of 7 leaf trifoliates were removed from each plant through two LAI treatments, resulting in an expected potential loss of a LAI of 4.3. However, only a difference of 0.5 was achieved between LAI control and treatment plots, and this was attributed to internal regulatory mechanisms. This further shows evidence of sub-optimal behavior. Nevertheless, statistically significant decreases in LAI was achieved through the LAI treatment performed in this study, with a maximum of 8.1% decrease in LAI between control and LAI treatment sub-plots. The experiment also confirmed the widely observed canopy structural acclimation due to elevated CO\textsubscript{2} whereby LAI increases due to photosynthetic stimulation.

The end of season seed biomass was collected for all the sets of treatments and their corresponding dry weight values were obtained. Statistical analysis of these measurements reveal that a reduction in LAI causes a significant increase in end of season seed yield of up to 8.1%. This result is in agreement with the prior modeling results. The experiment also confirmed the widely reported increase in seed yield for plants grown under elevated CO\textsubscript{2}. However, the extent of yield increase was observed at 24%, which is much higher than the 15% which has been previously recorded at this site [Morgan et al., 2005].

Hence, the experimental results presented in this study demonstrate that decreasing LAI in soybean canopies increases end of season seed yield under both ambient and elevated CO\textsubscript{2} conditions. This is consistent with our earlier model result which indicated that soybean
canopies are sub-optimal by having a higher LAI with respect to maximizing NPP. In the following chapter we investigate these results in the light of strategies that plants use to allocate carbon.
CHAPTER 4

PLANT CARBON ALLOCATION ACCLIMATION AND SUB-OPTIMALITY WHEN SUBJECT TO GROWTH UNDER ELEVATED CARBON DIOXIDE CONDITIONS

4.1 Introduction

Our modeling results in Chapter 2 illustrate that soybean canopies are sub-optimal with respect to maximizing their NPP and hence their end of season seed biomass. Our analysis indicates that plants have a larger than optimal LAI and this causes a lowering of NPP due to increased self shading and trade-offs between GPP gains and respiration losses. In Chapter 3, we tested this result using a LAI reduction experiment and our results show that a decrease in LAI resulted in an increase in end of season seed biomass thus confirming our modeling results. In this chapter we develop a carbon allocation and growth model, and couple it with a coupled multi-layer canopy and soil root system vegetation model (MLCan) [Drewry et al., 2010a]. We use this coupled model to infer the acclimation in carbon allocation due to elevated CO₂. Furthermore, we develop a framework for obtaining an optimal carbon allocation and growth strategy to maximize end of season seed biomass and use it to test against observed results under ambient and elevated CO₂ conditions.

4.2 Carbon allocation model framework and equations

4.2.1 Carbon mass balance

Building on the framework presented by Arora and Boer [2005] the plant is divided into 4 parts, leaf, stem, seeds and root. Note that in the formulation of Arora and Boer [2005] there were no specific allocation for seeds. Mass balance equations are performed at daily time scales to determine the temporal evolution of carbon among all the plant parts. The
daily GPP Kg of CO2/day/m² is allocated to different plant parts. This is expressed as:

$$\beta_{GPP} = A_L + A_S + A_P + A_R$$  \hspace{1cm} (4.1)$$

where; $\beta$ Kg of C/Kg of CO₂ represents the conversion from kilograms of CO₂ to kilograms of carbon. $A_L$, $A_S$, $A_P$ and $A_R$ Kg of C/day/m² represent the carbon flux allocated to the leaf, stem, seed and root respectively. Normalizing the carbon allocation to different plant parts with respect to the GPP we get the carbon allocation fractions to each plant part. This is expressed as:

$$a_L = \frac{A_L}{\beta_{GPP}}$$  
$$a_S = \frac{A_S}{\beta_{GPP}}$$  
$$a_P = \frac{A_P}{\beta_{GPP}}$$  
$$a_R = \frac{A_R}{\beta_{GPP}}$$  \hspace{1cm} (4.2)$$

where; $a_L$, $a_S$, $a_P$ and $a_R$ – represent GPP normalized carbon allocation fractions to the leaf, stem, seed and root respectively. Note that $a_L + a_S + a_P + a_R = 1$.

The mass balance equations for the different plant parts is expressed as:

$$\frac{dC_L}{dt} = A_L - R_{gL} - R_{mL} - D_L$$

$$\frac{dC_S}{dt} = A_S - R_{gS} - R_{mS} - D_S$$

$$\frac{dC_P}{dt} = A_P - R_{gP} - R_{mP}$$

$$\frac{dC_R}{dt} = A_R - R_{gR} - R_{mR} - D_R$$  \hspace{1cm} (4.3)$$

Where, $C_L$, $C_S$, $C_P$ and $C_R$ Kg of C/m² represent the carbon content in the biomass of the leaf, stem, seed and root plant part respectively. $R_{gL}$, $R_{gS}$, $R_{gP}$ and $R_{gR}$ Kg of C/day/m² represent the carbon flux out of the leaf, stem, seed and root respectively caused due to growth respiration. $R_{mL}$, $R_{mS}$, $R_{mP}$ and $R_{mR}$ Kg of C/day/m² represent the carbon flux out of the leaf, stem, seed and root respectively caused due to maintenance respiration. $D_L$, $D_S$ and $D_R$ Kg of C/day/m² represent litter fall fluxes of carbon in the leaf, stem and root respectively. Note that we do not include litter fall for the seed component in our carbon
allocation model.

In our formulation, we ignore the costs associated with herbivory, hormones, mutualisms, root exudates, flowering, active transport, remobilization, chemical defenses, etc.

4.2.2 Growth respiration

Growth respiration represents the cost to build plant tissue from photo-assimilates, and in our work this is represented as:

\[ R_{gL} = \alpha_L (A_L - R_{mL}) \]
\[ R_{gS} = \alpha_S (A_S - R_{mS}) \]
\[ R_{gP} = \alpha_P (A_P - R_{mP}) \]
\[ R_{gR} = \alpha_R (A_R - R_{mR}) \]  \hspace{1cm} (4.4)

where, \( \alpha_L, \alpha_S, \alpha_P \) and \( \alpha_R \) are constant fractions called as growth respiration fractions typically talking the values between 0 and 1 in general. It has been suggested that, for vegetative plant material, it is common to have a growth respiration fraction of 0.25 [Thornley, 2011]. Thornley and Cannel [2000] use a growth respiration fraction value of 0.2 to model for vegetative plant material. Furthermore, the authors state that for reproductive parts, higher growth respiration losses are expected [Thornley and Cannel, 2000]. Lavigne and Ryan [1997] observe stem growth respiration fractions between 0.2 and 0.4 in trees.

Bunce and Ziska [1996] performed whole plant respiration experiments using soybean plants at different temperatures and CO\(_2\) concentrations and obtained growth respiration fractions between 0.28 and 0.35. Furthermore, their results concluded that there was no significant effect of growth conversion efficiency due to changes in growth temperatures. However, the authors found a slight (0.01) decrease in losses due to growth respiration with a 24% decrease in leaf nitrogen caused by elevated CO\(_2\) conditions. For the plant functional type C3 crops, Arora and Boer [2005] use a growth respiration fraction value of 0.15, while Knorr et al. [2007] uses a range between 0.2 and 0.3. In our work, we use a value of 0.15 as the growth respiration fraction for all plant parts based on the values given by Arora and Boer [2005].
4.2.3 Maintenance respiration

Maintenance respiration is represented as:

\[ R_{mL} = \beta \text{LAI} \ R_{mLT_0} \exp \left( c_{mL} - \frac{\Delta H_{mL}}{RT_L} \right) \]
\[ R_{mS} = \beta C_S R_{mST_0} \left( Q_{10S} \right) \frac{T_S - T_0}{10} \]
\[ R_{mP} = \beta C_P R_{mPT_0} \left( Q_{10P} \right) \frac{T_P - T_0}{10} \]
\[ R_{mR} = \beta C_R R_{mRT_0} \left( Q_{10R} \right) \frac{T_R - T_0}{10} \]

(4.5)

where, \( R_{mLT_0} \) Kg of CO\(_2\)/day/m\(^2\) of; LAI represents the base leaf respiration rate per unit leaf area. \( R_{mST_0}, R_{mPT_0} \) and \( R_{mRT_0} \) Kg of CO\(_2\)/Kg of C/day represent the base respiration rate per unit carbon biomass of stem, seed and root respectively. \( c_{mL} = 18.72 \) – represents the scaling constant, \( \Delta H_{mL} = 46.39 \) KJ/Mole represents the energy of activation, and \( R \) KJ/Mole/K represents the universal gas constant. \( Q_{10S}, Q_{10P} \) and \( Q_{10R} \) – represent the ratio of respiration at reference temperature \( T_0 \) K to that at temperature \( T_0 - 10 \) K. \( T_S, T_P \) and \( T_R \) K represent the temperature of the stem, seed, and root respectively.

The leaf maintenance respiration is modeled based on leaf respiration expressions from Bernacchi et al. [2003], Collatz et al. [2001], Drewry et al. [2010a]. The stem, seed and root respiration are modeled using the formulation based on Drewry et al. [2010a]. Note that Drewry et al. [2010a] uses a similar expression to the one given in 4.5 (root respiration example) to model soil respiration. The base respiration rates for stem and root are given as \( R_{mST_0} = 0.0365 \) and \( R_{mRT_0} = 0.16 \) in units of Kg of C/Kg of biomass/year for a C3 crop plant function type in the CTEM model [Arora and Boer, 2005]. For our model, we use a decreased \( R_{mRT_0} \) parameter to consider only root respiration and exclude other soil respiration fluxes.

Tang et al. [2005] performed root exclusion chamber experiment in a ponderosa pine ecosystem in the Sierra Nevada region. This experiment attempted to distinguish between root respiration and heterotrophic respiration. Their results indicate that soil respiration is higher in the presence of roots due to the contribution of root respiration. A strong diurnal variation in CO\(_2\) fluxes was observed in the exclusion plots attributed to a strong diurnal variation in the temperature. In the control plots, where the diurnal variation in temperature was dampened due to canopy shading, a strong nocturnal root respiration flux could have contributed to additional CO\(_2\) especially during the nighttime when soil microbial
respiration is low. Temperature plays an important role in determining soil respiration with increased temperatures causing increased respiration. Soil moisture plays a secondary role in determining soil respiration where both very low and very high soil moisture limiting soil respiration and an intermediate soil moisture enhancing soil respiration. The average ratio of root to total soil respiration during the growing season was observed to be 0.56 and during the non-growing season to be 0.16 for ponderosa pine.

Black et al. [2009] performed root exclusion chamber experiments to obtain soil and root respiration in a soybean agricultural ecosystem under both control and elevated CO$_2$ and elevated temperature conditions. While a strong seasonal variation was observed in the soil and root respiration, both root respiration and heterotrophic respiration were about half of the total soil respiration under ambient CO$_2$ and temperature conditions. In this work, we assume that $R_{mST_0}$ is 50% of the value used in Drewry et al. [2010a] implying that 50% of the soil respiration is root respiration. Note that plants acclimate their respiration response to long term changes in temperature. The values of $Q_{10S}$, $Q_{10P}$, and $Q_{10R}$ can change depending on the long term temperature exposure [Arora and Boer, 2005]. However, we ignore such effects in this work.

The NPP Kg of CO$_2$/day/m$^2$ which is the GPP less the maintenance respiration is represented as:

$$\beta NPP = \beta GPP - R_{mL} - R_{mS} - R_{mP} - R_{mR}$$ (4.6)

4.2.4 Litter fall

Litter fall is modeled as:

$$D_L = \frac{C_L}{\tau_L}$$
$$D_S = \frac{C_S}{\tau_S}$$
$$D_R = \frac{C_R}{\tau_R}$$ (4.7)

where, $\tau_L$, $\tau_S$ and $\tau_R$ are the lifespan days of each plant part. Note that the seed does not have any litter fall losses associated with it. For soybean, the leaf life span is 80 days. The stem and root life span are taken to be 7300 days and 1095 days respectively based on a C3 crop plant functional type from the CTEM model [Arora and Boer, 2005]. Note that we ignore the effects of crop harvest that causes changes to the natural litter fall rates.
Based on the experimental data from Miyaji [1984], we see that the average leaf life span for soybeans is 80 days. Unlike the model developed by Arora and Boer [2005], we do not include accelerated leaf litter fall due to stress conditions such as drought or extremes in temperature. This can lead to non-closure of biomass when the ecosystem undergoes a stress based enhanced leaf senescence. The data taken from CTEM Arora and Boer [2005] has an unrealistically high root life span value of about 3 years.

4.2.5 Carbon to biomass

Empirical relationships are used to convert from carbon content in each plant part to their respective biomass. The equation representing this conversion is given as:

\[
\begin{align*}
B_L &= \frac{C_L}{\gamma_L} \\
B_S &= \frac{C_S}{\gamma_S} \\
B_P &= \frac{C_P}{\gamma_P} \\
B_R &= \frac{C_R}{\gamma_R}
\end{align*}
\]

where, \(B_L, B_S, B_P\) and \(B_R\) Kg of biomass/m\(^2\) represent the biomass in the leaf, stem, seed and root respectively and \(\gamma_L, \gamma_S, \gamma_P\) and \(\gamma_R\) Kg of C/Kg of biomass represent the carbon content of the biomass in leaf, stem, seed, and root respectively. In this model we assume that the carbon content in biomass is time invariant, however it can vary between plant parts. In this work, we assume that 40% of biomass is carbon hence all \(\gamma\) values are 0.4.

4.2.6 Biomass to plant properties

Finally, the biomass is converted into different plant properties using the following empirical relationships:

\[
\begin{align*}
LAI &= \lambda B_L \\
K_{rad} &= \delta_{rad} f_{rad} B_R \\
K_{axi} &= \delta_{axi} f_{axi} B_R
\end{align*}
\]

(4.9)
where, $SLAI$ is the specific leaf area LAI/Kg of biomass which converts leaf biomass to LAI and is a constant. $K_{rad}$ and $K_{axi}$ represent the radial and axial root conductivities respectively. $f_{rad}$ and $f_{axi}$ are the fraction of root biomass that constitutes to the radial and axial root conductivities to water respectively. Note that $f_{rad} + f_{axi} = 1$. $\delta_{rad}$ and $\delta_{axi}$ represent the conversion from biomass to conductivities for the radial and axial root parts respectively. In our simulations we use $f_{rad} = 0.6$ and $f_{axi} = 0.4$ and $\delta_{rad} = 3.47 \times 10^{-7}$ and $\delta_{axi} = 0.18$.

4.3 Inference of carbon allocation patterns in soybean canopies

Based on the carbon allocation and growth model proposed in Section 4.2 we infer the time course of daily carbon allocation patterns in soybean canopies. We test the model using data from SoyFACE for the year 2001 [Morgan et al., 2005, Rodriguez, 2004]. The climate forcings for this problem was obtained from Drewry et al. [2010a]. The framework that we use to perform carbon allocation is given in Section 4.2. Since our model framework is applicable for closed canopies, we simulate a 60 day growing window towards the end of the growing season where the LAI is greater than 3.0. For the year 2002, we model from day 200 to 260.

Figure 4.1a shows the variation of different biomass components as a function of time under ambient and elevated CO$_2$ conditions. The above-ground biomass data for this figure was obtained from Morgan et al. [2005] and the below-ground biomass data was obtained from Rodriguez [2004]. The temporal trends in biomass indicate an initial rise in the vegetative biomass (leaf, stem, and root) followed by a fall later in the growing season. It must be noted that the decline in biomass is the strongest in the leaf, and this is followed by the root and then the stem. However, the reproductive biomass (seed) although starts growing only later in the growing season, increases monotonically till the end of the growing season. Furthermore, the trends in the biomass data show that compared to ambient CO$_2$ conditions, the biomass of each and every plant part is increased under elevated CO$_2$ conditions. However, the increase is not proportional across all plant parts [Morgan et al., 2005]. The relative increases in vegetative components of the biomass (stem, leaf and root) is much higher than the reproductive part (seed) indicating that soybean plants are able to exhibit significant levels of plasticity. Among the vegetative parts, the highest relative increased are observed in the stem, followed by the root and then the leaves.

Figure 4.1b presents the variation of carbon allocation fractions for the different plant parts as a function of time. The temporal trends in the carbon allocation fractions closely mimic the rates of increases of the different biomass components. While the fraction of carbon
Figure 4.1: Summary of a) biomass and b) inferred carbon allocation fractions in soybean plants under ambient and elevated CO$_2$ conditions. The biomass data in a) illustrates the effect of plant plasticity, whereby the relative increases in biomass across different plant parts are not constant. The carbon allocation fraction data in b) illustrates the effect of allocation acclimation where plants change their carbon allocation strategy under climate change. Solid lines represent ambient CO$_2$ while dashed lines represent elevated CO$_2$ conditions. Simulations are performed for soybean plants at the Ameriflux site in Bondville, IL for the year 2002.
allocated to the vegetative parts decreases with time, the fraction of carbon allocated to the reproductive part increases. Among the different plant parts, the lowest fraction of GPP gets proportioned to the roots (Figure 4.1b). This can be attributed to the fact that roots which are the sinks of carbon are located the farthest from the leaves which are the source of carbon and hence experience the highest transport resistance [Thornley, 2011, Thornley and Cannel, 2000]. Also, it is interesting to note that while the roots and the leaves have similar biomass, the fraction of GPP allocated to the roots is significantly lower than the leaves. This is attributed to the fact that leaves have a higher maintenance respiration costs. Furthermore, the litter fall rates of the leaf are an order of magnitude greater than that of the roots costing additional carbon.

It is also important to note that the carbon allocation fractions have a high degree of variability at the daily time scales (Figure 4.1b). While, it is true that plant carbon allocation is a dynamic process and can vary at short time scales, we feel that the sudden jumps and dips in the carbon allocation fractions are an artifact of the lack of fine resolution temporal data of biomass. We interpolate biomass between observed time points at the bi-monthly time scale. We suggest that, in reality carbon allocation fractions vary in a more gradual fashion than what is observed in Figure 4.1b.

We know that the sum of the carbon allocation fractions is equal to 1. Negative carbon allocation fractions indicate that there is a remobilization of carbon that leaves the particular plant part. Based on the Figure 4.1b, we see that the stem and root plant parts are able to remobilize and translocate significant amounts of carbon out of their tissue and the majority of this remobilized carbon reaches the pods. It is interesting to note that towards the end of the growing season, the fraction of GPP that is allocated to the seeds is more than 1, and remobilization of carbon enables this phenomenon. The extent of remobilization is higher under ambient CO$_2$ conditions compared to elevated CO$_2$ conditions. However, it must be noted that this is the GPP normalized fraction. The true carbon flux remobilized is actually higher, since the GPP is higher under elevated CO$_2$ compared to ambient CO$_2$ conditions.

The presence of allocation acclimation is illustrated in Figure 4.1b. Allocation acclimation is identified by the difference in allocation strategies as indicated by differences in carbon allocation fractions between ambient and elevated CO$_2$ conditions. It must be noted that the acclimation effects is highest for the reproductive portion of the plant (seed) compared to the other vegetative parts (leaf, stem, and root). The well documented phenomenon of lower than expected increases in seed biomass [Morgan et al., 2005] is also explained using the help of carbon allocation (Figure 4.1b). While the effect of allocation acclimation is
to mostly increase the fraction of GPP allocated to the vegetative parts, it significantly decreases the fraction of GPP allocated to the reproductive part (seeds). This provides a conclusive explanation for the lower than expected increases in yield for soybean plants growing under elevated CO$_2$ conditions [Morgan et al., 2005].

From the biomass data we observe that under elevated CO$_2$ conditions, the relative increases in stem biomass are the highest (Figure 4.1a). However, the carbon allocation data shows that under elevated CO$_2$ the fraction of GPP allocated to the stem is lower especially in the early time periods. This anomalous behavior is explained by the fact that, stem respiration and litter fall rates are several orders of magnitude smaller compared to other plant parts (Figure 4.2d). This example illustrates the significance of the interplay between the different carbon fluxes that determine the growth of each plant part.

From the carbon allocation fluxes in Figure 4.2 we can observe that maximal maintenance respiration fluxes are observed in the leaf. Similarly, maximal litter fall fluxes are also observed in the leaf tissue. Hence, the cost of maintaining leaf tissue is the highest among all plant parts. From the perspective of storage and remobilization of carbon, it would be advantageous for the plant to invest more in stem and root where the losses due to maintenance respiration and litter fall are minimal.

The results presented in this section, illustrate the presence of carbon allocation acclimation in soybean plants when subjected to growth under elevated CO$_2$ conditions. In the following section, we test the degree of sub-optimality of this observed carbon allocation strategy through the help of an optimal plant carbon allocation model framework.

### 4.4 Optimality framework for carbon allocation in plants

Based on the work of Iwasa [2000], we develop an optimal carbon allocation model in which we maximize the end of season seed biomass under ambient and elevated CO$_2$ conditions. The conceptual framework for the optimality is presented in Figure 4.3. We employ this optimality model for a 60 day time period towards the end of the growing season. As illustrated in the figure, there are several time scales of partitioning that are involved in this modeling effort. At the shortest time scales (half hourly), the variable that we allow to change is the stomatal conductance. We fix the LAI, and the axial and radial root conductivities. Based on the carbon allocation strategy chosen, the GPP at the end of the day is allocated to the different plant parts and this this results in the subsequent growth of the different plant parts at the daily time scale. Hence, LAI, and axial and radial root conductivities change
Figure 4.2: Summary of the different components of the carbon allocation fluxes for each of the plant part. Note that the seeds do not have any litter fall associated with them. a) Leaf, b) Stem, c) Seed and d) Root. Solid lines represent ambient CO$_2$ while dashed lines represent elevated CO$_2$ conditions. Simulations are performed for soybean plants at the Ameriflux site in Bondville, IL for the year 2002.
at daily time scales. However, we fix the particular carbon allocation strategy and allow it to change in steps of 0.2 once every 20 days. Note that, the carbon allocation fractions are linearly interpolated between the time points for change. For the entire duration of the simulation, the leaf area distribution, rooting depth, and root distribution are kept constant.

Figure 4.3: Illustration of the approach towards obtaining optimal carbon allocation strategy.

While it is true that the carbon allocation strategies can change at a finer time scale, as we show in our modeling exercise in the previous section, the changes in carbon allocation fraction are more gradual than rapid. We feel that a 20 day window provides an adequate representation to capture the acclimation effects of interest for us. For our 60 day time period, we have 3 time points of change of carbon allocation strategy. It must be noted that the sum of the different carbon allocation fractions should be equal to 1. Based on this, we develop an expanding web of all the possible permutations of carbon allocation fractions and
simulate the end of season seed biomass. It must be noted that the strategies which do not provide sufficient carbon fluxes for maintenance respiration are discarded.

The cost versus benefit trade-offs in this framework can be summarized as follows:

- Investment in leaf, leads to higher LAI and this can potentially result in a higher NPP. However, over investment in leaf will be detrimental to the NPP due to respiration trade offs.

- Investment in the stem can result in increased light availability and hence a higher NPP. However, there are upper limits to the amount of light that can be absorbed and investment in stem beyond this limit does not yield any NPP return.

- Investment in the seeds directly increases the optimal function. However, seeds to not contribute to increasing NPP and hence the timing and the quantity of investment to seeds must be done accurately so that carbon investment other plant parts yield maximal NPP.

- Investment in the roots results in increased access to water and hence prevention of wilting and the ability to continue photosynthesis without additional stomatal closure caused by water stress. However, having more than necessary roots results in increased respiration losses.

While our 1-D model can capture the trade-offs in leaf, seed, and root, the model currently cannot capture the effects of light competition due to increased height. While recent advances have been made in this area [Quijano et al., 2012], to simplify our analysis these are not included in this study. To account for stem carbon allocation, we calibrate the carbon allocation portion to the stem based on observed stem biomass values. Hence, in this study we optimize for leaf, stem and seed only. The optimality approach involves a simple mesh based search algorithm, however, as mentioned above, obtaining the mesh can be challenging. After, simulating for all possible combinations of carbon allocation strategy, and eliminating the strategies that are incapable of maintenance respiration, and the strategy that yields the highest end of simulation seed biomass is selected as the optimal strategy (Figure 4.3).

4.5 Optimal carbon allocation strategy

Figure 4.4 shows the location of the optimal and observed carbon allocation strategies under ambient and elevated CO$_2$ conditions. It can be observed from the figure that the results
from the optimality model match the trends in the observed results well. In particular, the temporal trends of decreasing carbon allocation to vegetative plant parts and increasing allocation to reproductive parts is well captured by the optimality model. Furthermore, the optimality model captures the trends with respect to allocation acclimation well. Under acclimation to elevated CO$_2$, the optimal carbon allocation model allocates more carbon to vegetative plant parts and less to reproductive parts (Figure 4.4). These results demonstrate that the optimality framework is able to capture allocation acclimation aspects well.

It must be noted that overall, the optimality model allocates less to the vegetative plant parts and more to the reproductive plant parts. This results in a higher than optimal observed end of simulation seed biomass (Figure 4.5c). The increase in seed yield resulting from an optimal carbon allocation strategy under ambient and elevated CO$_2$ conditions are 23% and 42% respectively. These predicted increases in seed yield due to optimal allocation acclimation result in much higher jumps in seed yield compared to the predicted yield increases without including the effects of acclimation.

Figure 4.6 illustrates the differences between optimal and observed LAI under ambient and elevated CO$_2$ conditions. The results of the carbon allocation and growth model show that the optimal LAI is about 50% of the observed LAI. Furthermore, under elevated CO$_2$ conditions, while the observed stimulation in LAI is only 10% the stimulation can be up to 25% under optimal conditions. The effects of decreased LAI on canopy and ecosystem fluxes have been thoroughly investigated in Chapter 2 and hence are not presented in this chapter.

4.6 Conclusions

In this chapter, we present a carbon allocation and growth model for vegetation at daily time scales. The model considers 4 plant parts, namely; leaf, stem, seed, and pod. The GPP is allocated to the different plant parts and there are losses resulting from growth respiration, maintenance respiration, and litter fall. Mass balance equations for each plant part is computed based on carbon influx and out flux. This model framework is then used to infer carbon allocation patterns under ambient and elevated CO$_2$ conditions by providing the biomass as one of the inputs in the model.

The results of this study indicate that soybean plants undergo allocation acclimation whereby, they alter their carbon allocation strategy when grown under elevated CO$_2$ conditions. In particular, under elevated CO$_2$ conditions, soybean plants decrease the fraction of GPP allocated to the seeds and increase the fraction allocated to vegetative plant parts.
Figure 4.4: Comparison of the optimal carbon allocation strategy with observed carbon allocation strategy for soybeans under ambient and elevated CO₂ conditions. a) Leaf, b) Stem, c) Seed and d) Root. Black lines indicate all possible allocation fraction combinations and solid and dashed colored lines represent data derives ambient and elevated CO₂ values respectively. Squares and circles represent optimal ambient and elevated CO₂ values respectively. Simulations are performed for soybean plants at the Ameriflux site in Bondville, IL for the year 2002.
Figure 4.5: Comparison of the optimal biomass with observed biomass for soybeans under ambient and elevated CO$_2$ conditions. a) Leaf, b) Stem, c) Seed and d) Root. Solid and dashed colored lines represent data derived from ambient and elevated CO$_2$ values respectively. Squares and circles represent optimal ambient and elevated CO$_2$ values respectively. Simulations are performed for soybean plants at the Ameriflux site in Bondville, IL for the year 2002.
Figure 4.6: Comparison between optimal and observed LAI under ambient and elevated CO₂ conditions illustrating that while LAI is lower at ambient CO₂ conditions compared to elevated CO₂ conditions, more importantly optimal LAI is lower than observed LAI under both ambient and elevated CO₂ conditions. Simulations are for the year 2002 for soybean grown at SoyFACE research facility, IL.

This explains the widely observed lower than expected yield in soybean plants when grown under elevated CO₂ conditions.

We further develop an optimality framework for carbon allocation and test the data inferred GPP allocation fractions against the carbon allocation strategy that maximizes end of simulation seed biomass. The results of the optimality studies indicate that the optimal carbon allocation strategies are able to capture the tendencies of allocation acclimation well. However, it also points out that there exists serious inefficiencies in carbon allocation in soybean plants under ambient and elevated CO₂ conditions. These results can be used to design crops that have the capability to significantly improve yield and can have important consequences in the area of food security. In the following section, we attempt to address some of the reasons for the observed sub-optimality.
CHAPTER 5

A FRAMEWORK TO QUANTIFY RESILIENCE IN NON-LINEAR DYNAMICAL SYSTEMS WHEN SUBJECT TO DISTURBANCE

5.1 Introduction

In the previous chapters we demonstrated the sub-optimal nature vegetation in terms of maximizing end of season seed biomass. We tested this for a soybean agricultural ecosystem using canopy optimization modeling studies in Chapter 2 and performed field experiments to test our modeling studies using canopy manipulation techniques. As illustrated in Chapter 3 the experimental results in agreement with the modeling studies demonstrated the sub-optimal nature of plant canopies. In Chapter 4, we further quantified the extent of sub-optimality using a coupled vegetation carbon allocation and growth model and identified the presence of allocation acclimation that causes increased sub-optimality for growth under elevated CO$_2$ conditions.

While we review several criticisms of the optimality approach to modeling vegetation acclimation in 1, we argue that unconstrained optimality models give a predictive knowledge of the direction in which the mean behavior of the trait would move under altered environmental conditions, rather than the present value of the trait [Makela et al., 2002]. We hypothesize that adding additional constraints such as the need to survive extreme events by maintaining resilience acts as a significant trade off towards achieving the optimality peaks. Since quantitative characterizations of resilience are not readily available in the literature, we develop a mathematical framework to to quantify resilience. We propose that using this resilience framework, we can obtain quantifiable measures of resilience which can then be used as constraints on the optimality model. We hypothesize that such a constrained optimality model would help us to not only bridge the gap between model outputs and observations, but also enhance our overall understanding of ecosystems under climate change.

1A slightly modified version of this chapter has been submitted to Ecological modeling journal and is under a second round of review: V. Srinivasan and P. Kumar. Emergent and divergent resilience behavior in disturbance driven catastrophic shift systems
The primary goal of this chapter is to define resilience measures for a non-linear dynamical system subject to disturbance modeled as stochastic noise. We use catastrophic shift system as the canonical form of the model for illustration purposes. Two ecological models are used as illustrations to provide context for comparing and contrasting these resilience measures. Our goal here is not to study these ecological systems in conventional detail, but to provide insights into the use on resilience measures as applied into these systems. In section 5.2 we review some of the recent literature in catastrophic shift systems and resilience and in section 5.3, we develop the mathematical framework for the resilience measures in a catastrophic shift system subject to singular and continuous disturbance disturbance events characterized as (a) Gaussian white noise and (b) Markovian dichotomous noise. Gaussian white noise captures random uncorrelated disturbance while Markovian dichotomous noise allows us to capture more structure in the disturbance. Using this mathematical framework, we develop resilience measures under singular and continuous disturbances (sections 5.4 and 5.5 respectively) and analyze the characteristics of these measures under varying system parameters. We then analyze the characteristics of these resilience measures under varying parameter conditions and disturbance intensities and highlight the emergent behavior. Subsequently, in section 5.6 we develop the concept of iso-resilience and in section 5.7 we provide discussions on the applications of our modeling approach. In section 5.8 we provide concluding remarks along with some broader implications of the results.

5.2 Literature review

Catastrophic shift systems have been used as a model to explain a range of phenomenon from lake eutrophication [Carpenter et al., 2001, Dent et al., 2002], shrub grass transition [Carpenter et al., 2001, Scheffer et al., 2001], algal overgrowth in corals [Bellwood et al., 2004, Cote and Darling, 2010], insect outbreak dynamics [Strogatz, 1994] and others [Folke et al., 2004]. The ubiquitous characteristics that these phenomena share are bi-stability, abrupt switching between alternate dynamic regimes, and hysteresis [Carpenter et al., 2001, Folke et al., 2004, Holling, 1996, Scheffer and Carpenter, 2003, Scheffer et al., 2001, Walker et al., 2004]. Bi-stability implies that the long-term dynamics converges to one of two stable points depending on the initial condition. The set of all initial states that converge to a specific stable point is referred to as its basin or domain of attraction (DOA). When the system is stochastic in nature, then the deterministic concept of DOA is replaced by the probabilistic concept of dynamic regime [Brand and Jax, 2007, Scheffer and Carpenter, 2003]. Each DOA
or dynamic regime is typically associated with its unique characteristic dynamics, processes, and feedbacks, such as turbid versus clear lake, shrub versus grass dominated landscape, etc. [Scheffer et al., 2001]. These systems have the capacity to switch to the alternate DOA or dynamic regime through a sudden or rapid transition, when system parameters, typically under the influence of external stress such as climate change, cross a critical threshold. More importantly, they exhibit a hysteresis effect, where the new dynamic regimes are sustained even after the removal of the stressor that caused the transition.

Resilience is broadly understood as the ability to withstand a change such that the dynamical behavior remains relatively unaffected [Folke et al., 2004, Holling, 1973, 1996, Turner, 2010]. The concept of resilience has also been associated with other related and often overlapping concepts such as vulnerability, adaptability, persistence, robustness, resistance, redundancy, stability, recovery, ability to self organize, transformability, flexibility, and ability to learn [Brand and Jax, 2007, Carpenter et al., 2001, Cote and Darling, 2010, Folke et al., 2004]. Resilience also holds one of the key wedges in sustainability science [Brand and Jax, 2007, Carpenter et al., 2001, Cote and Darling, 2010, Perrings, 2006] and is increasingly being used for developing strategies to mitigate climate change [Cote and Darling, 2010, Folke et al., 2004, Janssen et al., 2006, Turner et al., 2006]. Climate scientists have predicted changes in both the mean and the extremes in future climate forcings due to anthropogenic climate change [Field et al., 2012, Solomon et al., 2007]. Increases in climate variability and occurrence of extreme events such as temperature extremes in the form of heat and cold waves [Schar et al., 2004, Stott et al., 2004], increased occurrences of droughts and floods [Pall et al., 2011, Timmermann et al., 2011], increased frequency of hails [Mahoney et al., 2012] etc. can have significant impact on ecosystem processes such as vegetation growth and mortality [Hirota et al., 2012], occurrence of fires [Hirota et al., 2012], patterns of herbivory [Hamilton et al., 2005] etc. Hence, climate change can alter ecosystem behavior by: i) directly changing the system parameters and; ii) alter other aspects of disturbance such as frequency, intensity, variability and asymmetric bias etc.

An understanding of concept of resilience helps us to answer questions such as; how does a complex system absorb and respond to unexpected disturbances [Cumming et al., 2005]; what aspects of the complex systems are prone to behavioral changes under such a disturbance [Brand and Jax, 2007, Folke et al., 2004]; what type and strength of disturbance does it take to cause behavioral changes in particular aspects of a complex system [Carpenter et al., 2001]; which direction should our efforts be invested to prevent dynamic regime transitions [Cote and Darling, 2010, Holmgren and Scheffer, 2001] etc. In this context, the space and
time scales at which we analyze the problem play a significant role in the formulation of resilience measures [Carpenter et al., 2001]. We define resilience as the ability of a system’s DOA or dynamic regime to maintain its structure, process and feedbacks when subject to disturbances at a particular spatial and time scale of interest. Resilience can thus be interpreted as a higher order description of system dynamics [Anderies et al., 2006, Brand and Jax, 2007, Folke, 2006] that can capture characteristics of emergent behavior such as catastrophic shifts, hysteresis, dynamic regime change etc. for which simple space and time derivative based equilibrium and stability analysis are not suitable [Holling, 1973].

Two of the most commonly used resilience attributes are ‘engineering resilience’ and ‘ecological resilience’ [Gunderson, 2009, Holling, 1996]. While engineering resilience is defined as the time taken by the system to recover to the stable state following an isolated disturbance event [Holling, 1973, 1996], ecological resilience is defined as the amount of disturbance that a system can withstand without a change in the dynamic regime [Gunderson, 2009, Tilman and Downing, 1994]. More recently, there have been efforts to include other resilience attributes such as ‘latitude’, ‘precariousness’ and ‘resistance’ [Brand and Jax, 2007, Folke et al., 2004, Walker et al., 2004]. While the definition of precariousness measure seems to be identical to that of ecological resilience, latitude measure is defined as the size of the DOA, and resistance measure is associated with the depth of the potential well of a DOA. Several other resilience measures based on thermodynamic and information theory [Fath et al., 2003, 2006] have also been proposed. In general, there can be multiple representations of resilience, each of which capture in general overlapping but different attributes. A particular attribute of a DOA or dynamic regime might be highly resilient to one type of disturbance but less resilient to other types of disturbances [Cote and Darling, 2010, Folke et al., 2004]. For example, tropical savanna are highly resilient to fires, but not to over grazing [Folke et al., 2004, Holmgren and Scheffer, 2001, Scheffer et al., 2001]; managed marine coral communities might be able to bounce back from small scale thermal or nutrient shocks faster by increasing engineering resilience, however, this would be at the risk of being wiped off by large scale shocks thereby decreasing ecological resilience [Cote and Darling, 2010].

Although these past studies provide insights into resilience, a theoretical framework for understanding resilience in systems driven by stochastic disturbance has not been developed. In this chapter we develop a stochastic framework that provides important insights on different resilience measures and how they change with the attributes of the properties of the system and the disturbance. We hope that this development will also provide an interpretive framework for data driven investigations that use a probabilistic approach for interpretation
of the empirically observed dynamics [Marani et al., 2013, Scheffer et al., 2012]. We use catastrophic shift systems to develop this framework to quantify resilience at aggregate spatial scales (spatially averaged) and stationary time scales (transient behavior is not considered) by arguing that different resilience attributes give rise to different measures [Brand and Jax, 2007, Holling, 1973]. We consider the response of the system subject to both singular or isolated and continuous stochastic disturbance events. Developing on the work of past resilience quantifications [Carpenter et al., 2001, Folke et al., 2004, Walker et al., 2004], we propose a system-disturbance-attribute triplet framework to quantify resilience measures. This triplet framework is best captured by asking the question: ‘resilience of which behavioral characteristics, to what disturbance, and in what attribute’. Resilience ‘of’ can be system DOA or dynamic regime or other behavioral characteristics [Kumar, 2001] which include function, process, feedbacks etc. resilience ‘to’ can be the specific disturbance type in external forcing such as singular or stochastic disturbance etc. resilience ‘in’ can be distance to unstable threshold (ecological resilience), size of the DOA (width of the stability domain), mean dynamic regime residence time (fraction of time spent in the dynamic regime), mean passage times (switching frequency between adjoining connected dynamic regimes) etc. We also note that scale at which our resilience measures are proposed are important and in this study we deal with aggregate spatial scales and stationary time scales.

5.3 Mathematical formulations

5.3.1 Example A: Bistable population dynamics

In this example we consider the dynamics of bistable populations with refuge and outbreak dynamic regimes subject to immigration and emigration, population growth, non-linear interspecific competitive effects and random stochastic fluctuations in population fluxes. The governing equation that describe the dynamics of this population $P$ [number] at annual time scales is adapted from the logistic equation [Morin, 1999, Pearl and Reed, 1920] as:

$$\frac{dP}{dt} = I + rP + c\left(\frac{P_0 - P}{P_0}\right)^k + N\eta(t)$$  \hspace{1cm} (5.1)

The immigration and emigration rate $I$ [number/year] is a constant that can be positive or negative and population growth is governed by first order kinetics dependent on the intrinsic
growth rate \( r \) [1/year]. Interspecific competitive effects such as consumption, preemption, overgrowth, chemical interactions, territoriality and encounter competition etc. [Schoener, 1983], are driven by a power law relationship dependent on the: i) population carrying capacity \( P_0 \) [number], ii) the strength of the competitive effects \( c \) [number/year], and iii) the non-linearity of the competitive effects \( k \) [-]. The random fluctuation effects such as inter-annual variations in immigration and emigration rates, mortality due to disease etc. are represented by a Gaussian white noise \( \eta(t) \) [number/year] with standard deviation \( N \) [-]. \( k = 3 \) gives rise to catastrophic shift behavior. The range of admissible values for these parameters are: \( P \geq 0, t > 0, \infty < I < \infty, r > 0, c > 0, P_0 > 0 \) and \( N \geq 0 \). The population variable \( P \) in equation (5.1) can be non-dimensionalized by using a relative population variable \( x = \frac{P-P_0}{P_0} \) [-]. Performing this substitution in equation (5.1) and simplifying for \( k = 3 \) we get:

\[
\frac{dx}{dt} = \frac{I}{P_0} + r + rx - \frac{c}{P_0} x^3 + \frac{N}{P_0} \eta(t) \tag{5.2}
\]

5.3.2 Example B: Multi-stable vegetation dynamics

The second example describes the dynamics of multi-stable vegetation cover dynamics with desert, intermediate and vegetated dynamic regimes subject to reforestation and deforestation, vegetation growth and colonization, competition, and random fluctuations in vegetation mortality caused by stress and non-stress conditions induced by environmental fluctuations. The governing equation for the dynamics of vegetation as determined by its fractional cover \( F \) [m\(^2\)] at annual time scales is based on a simplified modeling framework presented by Ridolfi et al. [2011] and is given as:

\[
\frac{dF}{dt} = A + gF + S \left( \frac{F_0 - F}{F_0} \right)^k + N \eta(t) \tag{5.3}
\]

The deforestation and reforestation rate \( A \) [m\(^2\)/year] is a constant that can be positive or negative and vegetation cover growth is governed by first order kinetics dependent on the intrinsic growth rate \( g \) [1/year]. Competitive effects such as consumption, overgrowth, chemical interactions etc. [Schoener, 1983], are driven by a power law relationship dependent on i) the vegetation cover carrying capacity \( F_0 \) [m\(^2\)], ii) the strength of the competitive effects \( S \) [m\(^2\)/year], and iii) the non-linearity of the competitive effects \( k \) [-]. The random fluctuation effects such as inter-annual variations in mortality rates are modeled as a Markovian
dichotomous noise \( \eta(t) \) [\( \text{m}^2/\text{year} \)] with a disturbance strength \( N \) [-]. \( k = 3 \) gives rise to the catastrophic shift behavior. The range of admissible values for these parameters are: \( F \geq 0, t > 0, -\infty < A < \infty, g > 0, S > 0, F_0 > 0 \) and \( N \geq 0 \). The vegetation cover variable \( F \) in Equation (5.3) can be non-dimensionalized by using a normalized fractional vegetation variable \( x = \frac{F - F_0}{F_0} [-] \). Performing this substitution in equation (5.3) and simplifying for \( n = 3 \) we get:

\[
\frac{dx}{dt} = \frac{A}{F_0} + g + g x - \frac{S}{F_0} x^3 + \frac{N}{F_0} \eta(t) \tag{5.4}
\]

These two systems will henceforth be referred to as Example A and Example B. We note that, both equations (5.2) and (5.4) can be written in the generic form:

\[
\frac{dx}{dt} = \theta_1 + \theta_2 x + \theta_3 x^3 + K \eta(t) \tag{5.5}
\]

where, \( \theta_1, \theta_2 \) and \( \theta_3 \) are the parameters of the model and \( K \) characterizes the strength of the noise. We note that in the absence of noise i.e. \( \eta(t) = 0 \), the dynamics corresponds to that of a double well potential. However, under noise, this behavior can be altered and the implications of this is explored in greater detail in this chapter.

5.3.3 Catastrophic shift system dynamics

The governing equation for a general univariate deterministic dynamical system can be expressed as [Anishchenko et al., 2002]:

\[
\frac{dx}{dt} = -\frac{dV}{dx} \tag{5.6}
\]

where, \( x \) is the system state [in units of quantity \( Q \)], \( t \) is time [\( T \)] and \( V(x) \) is the potential function [\( Q^2/T \)]. The canonical form for the dynamics describing a catastrophic shift system is [Strogatz, 1994]:

\[
\frac{dx}{dt} = \theta_1 + \theta_2 x + \theta_3 x^3 \equiv F(x) \tag{5.7}
\]

where \( \theta_1, \theta_2 \) and \( \theta_3 \) are the imperfection parameter (or flux parameter) [\( Q/T \)], rate parameter (or growth/decay parameter) [\( 1/T \)], and non-linear recovery parameter (or feedback parameter) [\( 1/(Q^2T) \)], respectively. Comparing equation (5.2) (assuming \( N = 0 \)) with (5.7) we see that the flux parameter is the sum of the relative immigration and emigration rate and the relative population growth rate at the carrying capacity i.e. \( \theta_1 = \frac{I}{F_0} + r \) [\( 1/\text{year} \)],
the rate parameter is the intrinsic population growth rate $\theta_2 = r$ [1/year], and the feedback parameter is the normalized strength of competitive effects $\theta_3 = -\frac{c}{F_0}$ [1/year]. And comparing equation (5.4) (assuming $N = 0$) with (5.7) we see that the flux parameter is the sum of the relative deforestation and reforestation rate and the normalized fractional vegetation growth rate at the carrying capacity i.e. $\theta_1 = \frac{A}{F_0} + g$ [1/year], the rate parameter is the intrinsic vegetation cover growth rate $\theta_2 = g$ [1/year], and the feedback parameter is the normalized strength of competitive effects $\theta_3 = -\frac{S}{F_0}$ [1/year].

The expression for the potential function $V$ in equation (5.7) is governed by $-\frac{dV}{dx} = \frac{dx}{dt}$ and is obtained as:

$$V(x) = - \left( \theta_1 x + \frac{\theta_2 x^2}{2} + \frac{\theta_3 x^4}{4} \right)$$ (5.8)

Three cases are possible depending on the parameter combinations of $\theta$. Case 1: When $27\theta_1^2 < 4\theta_3^3$ three real fixed points are obtained. If $\theta_3 < 0$, then two of the three fixed points will be stable giving rise to the well known bi-stable system. For the rest of this chapter, we will use equation (5.7) and without loss of generality assume $\theta_3 = -1$. Case 2: When $27\theta_1^2 = 4\theta_3^3$ two real fixed points are obtained, and Case 3: When $27\theta_1^2 > 4\theta_3^3$ one real fixed point is obtained.

We denote the $i^{th}$ stable fixed point, or attractor, as $x_i$ and $X_i$ as its DOA (Fig.5.1a). $x_{i,j}$ is the unstable (fixed point) boundary between the DOAs $X_i$ and $X_j$. DOA $X_i$ can be bounded by the unstable boundaries $x_{i,j}$ and $x_{i,k}$ or an externally imposed system boundary $x_i$.

In Example A, when $N = 0$, and under the condition $27\theta_1^2\theta_3 < 4\theta_2^3$, we have bistable population dynamics with the stable low relative population level $x_1$ termed as ‘refuge population’ and the stable high relative population level $x_2$ termed as ‘outbreak population’ [Strogatz, 1994]. The unstable relative population level $x_{1,2}$ separating the refuge and outbreak relative population levels is termed as ‘threshold population’ [Strogatz, 1994]. When the initial relative population is higher than the threshold population, the population eventually reaches the outbreak population, and when the initial relative population is lower than the threshold population, the population eventually reaches the refuge population. The two DOAs $X_1$ and $X_2$ are called ‘refuge DOA’ and ‘outbreak DOA’ and these correspond to the stable attractors $x_1$ and $x_2$ respectively.

Similarly, in Example B, when $N = 0$, and under the condition $27\theta_1^2\theta_3 < 4\theta_2^3$, we have multi-stable vegetation cover dynamics with the stable low normalized fractional vegetation cover $x_1$ termed as ‘desert cover’ and the stable high normalized fractional vegetation cover $x_2$ termed as ‘vegetated cover’ [Ridolfi et al., 2011, Scheffer et al., 2001]. The unstable
Figure 5.1: Concepts of (a) DOA for singular disturbance events (equation (5.7)) and (b) dynamic regime for continuous disturbance events (equation (5.10)) for a catastrophic shift system. The system parameters used for both (a) and (b) are \( \theta_1 = 0.2, \theta_2 = 2.0 \) and \( \theta_3 = -1.0 \) and the additional parameter for (b) is Gaussian white noise disturbance scale \( D = 0.5 \). When the system is subject to a singular disturbance, DOAs can be obtained from a potential function \( V(x) \) plot such as in (a) where the peaks in the potential function (occurring at the unstable fixed point \( x_{1,2} = -0.10 \)) represented by the white circle separate the two DOAs. The troughs of the potential function (occurring at the stable fixed points \( x_1 = -1.36 \) and \( x_2 = 1.46 \)) are represented by the black circles. The ecological resilience \( R^E_1 \) (1.26) and \( R^E_2 \) (1.56) and the activation potential \( R^a_1 \) (0.73) and \( R^a_2 \) (1.30) resilience measures for the two DOAs are illustrated. When the system is subject to a continuous disturbance, dynamic regimes can be obtained from a stationary PDF such as in (b) where the troughs in the PDFs (occurring at the anti-mode \( x_{1,2} = -0.10 \)) represented by the white circle separate the two dynamic regimes. The peaks of the PDF (occurring at the stable fixed points \( x_1 = -1.36 \) and \( x_2 = 1.46 \)) are represented by the black circles. The stochastic ecological resilience \( R^{sE}_1 \) (1.26) and \( R^{sE}_2 \) (1.56) and the regime probability \( R^R_1 \) (0.27) and \( R^R_2 \) (0.73) resilience measures for the two dynamic regimes are also illustrated.
normalized fractional vegetation cover $\hat{x}_{1,2}$ separating the desert and vegetated covers is termed as ‘threshold cover’. When the initial normalized fractional vegetation cover is higher than the threshold cover, the ecosystem eventually reaches the vegetated cover, and when the initial normalized fractional vegetation cover is lower than the threshold cover, the ecosystem eventually reaches the desert cover. The two DOAs $X_1$ and $X_2$ are called ‘desert DOA’ and ‘vegetated DOA’ and these correspond to the stable attractors $\hat{x}_1$ and $\hat{x}_2$ respectively.

The fixed points for equation (5.7) can be obtained as:

$$\begin{align*}
\cdot x_1 &= -\left(\frac{\sqrt{3}i}{2} + \frac{1}{2}\right) a^{\frac{1}{3}} - \left(\frac{\sqrt{3}i}{2} - \frac{1}{2}\right) \frac{\theta_2}{3\theta_3 a^{\frac{1}{3}}} \\
\circ x_{1,2} &= \left(\frac{\sqrt{3}i}{2} - \frac{1}{2}\right) a^{\frac{1}{3}} + \left(\frac{\sqrt{3}i}{2} + \frac{1}{2}\right) \frac{\theta_2}{3\theta_3 a^{\frac{1}{3}}} \\
\cdot x_2 &= a^{\frac{1}{3}} - \frac{\theta_2}{3\theta_3 a^{\frac{1}{3}}}
\end{align*}$$  

(5.9)

where, $a = \frac{1}{2\theta_3}(3 - \sqrt[3]{\frac{27\theta_3^2\theta_2^4 + 4\theta_2^3}{\theta_3^2} - \theta_1})$. Note that, while the expressions for the fixed points involve complex numbers $i = \sqrt{-1}$, these simplify under the required range of parameters to yield real fixed points.

### 5.3.4 Catastrophic shift system dynamics under disturbance

In this work, we consider two different types of disturbances; (i) singular or isolated disturbances and, (ii) continuous disturbances, where the effect of disturbances on the systems dynamics are tightly coupled. A singular disturbance event is characterized by the Dirac delta function where the disturbance is applied on a steady state initial condition at an instantaneous time point and the system state is allowed to relax in response to this disturbance eventually returning to one of the attractors. In Example A, the singular disturbance event can be an externally imposed instantaneous shock (time scales much smaller than that of the population dynamics) population in flux or out flux. Typically these shocks can be sudden changes in immigration and emigration or sudden mortality events etc. In Example B, the singular disturbance event can be an externally imposed instantaneous shock (time scales much smaller than that of the vegetation dynamics) vegetation cover in flux or out flux. Typically these shocks can be extreme events such as rapid deforestation or reforestation, insect attack, forest fires etc.
The dynamics of a system when subject to singular disturbance can be analyzed using the mathematics described in section 5.3.3. However, when the system given by equation (5.7) is driven by a disturbance modeled using a continuous additive noise, it can be expressed as [Anishchenko et al., 2002]:

\[
\frac{dx}{dt} = \theta_1 + \theta_2 x + \theta_3 x^3 + \sqrt{2D}\eta(t)
\]  

(5.10)

where \(\eta(t)\) is the noise (disturbance) term \([Q/T]\) and \(D\) is its scaling factor [-]. If we consider noise with zero mean, then increasing \(D\) results in increasing the variability of the disturbance. Note that the mean of the disturbance can be factored out and combined with the \(\theta_1\) term, hence changes in the mean values of the disturbance can be represented as changes in \(\theta_1\). We consider two different disturbance types, namely: Gaussian white noise and Markovian dichotomous noise. While Gaussian white noise captures uncorrelated disturbance, Markovian dichotomous noise is a switching process between two states \(\Delta_1\) or \(\Delta_2\) \([Q]\). The transition rates from \(\Delta_2\) to \(\Delta_1\), and from \(\Delta_1\) to \(\Delta_2\), are distributed as \(\exp(\gamma_1)\) and \(\exp(\gamma_2)\), respectively, where \(\gamma_1\) and \(\gamma_2\) are the mean switching frequencies \([1/T]\). Note that \(1/\gamma_1\) and \(1/\gamma_2\) are the mean residence times in states \(\Delta_2\) and \(\Delta_1\) respectively. These noise types allow us to capture changes in the intensity (by changing \(\Delta_1\) and \(\Delta_2\)), variability (by changing \(D\)), frequency (by changing \(\gamma_1\) and \(\gamma_2\)) and asymmetric bias (by making \(\Delta_1 \neq \Delta_2\)) of disturbance events.

Gaussian white noise has been used to model the fluctuations in mean nutrient loading in lakes or oceans [Carpenter et al., 2001], temporal variation in population reproduction rate and/or population carrying capacity [May, 1973, Ridolfi et al., 2011], variation in precipitation-soil moisture feedback strength [Rodriguez-Iturbe et al., 1991], etc. Example applications of dichotomous noise include the switching between stress and non-stress conditions in resource availability [Ridolfi et al., 2011], occurrence of fires in savanna [Higgins et al., 1993], switching between wet and dry seasons in precipitation patterns such as drought versus no drought [Ridolfi et al., 2011] etc.

The resilience attributes of the system given by equation (5.10), driven by continuous disturbance, are best described in terms of the properties of the probability density function (PDF) \(P_S(x)\), of the state variable \(x\), at the appropriate space and time scale of interest. In the context of a stochastically driven catastrophic system, the peaks or modes \(\hat{x}_i\) of \(P_S(x)\) represent locations of maximum probabilities of system state (most preferred state) whereas the troughs or anti-modes \(\tilde{x}_{i,j}\) (between the modes \(\hat{x}_i\) and \(\hat{x}_j\)) represent locations of minimum probabilities of system state (least preferred state). We define \(X_i\) as the dynamic
regime of the mode $\dot{x}_i$, bounded by anti-modes $\ddot{x}_{i,j}$ and $\ddot{x}_{i,k}$ or an externally imposed system boundary $\bar{x}_i$ (Figure 5.1b).

The concept of dynamic regime in the presence of a continuous disturbance is analogous to the concept of DOA in the absence of an external disturbance. Note that, the restriction of $27\theta^2\theta_3 < 4\theta^3_2$ for the existence of multi-stability does not apply for the case of dichotomous noise. This is because, non-linear systems subject to noise can exhibit noise-induced bifurcation where the structural characteristics of the stationary PDFs change depending upon the characteristics and magnitude of the noise [Anishchenko et al., 2002, Horsthemke and Lefever, 2006, Ridolfi et al., 2011]. In Example A, we have two dynamic regimes $X_1$ and $X_2$ called ‘refuge dynamic regime’ and ‘outbreak dynamic regime’, and these correspond to the modes $\dot{x}_1$ and $\dot{x}_2$ respectively. Similarly, in Example B, depending on the value of the disturbance variability $\sqrt{2D}$ we can have up to four dynamic regimes $X_1$, $X_2$, $X_3$ and $X_4$ called ‘desert dynamic regime’, ‘intermediate desert dynamic regime’, ‘intermediate vegetated dynamic regime’ and ‘vegetated dynamic regime’, and these correspond to the modes $\dot{x}_1$, $\dot{x}_2$, $\dot{x}_3$ and $\dot{x}_4$ respectively (see section 5.5.3).

5.4 Singular disturbance events

5.4.1 Resilience measures for singular disturbance events

We now define the following resilience measures for a catastrophic shift system given by equation (5.7) subject to a singular disturbance event. A summary of these measures is provide in Table 5.1:

- **Size of DOA** $R^*_i = |\ddot{x}_{i,j} - \ddot{x}_{i,k}|$ [Q]: This measure captures the range of all possible values that the system state $x$ can take so that it will remain within the DOA at all future times. This measure has also been referred to as the latitude [Brand and Jax, 2007, Folke et al., 2004, Walker et al., 2004]. For the example illustrated in Figure 5.1a, the two measures $R^*_1$ and $R^*_2$ are $\infty$, since one of the boundaries of each domain goes to $\pm\infty$. In general it can be said that larger the $R^*_i$ the greater the allowance for the variation of $x$ where it will relax to $\dot{x}_i$ and hence greater the resilience. This is illustrated in Table 5.2c. However, this measure does not take into account the skewness of the location of the attractor $\dot{x}_i$ with respect to its boundaries. In Example A, the size of DOA measure $R^*_1$ represents the extent of the refuge DOA. A large $R^*_1$
<table>
<thead>
<tr>
<th>Name of measure</th>
<th>Variable</th>
<th>Definition</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size of DOA</td>
<td>$R_i^s$</td>
<td>$</td>
<td>\dot{x}<em>{i,j} - \dot{x}</em>{i,k}</td>
</tr>
<tr>
<td>Ecological resilience</td>
<td>$R_i^E$</td>
<td>$\min_j {</td>
<td>\dot{x}<em>i - \dot{x}</em>{i,j}</td>
</tr>
<tr>
<td>Engineering resilience</td>
<td>$R_i^e$</td>
<td>$\min_j \left{ \frac{1}{T_{i,j}} \right} [1/T]$</td>
<td>Minimum of the inverse of the time taken for the system state to travel from the unstable boundary $\dot{x}_{i,j}$ to the attractor $\dot{x}_i$ subject to a $\epsilon$ perturbation.</td>
</tr>
<tr>
<td>Attractor response rate</td>
<td>$R_i^\lambda$</td>
<td>$\left</td>
<td>\frac{dF(x)}{dx} \right</td>
</tr>
<tr>
<td>Activation potential</td>
<td>$R_i^a$</td>
<td>$\min_j \left{ V(\circ x_{i,j}) - V(\dot{x}_i) \right} [Q^2/T]$</td>
<td>Minimum potential required (using potential function) to excite the system from an attractor $\dot{x}<em>i$ to the unstable boundary $\dot{x}</em>{i,j}$.</td>
</tr>
<tr>
<td>Regime size</td>
<td>$R_i^r$</td>
<td>$</td>
<td>\dot{x}<em>{i,j} - \dot{x}</em>{i,k}</td>
</tr>
<tr>
<td>Regime probability</td>
<td>$R_i^R$</td>
<td>$\int_{\dot{x}_i} P_S(x) dx$ $[-]$</td>
<td>Probability of system state in regime $X_i$. For connected regimes, this also represents the average fraction of time spent in regime $X_i$.</td>
</tr>
<tr>
<td>Stochastic ecological resilience</td>
<td>$R_i^{sE}$</td>
<td>$\min_j {</td>
<td>\dot{x}<em>i - \dot{x}</em>{i,j}</td>
</tr>
<tr>
<td>Mean passage time</td>
<td>$R_i^\tau$</td>
<td>$\min_j {\tau_{i,j}} [T]$</td>
<td>Average time spent before a system state in regime $X_i$ transitions to transition to regime $X_j$.</td>
</tr>
</tbody>
</table>

Table 5.1: List of resilience measure formulations
generally requires a greater disturbance magnitude for the system undergo a transition to the outbreak DOA. Similarly, in Example B, the size of the DOA measure $R_2$ represents the extent of the vegetated DOA.

**Ecological resilience** $R_E = \min_j \{ |\dot{x}_i - \dot{x}_{i,j}| \} [Q]$: This measure captures how far the attractor of system state $\dot{x}_i$ is from the unstable DOA boundaries $\dot{x}_{i,j}$ [Gunderson, 2009]. This measure has also been referred to as precariousness [Brand and Jax, 2007, Folke et al., 2004, Walker et al., 2004]. For the example illustrated in Figure 5.1a, the two measures $R_1$ and $R_2$ are highlighted. The system state will be at the attractor at steady state, and is the preferred state of the DOA $X_i$. If the location of the attractor $\dot{x}_i$ is close to the unstable DOA boundary, then in terms of the difference in state values $x$, a smaller ‘push’ is sufficient to transition the system state into another DOA. Such a system is less resilient to DOA changes and hence we say that it has a smaller ecological resilience. In Example A, the ecological resilience measure $R_2$ represents the amount of ‘push’ in terms of shocks in immigration and emigration required for the population to undergo a transition from the outbreak population to the refuge population.

This measure takes into account the skewness associated with the locations of the outbreak and threshold population as demonstrated in Table 5.2a. In this example while the $R_1$ measures are the same, the $R_E$ measures are different. In Example A, if $\frac{R_1}{R_2} = 2$ we can say that the refuge population levels are two times more resilient than the outbreak population levels against undergoing a transition (to the alternate stable population level) when subject to a shock in immigration and emigration rate. In Example B, the ecological resilience measure $R_1$ represents the amount of ‘push’ (fraction of vegetation cover wiped out or planted) in terms of shocks in mortality required for the vegetation to undergo a transition from the desert cover to the vegetated cover.

**Engineering resilience** $R_e = \min_j \{ \frac{1}{T_{i,j}} \} [1/T]$: This measure captures the rate of recovery following a disturbance event, where $T_{i,j}$ denotes travel time from the unstable boundary $\dot{x}_{i,j}$ to the attractor $\dot{x}_i$ caused by an infinitesimally small perturbation $\epsilon$ [Holling, 1996]. If a DOA $X_i$ has a large $T_{i,j}$, it means that the recovery towards the attractor is slow and correspondingly the $R_e$ is low, and conversely a small $T_{i,j}$ results in a faster recovery and hence a higher $R_e$. We note that typically the system moves very slowly near the fixed points and contributes most to the total travel time. The
total travel time is therefore strongly dependent on the choice of $|\epsilon|$. In Example A, the engineering resilience measure $R^e_1$ is the rate of recovery for the relative population to travel from the threshold level to the refuge level when subject to an infinitesimally small singular perturbation $\epsilon$. Similarly, in Example B, the engineering resilience measure $R^e_2$ is the rate of recovery for the normalized fractional vegetation cover to recover from the threshold to the vegetated cover when subject to an infinitesimally small perturbation $\epsilon$.

The travel time $T_{i,j}$ from the unstable boundary $\overset{\circ}{x}_{i,j}$ to the attractor $\overset{\bullet}{x}_i$ when subject to an $\epsilon$ disturbance is computed using the following expression:

$$T_{i,j} = \int_{\overset{\circ}{x}_{i,j} + \epsilon}^{\overset{\bullet}{x}_i - \epsilon} \frac{dx}{F(x)} \quad (5.11)$$

For the illustration discussed later in section 5.4.2, the parameter $\epsilon$ is set as 0.01% of $|\overset{\circ}{x}_{i,j} - \overset{\bullet}{x}_i|$. While the choice of $\epsilon$ affects the actual numerical values of $T_{i,j}$, the trends in $T_{i,j}$ across a range of parameters remain unaffected. Substitution of $\overset{\bullet}{x}_1$, $\overset{\bullet}{x}_2$ and $\overset{\circ}{x}_{1,2}$ values from equation (5.9) in (5.11) and integrating numerically using the trapezoid method gives us the $T_{i,j}$ values. $R^e_i$ is readily obtained as the inverse of $T_{i,j}$.

- **Attractor response rate** $R^\lambda_i = \frac{1}{\tau_i} = \frac{1}{\left|\frac{dF(x)}{dx}\right|_{x=\overset{\bullet}{x}_i}^{-1}}$: This measure provides an alternate measure for the rate of recovery following a disturbance event in terms of the inverse of the characteristic time $\tau_i = \left|\frac{dF(x)}{dx}\right|_{x=\overset{\bullet}{x}_i}^{-1}$ when subject to a perturbation at its attractor $\overset{\bullet}{x}_i$ [Ridolfi et al., 2011]. The function $\left|\frac{dF(x)}{dx}\right|$ can be computed from equation (5.7) as:

$$\left|\frac{dF(x)}{dx}\right| = \theta_2 + 3\theta_3x^2 \quad (5.12)$$

$R^\lambda_i$ is obtained by direct substitution of the values of $\overset{\bullet}{x}_1$ and $\overset{\bullet}{x}_2$ from equation (5.9) in equation (5.12). A DOA with a small $R^\lambda_i$ indicates that the system converges to its stable state at a slower rate as compared to another DOA with a larger $R^\lambda_i$. Unlike $R^e_i$ which involves some subjectivity in the choice of $\epsilon$, $R^\lambda_i$ presents a more attractive alternative to capture this aspect of the resilience. However, it must be noted that, while $R^\lambda_i$ provides an indication of the recovery time only near the attractor, $R^e_i$ includes the entire DOA. This is illustrated in Table 5.2b and d. In Example A, $R^\lambda_2$ measures how fast the relative population recovers to the outbreak population level.
when subject to minor shocks. Similarly, in Example B, $R_1^\lambda$ measures how fast the normalized fractional vegetation cover recovers to the desert cover level when subject to minor shocks. Note that while $R_1^e$ measures the recovery rate from the unstable threshold cover to the stable desert cover, $R_1^\lambda$ only measures the recovery rate near the stable desert cover.

- **Activation potential** $R_1^a = \min_j \{ V(\dot{x}_{i,j}) - V(\dot{x}_i) \} \ [Q^2/T]$: This measures the energy needed to transition the system from its attractor to one of its unstable boundaries. This measure is related to the definition of resistance [Brand and Jax, 2007, Folke et al., 2004, Walker et al., 2004]. For the example illustrated in Figure 5.1a, the two measures $R_1^a$ and $R_2^a$ are highlighted. While the ecological resilience measure $R_1^e$ deals with the ‘push’ in terms of the difference in state values, the activation potential measure deals with the ‘push’ in terms of energy. This difference is highlighted in Table 5.2c. Using the potential function we can compute the minimum energy (potential) required to transition the system state from its attractor $\dot{x}_i$ to its boundary $\dot{x}_{i,j}$. The lower the energy required to achieve this, the easier it is to accomplish the transition and hence the lower the activation potential resilience. $R_1^a$ is easily computed by substitution of $\dot{x}_1$, $\dot{x}_2$ and $\dot{x}_{1,2}$ values from equation (5.9) in equation (5.8). In Example A, the activation potential measure $R_1^a$ measures the energy (in terms of relative population potential) needed to transition from a refuge population to an outbreak population. And in Example B, the activation potential measure $R_2^a$ measures the energy (in terms of normalized fractional vegetation cover potential) needed to transition from a vegetated cover to a desert cover.

While this is not an exhaustive list of resilience measures, we believe that it includes measures that would be encountered quite frequently across a wide spectrum of problems. Furthermore, these measures captures the key differences in the dynamics of system behavior as illustrated in Table 5.2. It is also possible to obtain derived resilience measures such as state recovery velocity $R_{i}^{Ev} = R_{i}^{E} R_{i}^{e}$ and activation potential recovery velocity $R_{i}^{av} = R_{i}^{a} R_{i}^{e}$ from the measures presented above. We now perform example simulations and analyze the behavior of these singular resilience measures under changing parameter conditions.
<table>
<thead>
<tr>
<th></th>
<th>Singular disturbance: Potential function</th>
<th>Continuous disturbance: PDF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a</strong></td>
<td>( R_s^1 = R_s^{1'} ) ( R_E^1 &gt; R_E^{1'} ) ( R_a^1 &gt; R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>b</strong></td>
<td>( R_s^1 = R_s^{1'} ) ( R_E^1 = R_E^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>c</strong></td>
<td>( R_s^1 &gt; R_s^{1'} ) ( R_E^1 = R_E^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>d</strong></td>
<td>( R_s^1 = R_s^{1'} ) ( R_E^1 = R_E^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>e</strong></td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>f</strong></td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 = R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
<tr>
<td><strong>g</strong></td>
<td>( R_r^1 &gt; R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
<td>( R_r^1 &gt; R_r^{1'} ) ( R_s^1 &gt; R_s^{1'} ) ( R_a^1 = R_a^{1'} )</td>
</tr>
</tbody>
</table>

Table 5.2: Illustration of the ability of the different resilience measures proposed in this study to capture different resilience attributes of a dynamical system when subjected to singular and continuous disturbance events. White circles represent DOA or dynamic regime boundaries and black circles represent stable fixed points or modes of the corresponding DOA or dynamic regime. Thin and thick lines correspond to two alternate shapes of potential functions or PDFs, identified as 1 and 1’ respectively, used for illustrating that not all resilience measures are different in each case.
5.4.2 Resilience behavior under singular disturbance events

For the system described by (5.7) with $-\infty < x_1 < \bar{x}_{1,2} < x_2 < \infty$ (in the allowable region determined by $27\theta_1^3\theta_3 < 4\theta_2^2$), the DOAs $X_1$ and $X_2$ are semi-infinite and therefore $R_{s1} = R_{s2} = \infty$. The variations of $R_E$, $R_a$, $R_e$ and $R_\lambda$ as a function of the variation in the imperfection parameter $\theta_1$ and the rate parameter $\theta_2$ are shown in Figure 5.2. It is immediately evident that, for the two DOAs, the four resilience measures show different variations as the parameters change. In the context of the ecological resilience, $R_E$ decreases while $R_2$ increases as the imperfection parameter $\theta_1$ increases (Figure 5.2a). This is because as $\theta_1$ is increased, the distance between $x_1$ and $\bar{x}_{1,2}$ becomes larger and the distance between $x_2$ and $\bar{x}_{1,2}$ becomes smaller. Unlike $\theta_1$, the effect of increasing $\theta_2$ is to increase both $R_E$ and $R_2$. This is because $\theta_2$ has the effect of pushing both the attractors $x_1$ and $x_2$ away from the unstable boundary $\bar{x}_{1,2}$ irrespective of the nature of the imperfection. Hence, the highest ecological resilience measures $R_E$ for a given DOA $X_i$ are obtained when we have high values of $\theta_2$, while the effect of increasing $\theta_1$ is dependent on the DOA under consideration.

In Example B, high reforestation rate along with high vegetation growth rate increases the $R_E$ of the vegetated DOA and decreases the $R_E$ of the desert DOA. The activation potential measure $R_a$ shows a pattern similar to that of $R_E$ although the gradients of change are quite different (Figure 5.2b). This is because there is a one to one mapping between the distance and the potential for our particular problem (equation (5.8)). However, it must be noted that in general this behavior need not be true for other systems.

In Example A, high emigration rates and low population growth rates increases the $R_a$ of the refuge population and decreases the $R_a$ of the outbreak population.

The engineering resilience measure $R_e$ (Figure 5.2c) shows patterns of variation that are distinctly different from those of $R_E$, $R_a$ and $R_\lambda$ (Figure 5.2 a, b and d). We see that as $\theta_2$ increases, the travel time decreases in both DOAs. Although $\theta_2$ increases the distance between the attractor and unstable boundary, it also significantly increases the travel velocity between these points (by making the slope steeper), with the net effect of decreasing travel time. The behavior of $R_e$ with respect to $\theta_1$ is more complex. Maximum values of $R_e$ are obtained at low $|\theta_1|$ values indicating that a symmetric system has the most travel time. When imperfection is introduced into the system ($\theta_1 \neq 0$), although the distance between the attractor and unstable boundary changes, there is a corresponding change in the travel velocity. The net effect is such that when distance increases the velocity decreases and vice versa. While larger $|\theta_1|$ results in increasing $R_E$ on one DOA and decreasing $R_E$ on the other DOA (Figure 5.2a), $R_e$ decreases with increasing $|\theta_1|$.
Figure 5.2: Variation of (a) Ecological resilience $R^E_i [Q]$, (b) Activation potential $R^a_i [Q^2/T]$, (c) Engineering resilience $R^e_i [1/T]$ and (d) Attractor response rate $R^\lambda_i [1/T]$ resilience measures for a catastrophic shift system as a function of imperfection parameter $\theta_1$ and rate parameter $\theta_2$ for the two DOAs $X_1$ and $X_2$ when subject to a singular disturbance event. DOAs $X_1$ and $X_2$ correspond to the lower and higher attractor value $\bullet x_1$ and $\bullet x_2$ respectively. White space represents parameter combinations for which the system does not exhibit catastrophic shift behavior $27 \theta_1^2 \theta_3 > 4 \theta_2^3$. The diagonal grey line indicates slopes of constant immigration or emigration rates $I$ [number/year] in Example A problem or deforestation and reforestation rates $A$ [m$^2$/year] in Example B.
The behavior of the attractor response rate measure $R^λ_i$ (5.2d) to changes in $θ_1$ and $θ_2$ are similar to the $R^E_i$ and $R^o_i$ measures 5.2 a and b) for identical reasons. In Example B, high vegetation growth rates increases $R^λ_i$ for both the desert and vegetated cover. While reforestation increases $R^λ_i$ in vegetated cover and decreases $R^λ_i$ in desert cover.

The above simulations illustrate the importance that attribute plays in determining the behavior of resilience under changing parameter conditions when subject to a singular disturbance event. In the following section, we illustrate the effect of variability in disturbance forcing on the resilience characteristics of a catastrophic shift system when subject to continuous disturbance.

5.5 Continuous disturbance events

5.5.1 Resilience measures for continuous disturbance events

We now define resilience measures for the stochastic dynamic system given by equation (5.10) and describe their properties under singular and continuous disturbance events.

- **Regime size** $R^r_i = \left| \overset{\circ}{x}_{i,j} - \overset{\circ}{x}_{i,k} \right|$ $[Q]$: This measure describes the extent of variability that the system state $x$ can take before it transitions out of dynamic regime $X_i$. For the example illustrated in Figure 5.1b, the two measures $R^r_1$ and $R^r_2$ are $∞$. A dynamic regime having a large size allows for greater variability in the system state while staying in the same dynamic regime and hence has greater $R^r_i$ resilience. Note that unlike the concept of DOA, where the system state cannot alternate between DOAs, the concept of dynamic regimes allows the system state to alternate between connected dynamic regimes. Table 5.2 e and g illustrates two dynamic regimes with equal and unequal regime size measures respectively. In Example A, the regime size measure $R^r_1$ represents the size of the refuge dynamic regime. In Example B, the regime size measure $R^r_2$ represents the size of the vegetated dynamic regime.

- **Regime probability** $R^R_i = \int_{X_i} P_S(x)dx$ $[-]$: This measure describes the probability of finding the system state $x$ in the dynamic regime $X_i$ for an ensemble of observations. For the example illustrated in Figure 5.1b, the two measures $R^R_1$ and $R^R_2$ are the areas under their corresponding stationary PDFs. Using ergodic property (for connected dynamic regimes), this measure can also be interpreted as the average fraction of time
that a system state stays in dynamic regime $X_i$ [Horsthemke and Lefever, 2006]. Hence a dynamic regime with a higher $R^R_i$ is more likely to be realized than a dynamic regime with a lower $R^R_i$. Table 5.2 e and f illustrates two dynamic regimes with unequal and equal regime probabilities respectively. In Example A, the dynamic regime probability measure $R^R_2$ captures the average fraction of time the relative population is in the outbreak dynamic regime. Similarly, in Example B, the regime probability measure $R^R_1$ captures the average fraction of time the normalized fractional vegetation cover is in the desert dynamic regime. However, this is only true for the case of connected dynamic regimes. When we have disconnected dynamic regimes at barrier regions (as illustrated in section 5.5.3), the regime probability needs to be normalized with the sum of regime probabilities of connected dynamic regimes to obtain the average time fraction.

**Stochastic ecological resilience** $R^{sE}_i = \min_j \{|\ddot{x}_i - \hat{x}_{ij}^o|\}$: This measure is similar to the ecological resilience measure $R^E_i$, however it deals with the ‘push’ in terms of the difference in state values between the dynamic regime mode $\hat{x}_i$ and the boundary $\hat{x}_{ij}^o$. For the example illustrated in Figure 5.1b, the two measures $R^{sE}_1$ and $R^{sE}_2$ are highlighted. Unlike $R^E_i$, which indicates the exact amount of ‘push’ required to perform one DOA transition, $R^{sE}_i$ only provides an indication of the amount of ‘push’ required to have a tendency for dynamic regime transitions. This is because, under a stochastic disturbance, dynamic regime changes occur infinitely often in the true limiting case of stationarity. Hence a higher $R^{sE}_i$ indicates that a larger ‘push’ in terms of differences in state values is required to undergo a tendency for dynamic regime changes. Table 5.2f illustrates two dynamic regimes with equal $R^r_i$, but unequal $R^{sE}_i$ due to the skewness in the location of the mode with respect to the boundaries of the dynamic regime. In Example A, the stochastic ecological resilience measure $R^{sE}_1$ represents the amount of ‘push’ in terms of shocks in immigration and emigration required for the population to undergo a tendency to transition from the refuge population to the outbreak population. Similarly, in Example B, the stochastic ecological resilience measure $R^{sE}_2$ represents the amount of ‘push’ in terms of shocks in mortality required for the vegetation cover to undergo a tendency to transition from the vegetated cover to the neighboring intermediate or desert cover.

**Mean passage time** $R^T_i = \min_j \{\tau_{i,j}\}$: This measure determines the minimum of the average time $\tau_{i,j}$ taken for a system in mode $\hat{x}_i$ of dynamic regime $X_i$ to transition
to one of its neighboring mode $x_j$ in dynamic regime $X_j$ [Ridolfi et al., 2011]. A higher mean passage time causes the system to stay on an average longer in the present dynamic regime and hence results in a higher resilience. The inverse of the mean passage time gives the mean rate of transition between dynamic regime modes. Note that, the concept of $R_i^\tau$ is different from $R_i^{R}$ because two adjoining dynamic regimes $X_i$ and $X_j$ having identical residence times (equal regime probabilities) can accomplish this either by frequent or by rare transitions (small or large passage times) between them. In Example A, the mean passage time measure $R_2^\tau$ represents the average time taken for the relative population to transition from the outbreak population to the refuge population levels. Similarly, in Example B, the mean passage time measure $R_1^\tau$ represents the average time taken for the normalized fractional vegetation cover to transition from the desert cover to the neighboring intermediate or vegetated cover levels.

We now discuss the behavior of these resilience measures for the two different disturbance types.

5.5.2 Resilience behavior under Gaussian white noise disturbance

For the case of $\eta(t)$ being a Gaussian white noise, the stationary PDF for equation (5.10) is (see page 111, equation 6.10 or 6.13 in [Horsthemke and Lefever, 2006]):

$$P_S(x) = N \exp \left\{ \frac{-V(x)}{D} \right\}$$  (5.13)

where $N = 1/ \int_X \exp \left\{ \frac{-V(x)}{D} \right\} dx$ is the normalizing factor computed numerically using trapezoid method, and $X$ represents the entire region where the stationary PDF exists. Note that both Ito and Stratanovich formulations yield the same result under additive Gaussian white noise disturbance. The modes $x_i$ and the antimodes $\bar{x}_{i,j}$ are the locations of the local maxima and minima of the stationary PDF and are computed numerically. The regions between two consecutive local minima $\bar{x}_{i,j}$ and $\bar{x}_{i,k}$ or one local minima $\bar{x}_{i,j}$ and one adjacent system boundary $\bar{x}_i$, or two system boundaries $\bar{x}_{i1}$ and $\bar{x}_{i2}$ (without any local minima between them) form dynamic regime $X_i$. For a catastrophic shift system driven by additive Gaussian white noise disturbance, when $27\theta_1^2 < \frac{4\theta_2^2}{\theta_1}$ and $D < D_t$, we have two dynamic regimes $X_1$ and $X_2$ coinciding with the two DOAs, with the locations of the modes coinciding with the
stable fixed points \( \dot{x}_1 \) and \( \dot{x}_2 \) (for the deterministic system) and the locations of the anti-mode coinciding with the unstable fixed point \( \ddot{x}_{1,2} \) (for the deterministic system) (Figure 5.3b). The modes have sharper peaks at low values of \( D \) and they gradually diffuse as \( D \) increases (Figure 5.3a). Note that, \( D_t \) is a threshold disturbance scaling parameter, beyond which the disturbance overshadows the dynamics governed by the potential function and the bimodal behavior of the stationary PDF is lost. In this study, we will only consider the case of \( D < D_t \).

\( R^r_i \) and \( R^{se}_i \) are computed from the locations of the boundaries and the modes of dynamic regime \( X_i \). \( R^r_i \) is computed by integrating the stationary PDF given by equation (5.13) between the boundaries of dynamic regime \( X_i \) numerically using the trapezoid method.

The mean passage time \( \tau_{i,j} \) for transitions from mode \( \dot{x}_i \) to mode \( \dot{x}_j \) is (see page 81, equation 3.60 in [Ridolfi et al., 2011]):

\[
\tau_{i,j} = \frac{1}{D} \int_{\dot{x}_1}^{\dot{x}_2} \left[ \exp \left\{ \frac{V(x)}{D} \right\} \int_{-\infty}^{x} \exp \left\{ \frac{-V(y)}{D} \right\} dy \right] dx
\] (5.14)

The integrals in equation (5.14) are evaluated numerically using the trapezoid method. Note that, \( R^r_i = \min_j \{ \tau_{i,j} \} \) and can be directly obtained from the above computation. We now perform example simulations and analyze the behavior of these continuous resilience measures under changing disturbance magnitudes and parameter conditions.

Increasing \( D \) has the effect of destabilizing the more stable dynamic regime, and since \( \sum_i R^r_i = 1 \), the less stable dynamic regime tends to gain more regime probability. Hence an increase in the Gaussian white noise intensity \( D \), (and correspondingly the disturbance variability), favors the otherwise less resilient dynamic regime, as measured by \( R^r_i \), at the cost of the more resilient dynamic regime (Figure 5.3c). This disturbance induced stabilization of less resilient dynamic regimes, and consequently the destabilization of more resilient dynamic regimes, can have significant consequences in several ecological applications. One example is the stabilization of tropical savanna by fire induced disturbances [Higgins et al., 1993]. In the absence of such a disturbance, savanna become less resilient in terms of \( R^r_i \) and can potentially lead to shrub or woody encroachment.

Different parameter combinations for \( \theta_i \) can give rise to different ‘regions of sensitivity’ where \( R^r_i \) changes more rapidly in response to changes in \( D \) (indicated by regions around the highest slopes \( \left| \frac{dR^r_i}{dD} \right| \) in Figure 5.3c). The range of values of \( D \) for which \( R^r_i \) is most sensitive represents a critical region in terms of determining sensitivity to dynamic regime.
Figure 5.3: Effect of Gaussian white noise disturbance on resilience measures at different intensities of disturbance variability on a catastrophic shift system with $\theta_1 = 0.01$, $\theta_2 = 1.0$ and $\theta_3 = -1.0$ bounded by $\bar{x}_1 = -\infty$ and $\bar{x}_2 = \infty$. (a) Sample PDFs for different magnitudes of disturbance variability $D$ illustrate the effect of leveling of the PDFs as $D$ increases. (b) Regime probabilities $R_i$ (color coded) as a function of disturbance variability $D$ along with the locations of modes $\dot{x}_1 = -1.00$ and $\dot{x}_2 = 1.01$ (black circles) and anti-modes $\dot{x}_{12} = -0.01$ (white circles). For all disturbance variability scales we have only two dynamic regimes $X_1$ and $X_2$. (c) Regime probability $R_i^R$ for case 1: $\theta_1 = 0.01$, for case 2: $\theta_1 = 0.05$ and for case 3: $\theta_1 = 0.1$ and mean passage time $R_i^\tau$ resilience measures as a function of disturbance variability $D$. The dotted lines in the three $R_i^R$ plots are $\left| \frac{d R_i^R}{d D} \right|$ values (not to scale) representing the sensitivity of $R_i^R$ to changing $D$ values. Note the effect of disturbance induced enhancement of regime probabilities of the weaker dynamic regime $X_1$ at the cost of the stronger dynamic regime $X_2$ in all three $R_i^R$ plots in (c). Comparison between the three $R_i^R$ plots demonstrates differences in the sensitivity regions of $R_i^R$ to changing $D$ values. The peak of the $\left| \frac{d R_i^R}{d D} \right|$ (dotted lines in (c)) represent regions of maximum sensitivity. The regime size measure $R_i^s$ (not shown in figure) is $\infty$ for both dynamic regimes since the dynamic regimes are semi-infinite. The stochastic ecological resilience measures $R_i^{sE}$ and $R_2^{sE}$ (not shown in figure) have a constant value at 0.985 and 1.015 respectively for all $D$ values. Note that for illustration purposes, the upper and lower bounds for the $R_i^\tau$ plot in (c) have been cropped.
dominance. Some parameter combinations exhibit behavior where increasing disturbance on a lightly disturbed environment significantly alters its $R_i^R$ resilience measure whereas increasing disturbance on an already disturbed environment may not cause any significant change in $R_i^R$. These types of behavioral response can have important consequences especially in the context of climate change induced ecosystem transitions [Cote and Darling, 2010, Folke et al., 2004, Ridolfi et al., 2011] caused by increased variability in climate forcings [Steffen et al., 2004]. For example, Knapp et al. [2002] demonstrate that increasing rainfall variability in grassland ecosystems resulted in decreased above-ground net primary productivity and increased plant community diversity or species richness, while D’Odorico and Bhattachan [2012] show that increasing hydrologic variability can enhance post-disturbance recovery (engineering resilience or mean passage time measures) in dryland ecosystems.

The behavior of the system state as a function of time for different values of $D$ is illustrated in Figure 5.4. It can be observed that when $D$ is increased, the frequency of switching between the two dynamic regimes increases. Furthermore, from the phase plots (Figure 5.4b) it can be inferred that the system state tends to stay closer to the modes at low values of $D$, and there is an increased diffusion in the location of the system state as $D$ increases. This corresponds to a diffusion in the peaks of the stationary PDF as $D$ increases (Figure 5.3).

The regime probability measure $R_i^R$ is highly sensitive to changes in $\theta_1$ (Figure 5.5a). In contrast, for a fixed $\theta_1$, variations in $\theta_2$ have significantly smaller change in $R_i^R$. In a bimodal system, these variations are complementary between the two dynamic regimes. As we increase the disturbance variability $D$, we observe greater diffusion in the probability densities and this causes the regime probabilities $R_1^R$ and $R_2^R$ to get closer to each other and eventually become equal in the limiting case of large noise levels. Interpreting this in the context of Example A, we infer that the fraction of time spent in the refuge dynamic regime and the outbreak dynamic regime are highly sensitive to changes in immigration and emigration rates, with the sensitivity decreasing with increasing disturbance variability.

Similar to $R_i^R$, $R_i^{sE}$ is highly sensitive to $\theta_1$ for identical reasons (Figure 5.5b). $\theta_2$ on the other hand has a mild effect of increasing $R_i^{sE}$ irrespective of the dynamic regime (Figure 5.5b). This is attributed to the fact that $\theta_2$ causes a stabilizing effect as mentioned earlier. Also, changing the disturbance variability $D$ does not affect $R_i^{sE}$. This is because, for our particular problem the modes occur at the attractors $\dot{x}_1$ and $\dot{x}_2$ and the anti-mode occurs at the DOA boundary $\ddot{x}_{1,2}$ irrespective of the disturbance variability $D$ resulting in $R_i^{sE} = R_i^E$. However, it must be noted that in general this need not be true for other systems where the behavior of $R_i^{sE}$ can be affected by $D$. 

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Figure 5.4: Effect of Gaussian white noise disturbance on the time trajectory of the system state $x$ at different intensities of disturbance variability on a catastrophic shift system with $\theta_1 = 0.01$, $\theta_2 = 1.0$ and $\theta_3 = -1.0$ bounded by $x_1 = -\infty$ and $x_2 = \infty$. Two different initial conditions at time $t = 0$ are selected; the blue line corresponds to $x(0) = -0.995$ and the green line corresponds to $x(0) = 1.005$. (a) Time trajectories for different magnitudes of disturbance variability $D$ illustrate the effect of increased switching between dynamic regimes and a corresponding decrease in $R_\tau$ as $D$ increases. (b) Phase plots illustrating the range of values that the system state can take when subjected to Gaussian white noise. The locations of the modes of the PDF are represented as black circles and the locations of the anti-modes are represented as white circles.
Figure 5.5: Effect of the variation of parameters $\theta_1$ and $\theta_2$ on resilience measures for Gaussian white noise disturbance at four different intensities of disturbance variability for the two dynamic regimes $X_1$ and $X_2$. Increasing the disturbance variability $D$ results in a (a) diffusive effect in regime probability $R_i^R$, an (b) invariant effect in stochastic ecological resilience $R_i^{sE}$ and a (c) weakening effect in mean passage time $R_i^\tau$. When $D = 0.01$ at $\theta_1 = 0.05$ the values for $R_i^\tau$ at $\theta_2 = 1.0$ and $\theta_2 = 2.0$ are $3.2496e+11$ and $5.9942e+43$ respectively (representing an increase of approximately 32 orders of magnitude), whereas when $D = 0.1$ the values are $6.6265e+01$ and $5.1054e+04$ respectively (representing an increase of approximately 3 orders of magnitude). Note that for illustration purposes, the upper and lower bounds for the $R_i^\tau$ plot in (c) have been cropped. The diagonal grey line indicates slopes of constant immigration or emigration rates $I$ [number/year] for the population dynamics example problem.
The mean passage time measure $\mathcal{R}_i^\tau$ increases with increasing $\theta_2$ (Figure 5.5c) due to the stabilizing effect of $\theta_2$. $\mathcal{R}_1^\tau$ decreases while $\mathcal{R}_2^\tau$ increases as the imperfection parameter $\theta_1$ is increased. This is because, when $\theta_1$ is increased, the distance between $\dot{x}_1$ and $\ddot{x}_{1,2}$ becomes larger and the distance between $\dot{x}_2$ and $\ddot{x}_{1,2}$ becomes smaller, and the probability peak at $\dot{x}_1$ increases while the peak at $\dot{x}_2$ decreases. This effect is weakened with increasing disturbance variability since disturbance facilitates dynamic regime changes. The effect of disturbance variability is such that at $\theta_1 = 0.0$ [Q/T] doubling $\theta_2$ from 1.0 to 2.0 [1/T] results in 32 orders of magnitude increase in $\mathcal{R}_1^\tau$ at $D = 0.01$ [-] but only a 3 orders of magnitude increase at $D = 1.0$ [-] (Figure 5.5c). Applying this to Example A, we infer that the mean passage time $\mathcal{R}_1^\tau$ decreases while $\mathcal{R}_2^\tau$ increases with increasing population growth rate. This means that on an average transitions from the outbreak to the refuge population levels occur less frequently as the population growth rate is increased. Also by increasing the immigration rate we can make the transition from the refuge to the outbreak population levels faster while simultaneously making the transition from the outbreak to the refuge population level slower.

### 5.5.3 Resilience behavior under Markovian dichotomous noise disturbance

For the case when $\eta(t)$ is a Markovian dichotomous noise, the stationary PDF for equation (5.10) is (see page 267, equation 9.50 in Horsthemke and Lefever [2006]):

$$P_S(x) = N' \frac{\sqrt{2D}}{\kappa(x)} \exp \left\{ - (\gamma_1 + \gamma_2) \int \frac{x}{\kappa(z)} \left( F(z) + I \sqrt{2D} \right) \right\}$$

(5.15)

where $\kappa(x) = \left\{ F(x) + \sqrt{2D} \Delta_1 \right\} \left\{ F(x) + \sqrt{2D} \Delta_2 \right\}$, $I = \frac{\gamma_1 \Delta_1 + \gamma_2 \Delta_2}{\gamma_1 + \gamma_2}$, $N'$ is a normalizing factor computed numerically using the trapezoid method. The integral in equation (5.15) is also performed numerically using the trapezoid method.

The solution boundaries for equation (5.15) are computed as follows [Ridolfi et al., 2011]. First, we compute the locations of fixed points for equation (5.10), by substituting the noise term $\eta(t)$ as $\Delta_1$ and $\Delta_2$. Combining the fixed points for these two cases, we look for regions where there are two consecutive stable fixed points. These regions form the valid solution boundaries for the stationary PDF. For the case when we have disconnected solution boundaries (barrier regions), we normalize each solution separately and finally scale all the stationary PDFs by the number of disconnected solutions. In some cases these solution
boundaries can be points of singularity in which case we perform the numerical integration by introducing appropriate shifts from the boundaries.

The modes $x_i$ and the antimodes $\bar{x}_{i,j}$ are the locations of the local maxima and minima of the stationary PDF and are computed numerically. The regions between two consecutive local minima $\bar{x}_{i,j}$ and $\bar{x}_{i,k}$ or one local minima $\bar{x}_{i,j}$ and one adjacent system boundary $x_i$, or two system boundaries $x_{i1}$ and $x_{i2}$ (without any local minima between them) form dynamic regime $X_i$. For a catastrophic shift system driven by additive Markovian dichotomous noise disturbance, we can have anywhere between one and four dynamic regimes depending on the parameter values. These are caused due to noise induced bifurcations. Qualitative changes in dynamics of a system when subject to parameter change are called bifurcations. Bifurcations arising due to change in intrinsic system parameters (in our case $\theta_1$, $\theta_3$ and $\theta_3$) are regular bifurcations. For the example considered in this study, we deal with catastrophic bifurcations. However, bifurcations can also occur when we change the characteristics of the noise in a noise-driven dynamical system. These bifurcations are referred to as noise induced bifurcations. For the case of Markovian Dichotomous noise, which has four intrinsic noise parameters $\Delta_1$, $\Delta_2$, $\gamma_1$ and $\gamma_2$ which can vary independent of one other, we can induce bifurcations corresponding to the variation in each of these noise parameters. When bifurcations are induced due to changes in $\Delta$, they are called ‘$\Delta$ bifurcations’ and when bifurcations are induced due to changes in $\gamma$, they are called ‘$\gamma$ bifurcations’.

$\mathcal{R}_i^R$ and $\mathcal{R}_i^{SE}$ are computed from the locations of the boundaries and the modes of dynamic regime $X_i$. $\mathcal{R}_i^R$ is computed by integrating the stationary PDF given by equation (5.13) between the boundaries of dynamic regime $X_i$ numerically using the trapezoid method. When we have disconnected dynamic regimes as is the case with barrier regions indicated by the ellipse in Figure 5.6b, we normalize each of the individual PDFs separately and then scale them by the number of disconnected regions.

The mean passage time $\tau_{i,j}$ for transitions from mode $x_i$ to mode $x_j$ is (see page 3524, equation 20 in Sancho [1985]):

$$\tau_{i,j} = (\gamma_1 + \gamma_2) \int_{x_1}^{x_2} \left[ -\frac{1}{\psi(x)\kappa(x)} \int_{x_1}^{x} \psi(y)dy \right] dx$$  \hspace{1cm} (5.16)

where $\psi(x) = \frac{|\Delta_1|\sqrt{2D} - F(x)}{\sqrt{2D}}P_S(x)$. Equation (5.16) is evaluated numerically using the trapezoid method. Note that, $\mathcal{R}_i^R = \min_j \{\tau_{i,j}\}$ and can be directly obtained from the above com-
Figure 5.6: Noise induced bifurcation effect on resilience due to a Markovian dichotomous noise for a catastrophic shift system with parameters $\theta_1 = 0.01$, $\theta_2 = 1.0$, $\theta_3 = -1.0$, $\Delta_1 = -1.2$, $\Delta_2 = 1.0$. Case 1 (subplots a, b and c) represent $\gamma_1 = 1.2$ and $\gamma_2 = 1.0$ and case 2 (subplots d, e and f) represent $\gamma_1 = 0.12$ and $\gamma_2 = 0.1$. (a and d) Sample PDFs for different magnitudes of disturbance variability $D$ illustrate the bifurcation in the PDFs. (b and e) Regime probabilities $R_i$ (color coded) as a function of disturbance variability $D$ along with the locations of modes (black circles) and anti-modes (white circles) demonstrate noise induced bifurcations at four locations resulting in changes in the number of dynamic regimes. Bifurcations caused by $\Delta$ and $\gamma$ are indicated by horizontal red $(D = 0.0545$ and $D = 0.0705)$ and black $(D = 0.01952$, $D = 0.0325$ and $D = 0.0935)$ lines respectively. The width of the individual color regions in (b and e) represents the size of the dynamic regimes $R_i$. The barrier region lies below the bifurcation line at $D = 0.0545$ and the region with trap or escape behavior is indicated by the ellipse. (c and f) Regime size $R_i$, regime probability $R_i^R$, stochastic ecological resilience $R_i^E$, and mean passage time $R_i^\tau$ resilience measures as a function of disturbance variability $D$. 

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putation. We now perform example simulations and analyze the behavior of these continuous resilience measures under changing disturbance magnitudes and parameter conditions.

Unlike for the case of Gaussian white noise disturbance, when a catastrophic shift system is subject to a Markovian dichotomous noise disturbance, we see structural changes in the stationary probability densities as the disturbance variability is increased (Figure 5.6a and d). These structural changes arise due to noise induced bifurcations [Horsthemke and Lefever, 2006, Ridolfi et al., 2011]. Distinction must be made between two regions which have four dynamic regimes each. For the example presented in Figure 5.6b, this occurs between $0.0 < D < 0.0545$ which represents disconnected dynamic regimes and between $0.0705 < D < 0.0935$ which represents connected dynamic regimes. While the system state is able to explore a continuous domain in the region of connected dynamic regimes, in the region of disconnected dynamic regimes, there exists a dynamical barrier that prevents the system state from transitioning between the disconnected dynamic regimes. We refer to these regions where the system states are disconnected as barrier regions (Figure 5.6b, $0.0 < D < 0.0545$). These dynamical barrier regions are illustrated through the use of time plots of the system state for different values of $D$ (Figure 5.7). It can be observed from the figure that for $D = 0.01$ and $D = 0.04$ (i.e. $0 < D < 0.0545$), the system state stays around its corresponding higher and lower initial values ($X(0) = 1.005$ and $X(0) = -0.995$ respectively) at all future times and hence the two regimes are disconnected. However, at $D = 0.07$ (i.e. $0.5455 < D < 0.0705$), when the system state starts at a higher initial value ($X(0) = 1.005$), it eventually reaches the dynamic regimes with lower values (around $X(0) = -0.995$). This illustrates the fact that the system state permanently escapes into the regimes with lower state values. However, at $D = 0.1$, the system state is able to move between all three dynamic regimes indicating that these are connected.

The existence of barrier regions coupled with the phenomenon of noise induced bifurcations can lead to the creation of trap and escape regions as indicated by the ellipse in Figure 5.6b. For the set of parameter combinations represented by case 1 in Figure 5.6, when a system state starts in this region (indicated by the ellipse) and the disturbance variability scale varies between $0.0 < D < 0.0545$, the system state will remain trapped in this region at all future times. However, once the disturbance variability is scaled up $D > 0.0545$, the system state permanently escapes out of this region. Unlike deterministic catastrophic shift systems which allow for the recovery of original state with hysteresis through parameter change, this region can never be recovered by decreasing the disturbance variability. The existence of these trap or escape regions can have important consequences in the context.
Figure 5.7: Effect of Markovian dichotomous noise disturbance on the time trajectory of the system state $x$ at different intensities of disturbance variability on a catastrophic shift system with $\theta_1 = 0.01$, $\theta_2 = 1.0$, $\theta_3 = -1.0$, $\Delta_1 = -1.2$, $\Delta_2 = 1.0$, $\gamma_1 = 1.2$ and $\gamma_2 = 1.0$. Two different initial conditions at time $t = 0$ are selected; the blue line corresponds to $x(0) = -0.995$ and the green line corresponds to $x(0) = 1.005$. (a) Time trajectories for different magnitudes of disturbance variability $D$ illustrate the effect of trap regions $D = 0.01$ and $D = 0.04$, escape regions $D = 0.07$ and connected regimes $D = 0.1$. (b) Phase plots illustrating the range of values that the system state can take when subjected to Markovian dichotomous noise. The locations of the modes of the PDF are represented as black circles and the locations of the anti-modes are represented as white circles.
climate change induced irrecoverable ecosystem transitions caused by increased variability in climate forcings [Ridolfi et al., 2011]. This is because, we can have catastrophic losses to ecosystem processes and function just by changing the variability in the climate, and more importantly the losses are irrecoverable even when the climate variability is decreased.

It must be noted that, for the case of Markovian dichotomous noise, we have four parameters $\Delta_1$, $\Delta_2$, $\gamma_1$ and $\gamma_2$. By varying each of these parameters independently, we can obtain noise induced bifurcations at four possible locations as illustrated in Figure 5.6b. It can be observed from Figure 5.6 b and c that, while both $\Delta$ bifurcations change the number of dynamic regimes, only one $\gamma$ bifurcation occurring at $D = 0.0935$ changes the number of dynamic regimes and the other two $\gamma$ bifurcations have no effect on the number of dynamic regimes. The $\gamma$ bifurcations occurring at $D = 0.0195$ and $D = 0.0325$ only cause structural changes in the PDFs (Figure 5.6a) to affect the mean passage time measure $R_i^\tau$ (Figure 5.6c).

Increasing $D$ has the general effect of increasing the regime size measure $R_i^r$ for all dynamic regimes (Figure 5.6c), with due accounting for the destruction and creation of dynamic regimes due to noise induced bifurcations. This is attributed to the fact that, a higher disturbance variability pushes the system farther, thereby enabling it to increase its regime size. The creation and destruction of dynamic regimes due to noise induced bifurcations causes the regime probability measures $R_i^R$ to jump at bifurcation points. For example, the $\Delta$ bifurcation at $D = 0.545$ destroys dynamic regimes 3 and 4 and transfers their probabilities to the remaining dynamic regimes 1 and 2 causing a jump in their regime probabilities. With respect to the regime probability measures $R_i^R$, for the given set of parameters, we find that for disturbance variabilities beyond the $\Delta$ bifurcations, dynamic regimes with lower stable states are preferred, while for disturbance variability within the $\Delta$ bifurcations all dynamic regimes are almost equally likely. Unlike for the case of Gaussian white noise disturbance where the two regime probabilities converge to 0.5 at very large disturbance variability ($D > D_t$), we cannot expect such a convergence for the case of dichotomous noise disturbance if asymmetry exists between the two $\gamma$ parameters.

In Example B, when we start with a vegetated cover increasing extremes in mortality and growth (stress and non-stress) favors dynamic regimes with higher (vegetated) fraction cover in terms of their regime probabilities until a threshold disturbance variability is crossed ($D = 0.0545$). When the stresses are higher than this bifurcation threshold, the system favors the desert dynamic regime with low vegetation cover. Increased variability in mortality and growth are expected due to climate change, where we could have: i) increased seedling
mortality rates [Hirota et al., 2012], ii) altered herbivory patterns [Hamilton et al., 2005], iii) temperature stresses, hail and flood damage [Mahoney et al., 2012] etc. Simultaneously, we can also experience increased growth rates due to elevated CO$_2$ [Solomon et al., 2007]. Hence, an understanding of this bifurcation threshold and its relative location to the present and future variability in climate forcings is critical in predicting the behavior of the state of ecosystems in future. Through the insights gained from this dynamical system example, we can identify ecosystems that are near the vicinity of this bifurcation threshold and prioritize our remediation and mitigation efforts accordingly.

Similar to the regime size measure, the stochastic ecological resilience measure $R_{SE}^i$ increases with increasing $D$ values for all dynamic regimes (after accounting for bifurcations). This is attributed to the increase in regime size with increasing disturbance variability. The mean passage time measure $R_\tau^i$ exhibits both increasing and decreasing trends with increasing $D$ values and is the only measure that is sensitive to all bifurcations.

As mentioned earlier, Markovian dichotomous noise allows us to change the frequency, intensity, variability and asymmetric bias of the disturbance. The changes in intensity and variability aspects of disturbance have been investigated earlier (Figure 5.6 a, b and c). This is performed by changing the $\gamma$ parameters. The effect of changes in the frequency of noise is illustrated in Figure 5.6 d, e and f. Comparing Figure 5.6 a, b and c with d, e and f, in the context of the example problems A and B, we see that decreasing the frequency of disturbances by an order of magnitude results in increased regime probability for the vegetated dynamic regime and decreased regime probability for the intermediate vegetated regime (Figure 5.6f, $R_{R}^i$). This illustrates the effect of frequency on the stabilization or destabilization of vegetated regime. Furthermore, there is an invariant effect for the regime size resilience measure (Figure 5.6f, $R_{r}^i$) and an overall decrease in mean passage time resilience measure (Figure 5.6f, $R_\tau^i$). It can be observed that the $\gamma$ parameters exert a strong influence on the mean passage time. When we decrease $\gamma$ values, we decrease the switching frequency between the two dichotomous states and increase the recovery time to each of the state causing a decrease in the mean passage time. Hence, higher $\gamma$ values result in higher $R_\tau^i$. This example illustrates converging, invariant, and diverging responses to changes in frequency of disturbances.

Figs.5.8 and 5.9 illustrate the effects of changing parameters and disturbance variability on resilience measures $R_{r}^i$, $R_{R}^i$, $R_{SE}^i$ and $R_\tau^i$ indicating the presence of noise induced bifurcations resulting in the creation and destruction of dynamic regimes. It can be observed from both the figures that the maximum variations in the resilience measures are observed near
the regions where there are noise induced bifurcations (around $\theta_1 = 0$ and when $\theta_2 < 1.0$). Furthermore, the effect of the parameter boundary where catastrophic shift occurs in the deterministic conditions ($27\theta_2^2\theta_3 < 4\theta_3^2$) is also strongly manifested in the resilience values.

The regime size measure $R_i^s$ generally increases with increasing $D$ values and decreases with increasing $|\theta_1|$ values (Figure 5.8a). A higher $D$ value enables the system to explore a larger domain thus increasing the regime size. Since bifurcations appear near $\theta_1 = 0$, we observe maximum regime size values around this region. The behavior of $R_i^s$ (Figure 5.8a) closely mimics the stochastic ecological resilience $R_i^{sE}$ (Figure 5.9a) for identical reasons.

The regime probability measure $R_i^R$ shows an interesting variation with increasing $D$ values where, there is a general enhancement in dynamic regime preference as the disturbance variability increases (Figure 5.8b). Dynamic regimes which are dominant at low $D$ values are more dominant at higher $D$ values, while dynamic regimes which are not dominant at low $D$ values become less dominant at higher $D$ values. This behavior is the opposite of the one we observe for the case of Gaussian white noise where we have a disturbance induced stabilization of weak dynamic regimes and destabilization of strong dynamic regimes. This illustrates the important role that the type of disturbance, its magnitude and variability play in determining the dynamical outcome of ecological systems.

While the mean passage time measure $R_i^\tau$ shows variations similar to those of the other measures, with strong influence of the deterministic catastrophic shift condition and bifurcation condition (Figure 5.9b), its behavior is more influenced by the values of $\gamma$ as discussed earlier. Furthermore, an asymmetry between $\gamma_1$ and $\gamma_2$ values would demonstrate a preference to the $R_i^\tau$ measures. For our example in Figure 5.9b, $\gamma_1 > \gamma_2$ and hence transitions from $\Delta_1$ to $\Delta_2$ take shorter time than transitions from $\Delta_2$ to $\Delta_1$. These can be easily observed in regions where only 2 dynamic regimes are present, where $R_i^\tau < R_i^\tau$, and in regions where 4 dynamic regimes are present, where $R_i^\tau < R_i^\tau$. This is because $R_i^\tau$ and $R_i^\tau$ correspond to $\Delta_1$ states and $R_i^\tau$ and $R_i^\tau$ correspond to the $\Delta_2$ states. Interpreting this result in the context of Example B, we infer that, the mean switching frequency of disturbance from stress to non-stress conditions is higher than from non-stress to stress conditions. Hence, it takes a longer time to transition out of the vegetated cover than the desert cover.

Based on these analyses we infer that there are several attributes to characterize the resilience of a system and the various resilience measures capture independent and complementary aspects of the system dynamics. The interactions between the system dynamics and the disturbance characteristics creates emergent behavior that are different for different resilience measures. This makes it possible to arrive at the same resilience values through sev-
Figure 5.8: Effect of the variation of parameters $\theta_1$ and $\theta_2$ on resilience measures (a) Regime size $R_i^R$ and (b) Regime probability $R_i^R$ for Markovian dichotomous noise at four different intensities of disturbance variability for the four dynamic regimes $X_1$, $X_2$, $X_3$ and $X_4$. The other parameters used in this simulation were $\Delta_1 = -1.2$, $\Delta_2 = 1.0$, $\gamma_1 = 1.2$ and $\gamma_2 = 1.0$. White spaces represent regions where the dynamic regimes do not exist. The effect of noise induced bifurcations can be observed with the changing locations of these white spaces across all four dynamic regimes when the disturbance variability $D$ is varied. The diagonal grey line indicates slopes of constant deforestation and reforestation rates $A$ [m$^2$/year] in Example B.
Figure 5.9: Same as figure 5.8 but for (a) Stochastic ecological resilience $R_s^E$ and (b) Mean passage time $R_t^E$ measures. Note that for illustration purposes, the upper and lower bounds for the $R_t^E$ plot in (b) have been cropped.
eral different combinations of system and disturbance parameters. This is captured through the concept of iso-resilience described in the next section.

5.6 Iso-resilience

Iso-resilience curves are contour lines that connect regions in the parameter space that have identical resilience measure values. The parameter space can be generated from a selection of the system and disturbance parameters. Figure 5.10 presents iso-resilience curves for measures $R_1^R$ and $R_1^r$ as a function of disturbance variability $D$ for a system driven by Gaussian white noise. Figure 5.10a illustrates the strong non-linearities in the behavior of $R_1^R$ as a function of $D$ and $\theta_2$. An interesting behavior can be observed where for a fixed $D$, $R_1^R$ decreases, reaches a minima and then increases with increasing $\theta_2$ values. Applying this behavior to Example A, we find that under low emigration rates, the average fraction of time the system state lies in the refuge dynamic regime ($R_1^R$) initially decreases, but later increases with increasing population growth rates. Therefore, to maintain a constant $R_1^R$ under increasing population growth rates, using the iso-resilience curves in Figure 5.10a we can decipher that we have to decrease $D$ when $D \lesssim 0.03$ but increase $D$ when $D \gtrsim 0.03$. $R_1^R$ exhibits a monotonously decreasing behavior when the parameter $\theta_1$ is increased (Figure 5.10c) whereas $R_1^r$ exhibits a different monotonously increasing behavior when the parameter $\theta_2$ is increased (Figure 5.10d). This further illustrates that changing parameters can increase one attribute of resilience while decreasing another attribute.

Iso-resilience curves can also be developed for derived resilience measures such as regime dominance, obtained as the difference in regime probabilities between two dynamic regimes, for example $R_1^R - R_2^R$ (Figure 5.10b). Regime dominance measures the average ‘excess’ fraction of time that the system state stays in one dynamic regime compared to another dynamic regime. A high value of regime dominance can indicate that the system state shows strong preference towards one dynamic regime over another.

5.7 Discussion

In this section, we highlight some potential applications of our resilience characterization in other catastrophic shift systems observed in nature. An example of two different disturbance types, fire and grazing on grasslands is discussed by Anderies et al. [2002]. Depending on the
Figure 5.10: Iso-resilience curves of different resilience measures for a catastrophic shift system subject to Gaussian white noise as a function of disturbance variability $D$ and parameters $\theta_1$ or $\theta_2$. (a) regime probability of dynamic regime 1 $R_1^R [-]$, (b) regime dominance obtained as the difference in regime probabilities between dynamic regimes 1 and 2 $R_1^R - R_2^R [-]$, (c) regime probability of dynamic regime 1 $R_1^R [-]$ and (d) natural logarithm of mean passage time $\log R_1^R [T]$. Z1 and Z2 are the starting and ending points for state transition and the bent and the straight arrows represent transition paths with and without the constraint $R_1^R > 0.8$ respectively.
particular set of parameters chosen, Anderies et al. [2002] show that fire causes a stabilization effect, while grazing causes a destabilization effect on the grassland dynamic regime. The regime probability measure $R^R_i$ captures this effect and the concept of disturbance induced stabilization, destabilization, or enhancement of dynamic regimes can be inferred in the example of Anderies et al. [2002]. In this context, we would like to point out that the popular notion ‘by controlling variability we shrink ecological resilience’ [Gunderson, 2009] is only partially true. As demonstrated from our simulations, depending on the system dynamics (parameters), the type and magnitude of disturbance and the particular attribute of resilience, we can have either an increasing, decreasing, or invariant resilience behavior to increasing variability for each and every dynamic regime.

Conflict between different attributes of resilience have been observed in several ecological scenarios in the literature. The classical conflict between engineering resilience and ecological resilience is highlighted in marine coral ecosystems [Cote and Darling, 2010], and other systems such as shrub grass ecosystems, population (insect, fish) dynamics, herbivory as a disturbance etc. [Holling, 1996]. A plot such as Figure 5.2 can be used as a tool to analyze this ‘efficiency versus existence’ trade off. For a stochastically driven system, the concept of mean passage time measure can be used instead of engineering resilience. Distinction must be made between dynamic regimes which have a very long mean passage time (long turn over times) indicating difficulty in achieving dynamic regime transitions and irreversible dynamic regimes which cannot theoretically accomplish such a transition due to the existence of barrier regions [Folke et al., 2004].

Oftentimes, there are conflicts between short term gains and long term resilience in resource exploitation, as in the case of using excessive fertilizer and pesticides, plowing, overstocking etc. in agricultural practices [Carpenter et al., 2001]. Similar resilience versus cost trade offs in other fields such as component failure of complex machines, resistance to diseases, resilience specialization to one type of disturbance versus another etc. have also been highlighted [Kitano, 2004]. An interesting case of such a trade off in conservation versus resilience in the case of marine coral ecosystems is discussed in Cote and Darling [2010]. In their paper Cote and Darling [2010] argue that, the development of marine conservation sanctuaries for the protection of coral ecosystems from increased variability in environmental forcings such as temperature changes, nutrient loading etc. could potentially result in decreasing the resilience of the ecosystem to extreme events. This is because, a coral ecosystem which was not protected from environmental variability, although will be in a slightly degraded state, has a higher resilience to extreme events. While Cote and Darling [2010] claim that such
phenomenon are plausible, we suggest that using the measures developed in this work, we can determine parameter conditions where this behavior is expected to occur, and whether increased disturbance variability stabilizes or destabilizes the current dynamic regime.

The framework developed in this chapter enables us to gain insights regarding several important questions in the context of catastrophic shift systems. For example, in shallow lake ecosystems, it is important to know whether inter-species competition or intrinsic growth rate dominates the system dynamics in the occurrence of algal blooms [Angeler et al., 2010]. These two processes can be captured by our parameters \( \theta_2 \) and \( \theta_3 \) and using plots similar to Figure 5.2 and Figure 5.10 one can identify regions in the resilience landscape that indicate dominance of different processes. Such characterizations can act as powerful tools to manage lake ecosystems from catastrophic transitions.

An interesting application of iso-resilience curves is that it enables us to devise paths for traversing the resilience landscape under changing parameter conditions. Specific paths can be designed that incorporate constraints such as, avoiding unfavorable regions and passing through favored regions [Folke et al., 2004, Folke and Others, 2002, Gunderson and Holling, 2002]. For example, in Figure 5.10a, if we start at Z1 and the \( D \) is increased from 0.02 to 0.08, in order to maintain the same regime probability \( R_1^R = 0.98 \), \( \theta_2 \) has to be decreased to 0.3 (represented as Z2). One possible path to accomplish this transition is indicated by the straight arrow. However, if we impose an additional constraint that \( R_1^R > 0.8 \) during the entire course of this transition, then we have to follow the path indicated by the bent arrow. The critical condition that must be met in this case is that \( \theta_2 < 0.3 \) before \( D > 0.044 \). Iso-resilience curves enable us to identify such critical points or bottlenecks when designing travel paths in a resilience landscape and hence can be used as valuable tools in managing resilience aspects of non-linear dynamical systems [Folke et al., 2004, Gunderson, 2009, Holmgren and Scheffer, 2001].

5.8 Conclusions

In this chapter, we use the canonical catastrophic shift system to develop a system-disturbance-attribute triplet framework to quantify resilience. This framework captures the interplay between intrinsic system dynamics and and extrinsic disturbance drivers. The concept of resilience does not just focus on the state of the system, but more importantly, the process dynamics and feedbacks which are captured by the DOA or dynamic regime. We propose several different resilience measures and interpret their variation to changing parameters
through the help of two ecological examples; (i) bistable population dynamics (Example A) (ii) multi-stable vegetation cover dynamics (Example B). Furthermore, we develop iso-resilience curves and use them to design travel paths in a resilience landscape, providing powerful tools to manage DOA or dynamic regime transitions in catastrophic shift systems. Several interesting behaviors were also observed through the help of these simulations. These include:

- Disturbance induced stabilization of weak dynamic regimes
- Disturbance induced enhancement of regime dominance
- Regions of sensitivity
- Barrier regions
- Trap or escape regions
- Bifurcation thresholds
- Bottlenecks in travel paths of resilience landscapes

This triplet framework can be readily applied to other non-linear dynamical systems including multi-state systems subject to multiplicative stochastic noise terms. These additional modifications enhance the complexity of the dynamical system (stochastic resonance, coherence, ratchet effect) and its associated DOA or dynamic regimes leading to the emergence of other interesting behaviors such as oscillations, pattern formations etc [Anishchenko et al., 2002, Ridolfi et al., 2011]. Extending to multiple dimensions would enable us to explore the quantification of more challenging resilience aspects such as adaptability, ability to self-organize, learning etc.

The mathematical framework developed in this chapter has enabled us to quantify and characterize different attributes of resilience when a non-linear dynamical system is subject to disturbance. In the final chapter, we propose a conceptual resilience constrained optimality framework to explain the widely observed sub-optimal behavior of plant canopies.
CHAPTER 6

CONCLUSIONS

Our experimental and modeling results presented in Chapters 2 and 3 indicated that soybean plant canopies are sub-optimal in NPP maximization that translates to sub-optimal seed yield. Our modeling results show that soybean plants have almost twice as much LAI compared to optimal conditions under peak LAI, and our experimental results indicate that a 0.5 decrease in LAI resulted in a 8.1% increase in end of season seed biomass. Furthermore, our carbon allocation modeling results from Chapter 4 indicated that plants allocate carbon in a sub-optimal manner whereby more carbon is allocated to the vegetative parts compared to reproductive parts. We further show that by changing plant carbon allocation, we can increase yield by upto 23% and 42% under ambient and elevated CO$_2$ conditions respectively.

We hypothesize that plants are sub-optimal so as to provide a “buffer” against unanticipated situations such as variability in weather, herbivory etc. which we have characterized as resilience constraints. In Chapter 5 we develop a mathematical framework to quantify resilience and develop resilience measures for a canonical catastrophic shift system. In this chapter we combine the results presented in the study and propose a unified resilience constrained optimality framework to predict plant acclimation due to environmental change. We further present a summary of some of the key findings of our research. Finally we provide some suggestions for avenues for future studies related to the findings of our research.

6.1 Framework for a resilience constrained optimality

Resilience against extreme events provide strong optimality constraints for plants, animals, and ecosystems in general [Whitfield, 2007]. For the case of soybean ecosystems, disturbance events occur in the form of water stress through flooding and droughts, heat stress due to hot or cold waves, diseases, herbivory due to insects, animals, windfall hail damage etc. [Morgan et al., 2005, Nabity et al., 2009, Schar et al., 2004]. Plants which are under optimum conditions are capable of maximizing seed yield (or any other optimality variable) without
the presence of disturbance events. However, under a disturbance regime the output for the optimality variable can be significantly deteriorated. For example, during the year of 2003, a hail damaged significant portion of the above-ground soybean biomass resulting in almost a 60% reduction in LAI [Morgan et al., 2005]. However, the plants exhibited resilience and the final seed yield was close to the annual average [Morgan et al., 2005]. Had the plants been under optimum LAI conditions, their performance in terms of seed yield would have been significantly smaller. We hypothesize that the presence of resilience in the plants enabled them to cope with this extreme event.

The concept of resilience constraints to optimality is illustrated in Figure 6.1. It can be observed from the figure that in the absence of resilience constraints, seed yield is maximized under a LAI that is lower than the observed values. This is what is illustrated in our optimality plots (Figure 2.6). However, we hypothesize that in the presence of resilience constraints, the optimal value for LAI shifts closed to the observed LAI values. More importantly, the optimal LAI values in the absence of resilience constraints results in a significantly deteriorated seed yield under the resilience constraint.

We suggest that the ability of plants to be resilient is an indicator of its acclimation potential. If we consider environmental change as an indicator of disturbance, our resilience constrained optimality framework can then be applied for acclimation scenarios as well.

6.2 Research summary

6.2.1 Acclimation effects decrease plant NPP uptake

Our results demonstrate that soybean ecosystems under acclimation to elevated CO$_2$ undergo acclimations that result in decreasing the NPP which in turn decreases their yield. For example, the combined effect of structural and biochemical acclimations are roughly additive and results in a 10% reduction in NPP. Our modeling results indicate that increased LAI due to structural acclimation causes increased self-shading resulting in a net decrease in NPP.

6.2.2 Plant canopy is sub-optimal with respect to maximizing NPP uptake

Our results demonstrate the trade off between gains in GPP and losses in respiration resulting in maximization of NPP at intermediate values of LAI. While optimal LAI values are in the
Figure 6.1: Conceptual illustration for the framework for resilience constrained optimality with LAI as the control variable. Without the presence of resilience constraints, the observed LAI is much higher than the optimal LAI, however, by introducing resilience constraints, we shift the optimality closer to the observed values.
range of 3.5 to 4.0, the observed LAI values are between 6.5 and 8.0. Furthermore, our results indicate that unlike carbon fluxes, which shows a peaking of NPP at intermediate LAI values, the variation of water and energy fluxes as a function of LAI are monotonic and either increase or decrease.

We also demonstrate the existence of interesting trade offs between canopy and soil energy fluxes resulting in compensating effect as LAI is varied. Typically, increases in canopy fluxes in water and energy are accompanied with decreasing soil fluxes. However, the rates of increase and decrease vary depending on the fluxes considered and these result in distinct patterns of changes in overall ecosystem fluxes.

6.2.3 LAI reduction experiments confirm sub-optimality in plant canopies

We performed LAI reduction experiments on soybean plants under ambient and elevated CO$_2$ conditions at the SoyFACE research facility in Illinois. Our experimental results show that an average reduction of LAI by 0.5, resulted in an overall 8.1% increase in seed yield confirming the existence of sub-optimality in soybean canopies. These results confirm our earlier modeling simulations and suggest that plants invest more carbon in vegetative parts compared to reproductive parts.

6.2.4 Carbon allocation strategies under acclimation

To investigate the reasons for the observed sub-optimality we develop a plant carbon allocation and growth model and couple it with an existing dynamic vegetation model. The results of the carbon allocation model indicate the presence of allocation acclimation whereby soybean plants change their carbon allocation patterns when subject to growth under elevated CO$_2$. In particular, the fraction of carbon allocated to reproductive parts is lower under acclimation under elevated CO$_2$. The presence of allocation acclimation further decreases the expected increases in yield in addition to eco-physiological, biochemical and structural acclimation.

6.2.5 Resilience can explain the observed suboptimal behavior

We hypothesize that resilience provides one of the key reasons for the observed sub-optimal behavior and develop a mathematical framework to quantify resilience using stochastic non-
linear dynamical systems. Resilience is defined as the ability of a system to withstand a disturbance and still maintain its dynamics. Our mathematical framework indicates that resilience is a function of system dynamics, disturbance properties and the resilience attribute of interest. In the presence of continuous stochastic disturbance events, we observe different emergent properties caused by noise induced bifurcations that can have important consequences in determining ecosystem behavior under disturbance. We develop iso-resilience curves that are contour lines of constant resilience values as system and disturbance parameters are changed. These curves can be used to manage resilience under changing climatic conditions.

6.2.6 Resilience constrained optimality framework to model acclimation

A resilience constrained optimality framework is proposed to explain the observed sub-optimality in soybean canopies. The conceptual framework suggests that in the absence of a resilience constraint a higher optimum can be reached. However, more importantly, it also suggests that the ecosystem states that give rise to optimum behavior without resilience constraints are different from those that give rise to optimum behavior under the presence of a resilience constraint.

To summarize, we conclude that soybean ecosystems, exhibit sub-optimality whereby the end of season seed yield is significantly lower than what is observed under both ambient and elevated CO$_2$ conditions. By making the plants invest more in reproductive parts compared to vegetative parts, we can significantly increase seed yield. We hypothesize that resilience constraints are one of the key factors that prevent plants from reaching their optimal values. Furthermore, our acclimation studies indicate that current soybean cultivars perform significantly poorer under acclimation to elevated CO$_2$. These results can be advantageously used to develop seeds to increase yield for current and future climate scenarios. In the following section we provide some suggestions for future research.
6.3 Future research

6.3.1 LAI reduction versus LAI manipulation

The experimental approach employed in this study involved decreasing LAI by removing young and emerging leaf trifoliates and this changes the plant carbon allocation pattern. This is because, in our experimental procedure we remove young and emerging leaves rather than fully flushed leaves. By removing young leaves, we change the carbon allocation patterns of the plant. Repeating the experiment by removing fully flushed leaves can provide an indication of the effect of LAI reduction in the absence of changes in carbon allocation. This experiment can yield further insights into the sub-optimal nature of plant canopies.

6.3.2 Explore storage mechanisms in allocation

Our plant carbon allocation model ignores the effects of transient carbon storage mechanisms. While, the effect of carbon translocation from leaves and stems can incorporate some aspects of long term carbon storage and retrieval, there are no mechanisms involved to include short term explicit carbon storage mechanisms. Plants can store carbon in leaf vacuoles, or in their phloem and its companion cells [Thornley and Cannel, 2000]. These can then be used under temporary carbon stress conditions such as nighttimes, cloudy days, or drought etc. While the effect of storage might not be significant for small annual plants, they play a crucial role for large perennial trees especially during leaf onset and bud burst during early spring.

6.3.3 Extend resilience framework for transient and multi-dimensional systems

The mathematical framework to quantify resilience presented in Chapter 5 is for a canonical one dimensional system under stationary conditions. However, natural ecosystems are multi-dimensional and are constantly changing due to the transient nature of disturbances. Hence, in order to effectively model most natural ecosystems, we need a multi-dimensional framework to explore ecosystem resilience characteristics. By computing the probability density function as a function of time, and using these to determine resilience quantifications, we can incorporate the transient effects. Including multi-dimensional and transient effect would enable us to model other emergent behavior such as oscillations, pattern formations,
adaptability, ability to self organize, learning etc.
REFERENCES


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