

# A Stage Structured Model of the Impact of Buffelgrass on Saguaro Cacti and their Nurse Trees

Lucero Rodríguez-Rodríguez<sup>1</sup>, Erin Stafford<sup>2</sup>, Anna Williams<sup>3</sup>, Brian Wright<sup>4</sup>, Christopher Kribs<sup>5</sup>, and Karen Ríos-Soto<sup>6</sup>

<sup>1</sup>University of Texas Rio Grande Valley

<sup>2</sup>Tulane University

<sup>3</sup>University of Texas at Austin

<sup>4</sup>University of Redlands

<sup>5</sup>University of Texas at Arlington

<sup>6</sup>University of Puerto Rico at Mayaguez

## Abstract

The saguaro cactus (*Carnegiea gigantea*), a keystone species in the Sonoran Desert, has faced population decline in recent years. The immediate threat to the saguaro cactus is the increase in wildfires fueled by the invasive species buffelgrass (*Pennisetum ciliare*). The increasing rate of wildfires could result in the collapse of the Sonoran Desert ecosystem. A stage structured model is developed and analyzed to capture interactions between saguaro cacti, their nurse trees, and buffelgrass. In order to model the impact of buffelgrass, the interactions between the saguaro growth stages, juvenile and adult, with the nurse trees, called the foothills palo verde (*Parkinsonia microphylla*), are studied. Then the presence of buffelgrass among the populations is analyzed to determine the influence of buffelgrass on nurse tree and cacti populations. This model consists of a system of non-linear ordinary differential equations which considers commensalism between juvenile saguaros and their nurse trees and their eventual competition as juveniles mature to adulthood. The analysis of this system includes qualitative analysis of the equilibria of the system as well as a numerical analysis of the sensitivity of key parameters. From this research, it was concluded that buffelgrass has led to an increase in wildfire frequency through the propagation of unnatural wildfires, which can lead to a decrease, or possible extinction, of the saguaro population. Therefore, in the interest of preserving the saguaro cactus population, the buffelgrass population must be limited through the use of herbicide and harvesting.

## 1 Introduction

### 1.1 The Saguaro Cactus

As a keystone species of the Saguaro National Park the saguaro cactus, or *Carnegiea gigantea*, serves not only as an icon of the national park, but also as a habitat and food source for many other species in the region [1]. Therefore, fluctuations in the saguaro cactus population can affect the health of the ecosystem [1]. Aside from the substantial ecological importance of saguaros, the cactus is also a large component of the local tourism industry, with tourism to the Saguaro National Park resulting in a cumulative economic benefit of \$66.5 million per year for Tucson, Arizona alone [2]. Furthermore, the saguaro also has cultural significance to the Papago and Pima nations, who have historically relied on the plant for food, drink, and religious traditions [1].

The saguaro cactus is a slow-growing, perennial plant that has been recorded to have a lifespan of 125 to 175 years and a maximum height of over 18 meters. Saguaros reproduce through cross pollination with other saguaros; however, they are not able to reproduce until they are 30 to 45 years of age. Most fragile in the early stages of growth, saguaro seeds flourish during infrequent weather patterns such as mild winters and summers, followed by increased rainfall. An example of their sensitivity can be noticed from past population bursts that have been linked to the subtle

weather fluctuations associated with volcanic activity and El Niño [3]. Since population bursts are observed from subtle weather changes, it can be inferred that the saguaro cactus reproduction is very sensitive to weather. This makes the saguaro population susceptible to the slightest weather fluctuations. Due to a long life span and slow growth many of the effects of population changes are not realized for decades or longer [4].

## 1.2 Palo Verdes, Nurse Trees of the Saguaro Cacti

The establishment and growth of young saguaros also depends on their nurse trees. Under their canopies, trees create a microclimate that is cooler in the summer and warmer in the winter. Nurse trees also help to protect saguaros from foraging animals and strong winds. Although saguaros can establish in the open, their likelihood to survive as a seedling is greatly increased under a nurse tree. The preference to shade results in an increased likelihood of a saguaro growing under a tree and there is a possibility of saguaro clusters around the base of trees. The most common nurse tree is the foothills palo verde, or *Cercidium microphyllum* [5]. The foothills palo verde is a small tree with maximum height of around 7.92 meters and can live for more than 100 years. Although palo verdes are shorter than fully grown saguaros, they are taller than young saguaros. The palo verde reproduces both sexually and asexually; however, due to animal consumption and water availability only 1.6% of all seedlings that are germinated survive, resulting in a low yearly recruitment rate for the species [6].

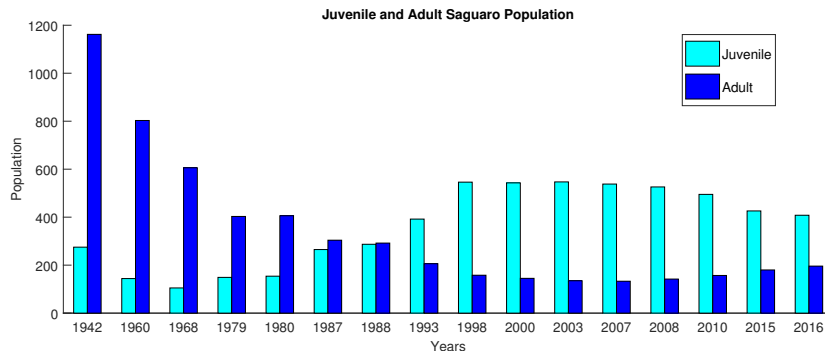


Figure 1: The changes in the distribution of adult and juvenile saguaro populations from 1942 to 2015 can be seen from data modified from Orum et.al.[7]. (It should be noted that there is a discrepancy in the reported data in 2013.)

## 1.3 Buffelgrass

Although saguaros are susceptible to many natural causes of death, such as freezing, drought, small animal consumption, and bacterial necrosis, the largest threat to the population is currently wildfire caused by buffelgrass [8]. Figure 1 was constructed by previously recorded saguaro census data [8, 7]. The figure shows a gradual decline in the population of both adult saguaros and juvenile saguaros starting from 1942. As a source for cattle feed and erosion control, buffelgrass was first introduced to the state of Arizona in the 1930's and was first identified in Saguaro National Park in 1989 [9]. Buffelgrass is a perennial invasive grass that can reproduce sexually or asexually, and its seeds are viable for up to 4 years before being germinated. Fluffy and nearly weightless, buffelgrass seed spread is facilitated by wind, water, and animal fur. Furthermore, germination can occur in a range of temperatures from 50°F to 104°F, requires about 0.124 inches of rain over two days, and at any time of year. Once germinated, seeds mature in about 18 months, and adults can reproduce within 6 weeks. Also, in the desert regions of Arizona, buffelgrass has no natural predators, meaning that removal is limited to the manual pulling of the plants by volunteers or chemical spraying, which is only viable for a couple of weeks in the rainy season when the plants are green. Buffelgrass resilience has led to an annual population increase of 35.5% in Saguaro National Park [10]. As an invasive species, buffelgrass is able to out-compete many native species in the Sonoran Desert. Further, the desert would only experience a natural wildfire about every 250 years without the presence of buffelgrass, meaning most native species are not equipped to deal with large fires. Buffelgrass, however, is a fire-adapted species, meaning it can quickly reemerge

after wildfires and provide fuel so that the fires burn longer and cover more area. Buffelgrass helps the quick spread of fire, which kills native species and leaves available space for the buffelgrass to invade at a faster rate than the native species [11].

The purpose of this study is to understand the long-term effects buffelgrass can have on the saguaro population as well as whether any resulting population decline can be reduced through the control of the buffelgrass population. The following outlines the remainder of the paper. In Section 2, a mathematical model is formulated to look at the interactions of saguaros and their nurse trees and the influence of buffelgrass on the system. Equilibria analysis will be performed on the model with and without the presence of buffelgrass in Section 3. In Section 4, parameters are explained in depth and provided numerical values. In Section 5, simulations are run to show the natural relationship between the nurse trees and saguaros. In Section 6 contrasts section 5, by simulating the effects of buffelgrass on the aforementioned natural relationship. Section 7 shows local sensitivity analysis on several parameters of interest. Finally, Section 8 discusses conclusions. Included in the appendix, is more detail about the mathematical analysis from this paper.

## 2 Model Formulation

In order to predict the impact of buffelgrass on the saguaro cactus, as well as the palo verde nurse tree, the dynamics of the saguaro and nurse tree populations are modeled with and without the presence of buffelgrass. This design will reveal the true impact of buffelgrass on the cactus and trees and allow us to analyze the extent of the buffelgrass wildfire damage. The model without the presence of buffelgrass serves to demonstrate the natural interaction of the saguaro cactus and the nurse trees. The introduction of buffelgrass to the model exhibits the extent of the damage caused by buffelgrass wildfires. These models will be systems of non-linear ordinary differential equations (ODEs) that represent the basic interactions between the populations. The inclusion of buffelgrass will predominantly reflect the effects of wildfires on saguaro cactus and their nurse trees.

### 2.1 Assumptions of the Model

Assumptions were made about the interactions between saguaros, nurse trees, and buffelgrass in order to maintain realistic dynamics and avoid unnecessary complexity. The first of these assumptions is that juvenile saguaros are assumed to be cacti in the age range of 1 to 35 years. The range starts at age 1, because this is when a cactus's susceptibility to death due to environmental conditions is greatly reduced. The range ends at 35, because this is when cacti are able to begin reproducing. Therefore, the adult saguaro population considers those to be at reproductive age, 35, and older. Another assumption is that the natural life span of all adult saguaros is 175 years, which is the average lifespan. It is also assumed that saguaros in both age groups are equally susceptible to death from conditions like extreme temperature, bacterial necrosis, and being eaten by rodents. Furthermore, the difference in the survival rates of the juvenile saguaros under nurse trees and in the open are not considered.

The model does not consider the effects of clustering of the adult population on the reproductive rate, since this is rarely seen. For the nurse trees, assumptions include that trees are not able to out compete adult saguaros for resources. Furthermore, the only competition that juvenile saguaros face is competition over space with adult saguaros. Thus, competition between juvenile saguaros and buffelgrass is not included. Competition between nurse trees and buffelgrass is also not included because the effects are not strong. Similarly, commensalism between adult saguaros and buffelgrass is not included because the effects do not greatly influence either species.

### 2.2 The Model Description

The model is formulated using the dynamics between the adult and juvenile saguaro cacti, their nurse trees, and buffelgrass. The interactions considered are given by the following system of equations.

$$\frac{dS_j}{dt} = rS_a \cdot \max \left\{ 0, \left( 1 - \frac{\epsilon S_j + S_a}{k_1 + bT} \right) \right\} - \gamma S_j - \mu_j S_j - \theta_j B S_j, \quad (1a)$$

$$\frac{dS_a}{dt} = \gamma S_j - \frac{\alpha_1}{k_2} S_a T - \mu_a S_a - \theta_a B S_a, \quad (1b)$$

$$\frac{dT}{dt} = \phi T \left( 1 - \frac{T + \sigma S_a}{k_2} \right) - \theta_T B T, \quad (1c)$$

$$\text{and} \quad \frac{dB}{dt} = \omega B \left( 1 - \frac{B}{k_3} \right) - \mu_B B. \quad (1d)$$

The growth of the juvenile saguaro population,  $S_j$ , from the reproduction of the adult saguaros,  $S_a$ , is best captured with a logistic growth term, given by

$$rS_a \left( 1 - \frac{\epsilon S_j + S_a}{k_1 + bT} \right). \quad (2)$$

The juvenile–adult interaction, Expression 2, represents the rate at which new juvenile saguaros enter the population. The parameter  $r$  is the rate that seeds germinate and survive to one year of age per adult saguaro. On the other hand the term,

$$\left( \frac{\epsilon S_j + S_a}{k_1 + bT} \right)$$

represents the proportion of space available for new juveniles to take root, including free space not taken by adults and space under nurse trees. The numerator,  $\epsilon S_j + S_a$  is the space that is already taken up by juvenile and adult saguaros. The parameter  $\epsilon$  converts juveniles to adults in terms of space, so that the carrying capacity term will be scaled to adults only. The denominator,  $k_1 + bT$ , represents the benefit nurse trees provide to juvenile saguaros by increasing their carrying capacity. Here,  $k_1$  is the carrying capacity of adult saguaros in open space and  $bT$  is the average number of saguaros one nurse tree can support. Therefore, nurse trees increase the number of juveniles that can survive in an area. Since this term has the possibility to be negative, we take the maximum value between zero and the term described previously, Expression 2, for the biological applicability of the model. Furthermore,  $\gamma$  is the rate at which juveniles mature into adults. Here it is assumed that juveniles become adults when they begin to reproduce.

For the adult population,  $\mu_a$  represents the death rate, and the rate at which adult saguaros die due to competition with trees for resources is  $\frac{\alpha_1}{k_2}$ . It is assumed that  $\alpha_1$  is nearly zero since the possibility of a nurse tree out competing an adult saguaro is rare. The dynamics of the tree population include natural germination and death rates, given by  $\phi$ , that is  $\phi = b - d$ . The rate that nurse trees reach their carrying capacity,  $k_2$ , is given by  $\phi T \frac{T}{k_2}$ . The term for the competition between adult saguaros and trees,  $\rho S_a T$ , can be rewritten as  $\phi T \frac{\sigma S_a}{k_2}$ , where  $\sigma$  is a proportion of the carrying capacity, and is dimensionless, that is given by  $\sigma = \frac{\rho}{\phi} k_2$ , where  $\rho$  is the rate adult saguaros out-compete trees.

Since the main effect of buffelgrass on native species in regions where it has invaded is the propagation of wildfire, the dynamics of buffelgrass interacting with native populations in the terms of competition or commensalism are neglected. The parameters  $\theta_i$  ( $i = j, a, \text{ or } T$ ) represent the effect of buffelgrass-related wildfire. Therefore, the terms in the saguaro and nurse tree equations,  $\theta_j B S_j$ ,  $\theta_a B S_a$ , and  $\theta_T B T$ , are the mechanism for the death of these species due to wildfires. The  $\theta$ 's terms are density dependent of buffelgrass and describe the average frequency of wildfires in the area under study per unit time.

It is assumed that the buffelgrass equation grows logistically, that is  $\omega B \left(1 - \frac{B}{k_3}\right)$ , where  $\omega$  is natural growth rate. When implementing mitigation strategies, such as seasonal chemical spraying,  $\omega$  will be decreased. The term for the space already occupied by buffelgrass is  $\frac{B}{k_3}$ , where  $k_3$  is the carrying capacity. Constant effort harvesting is also incorporated in the model, with  $\mu_B B$  representing efforts by volunteers to reduce the buffelgrass population through the manual pulling of buffelgrass. Thus,  $\mu_B$  is the harvesting rate. The System of Equations 1 representing the population dynamics can also be represented in a flow chart diagram given in Figure 2, while Table 1 include the parameters with their definitions and units.

Parameter Table		
Parameter	Definition	Units
$r$	Germination rate of saguaros	$\frac{\text{juveniles}}{\text{adults} \cdot \text{year}}$
$\epsilon$	Conversion of juveniles to adults in terms of space	$\frac{\text{adult}}{\text{adult}}$
$k_1$	Adult saguaro carrying capacity	$\frac{\text{juveniles}}{\text{adults}}$
$b$	Average juveniles under nurse tree	$\frac{\text{juveniles}}{\text{tree}}$
$\gamma$	Saguaro maturation rate	$\frac{1}{\text{year}}$
$\mu_j$	Juvenile death rate	$\frac{1}{\text{year}}$
$\alpha_1$	Rate nurse trees out-compete saguaros	$\frac{1}{\text{year}}$
$k_2$	Approximate carrying capacity of adults and nurse trees	Indv
$\mu_a$	Death rate of adult saguaros	$\frac{1}{\text{year}}$
$\phi$	Growth rate of palo verdes	$\frac{1}{\text{year}}$
$\rho$	Rate adult saguaros out-compete trees	$\frac{1}{\text{year} \cdot \text{indv.}}$
$\sigma$	Proportion of the $k_2$ carrying capacity	unitless
$\theta_i$	Frequency of buffelgrass caused wildfires and their effects on juvenile saguaros ( $\theta_j$ ), adult saguaros ( $\theta_a$ ), and trees ( $\theta_T$ )	$\frac{1}{\text{year} \cdot \text{grass}}$
$\omega$	Logistic growth term for buffelgrass population (birth-death)	$\frac{1}{\text{year}}$
$\mu_B$	Death of buffelgrass by harvesting	$\frac{1}{\text{year}}$
$k_3$	Average number of buffelgrass found in an area (one hectare)	<i>grass</i>

Table 1: Parameter definitions

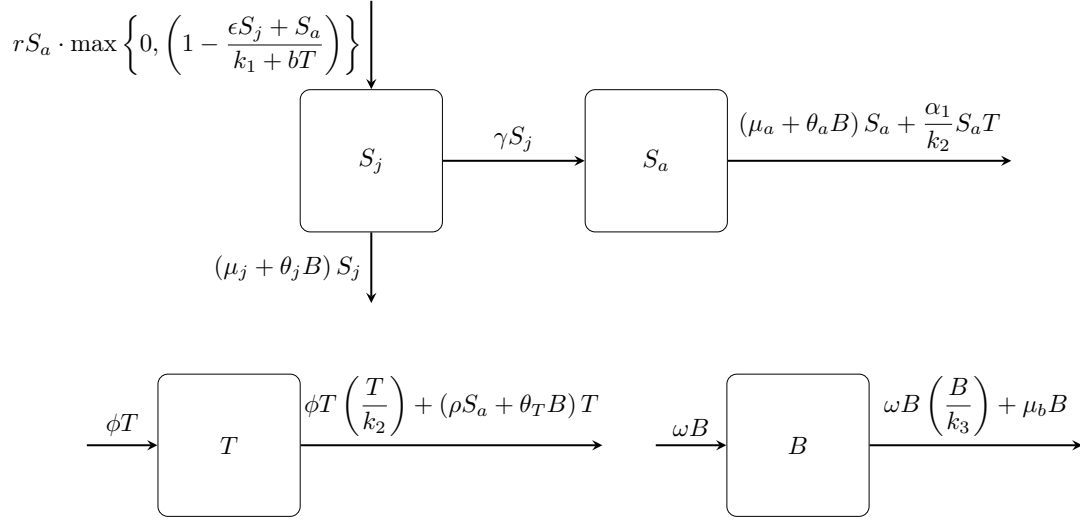


Figure 2: Flow chart diagram representing interactions between juvenile and adult saguaros, and nurse trees with the effects of buffelgrass

### 3 Analysis of the Model

In this section, the model is analyzed qualitatively by solving for equilibria and evaluating these points for stability. In order to find equilibria, the equations in System 1 are set equal to zero. These equilibria are then substituted into the Jacobian matrix, which can be found in Appendix 10.1, to study their respective stability. The simplest equation to solve is buffelgrass, 1d, as it is independent of any other state variables ( $S_j$ ,  $S_a$ , or  $T$ ). This results in the existence of two  $B^*$  equilibria. The system will be analyzed at the two equilibria according to their stability, one at buffelgrass extinction and the other is with buffelgrass presence among the population. To better analyze this model, it is important to first analyze the natural dynamics of saguaros and nurse trees, before the introduction of buffelgrass into the ecosystem. Therefore, the analysis of the model will be first performed at buffelgrass extinction equilibrium,  $B_1^* = 0$ , and then at buffelgrass existence equilibrium,  $B_2^* = k_3 \left(1 - \frac{\mu B}{\omega}\right)$ . Throughout this section, let the equilibrium points be denoted by  $E_k = (S_{jk}^*, S_{ak}^*, T_k^*, B_k^*)$ .

#### 3.1 Equilibria for Buffelgrass Extinction

For the purpose of the analysis of this section  $B_1^* = 0$ , which happens at  $\omega < \mu_b$ , and substitution the system of equations can be reduced to:

$$\frac{dS_j}{dt} = rS_a \cdot \max \left\{ 0, \left( 1 - \frac{\epsilon S_j + S_a}{k_1 + bT} \right) \right\} - \gamma S_j, \quad (3a)$$

$$\frac{dS_a}{dt} = \gamma S_j - \frac{\tilde{\alpha}_1}{k_4} S_a T, \quad (3b)$$

and

$$\frac{dT}{dt} = \tilde{\phi} T \left( 1 - \frac{T + \sigma S_a}{k_4} \right). \quad (3c)$$

### 3.1.1 Total Extinction

By setting Equation 1c equal to zero, an equilibrium value of  $T^*$  is found to be  $T^* = 0$ . Substituting  $T^* = 0$  into Equation 1b and setting the new equation equal to zero produces:

$$S_j^*(S_a) = \frac{\mu_a}{\gamma} S_a^*.$$

From here, substituting the values of  $T^*(S_a)$  and  $S_j^*(S_a)$  into Equation 1a gives  $S_a^* = 0$  as one of the equilibrium values of  $S_a$ , which also means  $S_j^* = 0$ . Using  $T^* = 0$ , then the total extinction equilibrium is found to be

$$E_1 = (S_j^*, S_a^*, T^*, B_1^*) = (0, 0, 0, 0).$$

### 3.1.2 Cacti Exclusion Equilibrium

The cacti exclusion equilibrium refers to the point with cactus population dies out, or  $(0, 0, T^*, 0)$ . Thus, if  $S_a^* = 0$ , then  $S_j^* = 0$ . To find the equilibrium value of  $T$ , when there is not total extinction, Equation 1c is set equal to zero; this gives

$$T^*(S_a) = k_2 \left( 1 - \frac{\rho}{\phi} S_a \right). \quad (4)$$

From the above Equation 4, it is important to note that for  $T^*(S_a) > 0$  (for the nurse tree population to exist, that is),  $S_a^* < \frac{\phi}{\rho}$ . Substituting in  $S_a^* = 0$  into Equation 4 above gives  $T^* = k_2$ . Therefore,

$$E_2 = (S_j^*, S_a^*, T^*, B_1^*) = (0, 0, k_2, 0).$$

### 3.1.3 Nurse Tree Exclusion Equilibrium

The nurse tree exclusion equilibrium refers to the point with nurse tree population dies out, such that  $(S_j^*, S_a^*, 0, 0)$ . Using the equilibrium values  $T^* = 0$ , and  $S_j^*(S_a) = \frac{\mu_a}{\gamma} S_a^*$ , it is possible to substitute these values into Equation 1a to get

$$r \left( 1 - \left( \frac{\frac{\epsilon \cdot \mu_a S_a^* + S_a^*}{\gamma}}{k_1} \right) \right) - \frac{(\gamma + \mu_j) \mu_a}{\gamma} = 0$$

Let  $R_{d1} = \frac{\gamma}{\gamma + \mu_j} \cdot \frac{r}{\mu_a}$  and  $E = \frac{\epsilon \cdot \mu_a}{\gamma}$ . By solving for  $S_a^*$ :

$$S_a^* = \frac{k_1 \left( 1 - \frac{1}{R_{d1}} \right)}{E + 1} \quad (5)$$

$R_{d1}$  is defined to be the threshold condition for adult saguaros existence in the absence of nurse trees. A more detailed explanation will be provided in Section 3.4. Thus,  $S_a^*$  exists as long as  $R_{d1} > 1$ . By substituting the value of  $S_a^*$  (Equation 5) into the definition of  $S_j^*$  above and using  $T^* = 0$  produces:

$$E_3 = (S_j^*, S_a^*, T^*, 0) = \left( \left( \frac{\mu_a}{\gamma} \right) \frac{k_1}{E + 1} \left( 1 - \frac{1}{R_{d1}} \right), \frac{k_1}{E + 1} \left( 1 - \frac{1}{R_{d1}} \right), 0, 0 \right).$$

Therefore,  $E_3$  exists if  $R_{d1} > 1$ .

### 3.1.4 Coexistence Equilibrium

The coexistence equilibrium,  $E_4 = (S_j^*, S_a^*, T^*, 0)$  represents when all species live in the same environment and share the same space and resources, with  $T^* \neq 0$ , thus:  $T^*(S_a^*) = k_2 \left( 1 - \frac{\rho}{\phi} S_a^* \right)$ .

Which, by requiring  $0 < \frac{\rho}{\phi} S_a^* < 1$ , can be rescaled by letting  $s_a^* = \frac{S_a^*}{\phi/\rho}$ . Hence,  $0 < s_a^* < 1$  and the rest of the equations in terms of  $s_a^*$  can be found.

$$T^*(s_a^*) = k_2(1 - s_a^*) \rightarrow T^* > 0 \text{ iff } \frac{S_a^*}{\phi/\rho} < 1$$

$$S_j^*(s_a^*) = \frac{\phi}{\rho} \left( \frac{\mu_a + \alpha}{\gamma} \right) s_a^* - \frac{\phi\alpha}{\rho\gamma} s_a^{2*}$$

Now, solving for  $s_a^*$  and letting  $R_{d2} = \frac{r}{\mu_a + \alpha} \cdot \frac{\gamma}{\gamma + \mu_j}$  produces:

$$0 = r \frac{\phi}{\rho} s_a^* \left[ 1 - \frac{\frac{\phi}{\rho} (s_a^* (\frac{\epsilon\mu_a}{\gamma} + 1 + \frac{\alpha}{\gamma}) - s_a^{2*} \frac{\epsilon\alpha}{\gamma})}{k_1 + bk_2(1 - s_a^*)} \right] - \frac{\phi}{\rho} \left( \frac{1}{R_{d2}} - \frac{\alpha s_a^*}{\mu_a R_{d1}} \right).$$

Where  $R_{d2}$  is defined to be the demographic threshold condition for adult saguaros in the presence of nurse trees. Setting  $E = \frac{\mu_a\epsilon}{\gamma}$  allows the equation to reduce to:

$$0 = \left( \frac{\alpha\phi\epsilon}{\rho\gamma} - \frac{bk_2\alpha}{\mu_a R_{d1}} \right) s_a^{2*} + \left[ (k_1 + bk_2) \frac{\alpha}{\mu_a R_{d1}} - bk_2 \left( 1 - \frac{1}{R_{d2}} \right) - \frac{\phi}{\rho} \left( 1 + E + \frac{\epsilon\alpha}{\gamma} \right) \right] s_a^* + (k_1 + bk_2) \left( 1 - \frac{1}{R_{d2}} \right).$$

Then, let

$$\begin{aligned} \tau_1 &= \left( \frac{\alpha\phi\epsilon}{\rho\gamma} - \frac{bk_2\alpha}{\mu_a R_{d1}} \right), \\ \tau_2 &= \left[ (k_1 + bk_2) \frac{\alpha}{\mu_a R_{d1}} - bk_2 \left( 1 - \frac{1}{R_{d2}} \right) - \frac{\phi}{\rho} \left( 1 + E + \frac{\epsilon\alpha}{\gamma} \right) \right], \text{ and} \\ \tau_3 &= (k_1 + bk_2) \left( 1 - \frac{1}{R_{d2}} \right), \end{aligned}$$

such that

$$f(s_a^*) = \tau_1 s_a^{2*} + \tau_2 s_a^* + \tau_3.$$

Notice that  $f(0) = \tau_3$ , and that  $\tau_3 > 0$  iff  $R_{d2} > 1$ . Also,  $f(1) = k_1 \left( 1 - \frac{1}{R_{d1}} \right) - \frac{\phi}{\rho} (1 + E)$  is less than zero iff  $\frac{\phi}{\rho} > \frac{k_1}{1+E} \left( 1 - \frac{1}{R_{d1}} \right)$ . In showing there exists at least one positive root of  $f\left(\frac{S_a^*}{\phi/\rho}\right)$  between 0 and 1. Meaning coexistence is possible if there is cactus population growth and the rate at which trees are out competed by cacti is less than the population growth rate of trees, more details can be found in Section 3.3. The following theorem can be concluded:

**Theorem 1** *If  $R_{d2} > 1$  and  $\frac{\phi}{\rho} > \frac{k_1}{1+E} \left( 1 - \frac{1}{R_{d1}} \right)$ , then there exists at least one coexistence equilibrium.*

## 3.2 Stability Analysis of the Equilibria with Buffelgrass Extinction

At  $B^* = 0$ , one of the eigenvalues from the general Jacobian matrix at  $B_1^* = 0$  will be  $\omega - \mu_b$ . For  $\omega < \mu_b$  the following stability analysis was found:

### 3.2.1 Total Extinction

The total extinction equilibrium point,  $E_1$ , is  $(0, 0, 0, 0)$ . The Jacobian at this point is given by Matrix 11 with zero substituted in for all of the state variable. The value of  $\phi$  is an eigenvalue of this matrix, and  $\phi$  is always positive. Therefore the equilibrium point for the extinction of all populations is unstable.



### 3.2.2 Cactus Exclusion Equilibrium

Next, the cactus exclusion equilibrium is analyzed. From this analysis, the following theorem is produced.

**Theorem 2** *If  $R_{d2} = \frac{r}{(\mu_a + \alpha_1)} \frac{\gamma}{(\mu_j + \gamma)} < 1$ , that is, if adult saguaros are producing less than one future adult saguaro throughout their lifetime, then there exists one **stable** equilibrium point where the saguaros have gone extinct, that is  $E_2 = (0, 0, k_2, 0)$ .*

**Proof** In order to test for local stability, the Jacobian matrix must be applied to the point,  $E_2 = (0, 0, k_2, 0)$ . From the Jacobian, it is evident that one eigenvalue is  $\lambda = -\phi$ , which is always negative. The remaining eigenvalues can be found with the characteristic polynomial:

$$\begin{aligned} (\lambda + (\gamma + \mu_j))(\lambda + (\alpha_1 + \mu_a)) - r\gamma &= 0 \\ \lambda^2 + (\alpha_1 + \mu_a + \gamma + \mu_j)\lambda + r\gamma \left( \frac{1}{R_{d2}} - 1 \right) &= 0 \end{aligned}$$

Here it can be observed that since parameter values will always be positive,  $m = (\gamma + \alpha + \mu_a + \mu_j)$  will always be positive. Additionally,  $g = r\gamma \left( \frac{1}{R_{d2}} - 1 \right)$  is greater than zero if and only if  $R_{d2} < 1$ . Since  $R_{d2} < 1$  is assumed and the analysis of the two remaining eigenvalues goes as follows:

$$\lambda_{2,3} = \frac{-m \pm \sqrt{m^2 - 4g}}{2}$$

Since  $m > 0$  and  $g > 0$ , then

$$\sqrt{m^2 - 4g} < m.$$

So,  $\lambda_2$  and  $\lambda_3$  will always be negative.

### 3.2.3 Nurse Tree Exclusion Equilibrium

The nurse tree exclusion equilibrium,  $E_3$ , was found to be  $E_3 = \left( \frac{\mu_a}{\gamma} S_a^*, S_a^*, 0, 0 \right)$ , where

$$S_j^* = \frac{\mu_a}{\gamma} \left( \frac{\gamma k_1}{\epsilon \mu_a + \gamma} \right) \left( 1 - \frac{1}{R_{d1}} \right)$$

and

$$S_a^* = \left( \frac{\gamma k_1}{\epsilon \mu_a + \gamma} \right) \left( 1 - \frac{1}{R_{d1}} \right).$$

That is,  $E_3$  exists as long as  $R_{d1} > 1$ .

**Theorem 3** *If  $\frac{\phi}{\rho} < \frac{k_1}{1 + \frac{\epsilon \cdot \mu_a}{\gamma}} \left( 1 - \frac{1}{R_{d1}} \right)$  and  $R_{d1} > 1$ , then the nurse tree extinction equilibrium,  $E_3 = (S_j^*, S_a^*, 0, 0)$ , is locally asymptotically stable.*

**Proof:**

Let  $E = \frac{\epsilon \mu_a}{\gamma}$  and  $S_{a2}^* = \frac{k_1}{E + 1} \left( 1 - \frac{1}{R_{d1}} \right)$ . Assume  $\frac{\phi}{\rho} < \frac{k_1}{1 + E} \left( 1 - \frac{1}{R_{d1}} \right)$  and  $R_{d1} > 1$  the Jacobian Matrix can be found in 11:

In order for  $\lambda_1$  to be negative:  $S_a^* > \frac{\phi}{\rho}$ . By substituting  $S_a^*$ ,  $\frac{\phi}{\rho} < \frac{k_1}{1 + \frac{\epsilon \cdot \mu_a}{\gamma}} \left( 1 - \frac{1}{R_{d1}} \right)$ , which requires  $R_{d1} > 1$ .

$\lambda_1$  and  $\lambda_2$  are given by the following:

$$\left( \lambda + \frac{\epsilon r}{k_1} S_a^* + (\mu_j + \gamma_j) \right) (\lambda + \mu_a) - \left( \gamma_j r \left( 1 - \frac{S_a^*(2 + E)}{k_1} \right) \right) = 0$$

By substituting  $S_a^*$ ,

$$\lambda^2 + \lambda F + L = 0$$

Where  $F = \left[ \mu_a + \epsilon r \left( \frac{1}{1+E} \left( 1 - \frac{1}{R_{d1}} \right) \right) + \mu_j + \gamma_j \right]$  and  $L = \mu_a \epsilon r \left( \frac{1}{1+E} \left( 1 - \frac{1}{R_{d1}} \right) \right) + \mu_a (\mu_j + \gamma) - \gamma r \left( 1 - \frac{2+E}{1+E} \right) \left( 1 - \frac{1}{R_{d1}} \right)$

Then  $F$  and  $L$  are greater than zero when  $R_{d1} > 1$  and  $S_a^* > \frac{\phi}{\rho}$ . Hence,  $E_3$  is locally asymptotically stable when  $R_{d1} > 1$  and  $S_a^* > \frac{\phi}{\rho}$ , more details of this can be found in Section 3.3.

### 3.2.4 Coexistence Equilibrium

Although the stability of the coexistence equilibrium was not determined analytically, stability was determined numerically using the baseline parameter values given in Table 4. This numerical analysis found the equilibrium point to be unstable. This is because for our baseline parameters the growth rate for buffelgrass is greater than the harvesting rate,  $\mu_B < \omega$ . Therefore, since buffelgrass is not affected by any of the other state variables, the buffelgrass population will always begin to increase if introduced to a system. However, if the harvesting rate were to surpass the growth rate  $\mu_B > \omega$ , the equilibrium point would be stable.

## 3.3 Biological Definitions of Stability Conditions

From analyzing the stability of equilibrium points for the case of the model without buffelgrass, conditions necessary for the survival of saguaros were found to include the following two expressions.

$$R_{d1} = \frac{r}{\mu_a} \cdot \frac{\gamma}{\gamma + \mu_j} \quad (6a)$$

$$R_{d2} = \frac{r}{\alpha_1 + \mu_a} \cdot \frac{\gamma}{\gamma + \mu_j} \quad (6b)$$

The value of  $R_{d1}$  (Equation 6a) represents the survival of saguaros in the absence of nurse trees. The term  $\frac{r}{\mu_a}$  gives the growth rate of the juvenile saguaro population multiplied by the average life span of an adult saguaro in the absence of nurse trees. The term  $\frac{\gamma}{\gamma + \mu_j}$  gives the proportion of juveniles that will survive to reproduce. Therefore,  $R_{d1}$  gives the expected number of new adult saguaros produced by one adult saguaro in the absence of nurse trees. This number must be greater than one for the survival and growth of the saguaro population.

The value of  $R_{d2}$  (Equation 6b) represents the survival of saguaros in the presence of nurse trees, so the competition between adult saguaros and nurse trees is taken into account. Therefore,  $\alpha_1$  is added to the adult death rate in the denominator of the equation for  $R_{d2}$ .

The condition necessary for saguaros to out-compete nurse trees and drive the tree population to extinction is given by:

$$\frac{\phi}{\rho} < \frac{k_1}{1 + \frac{\epsilon \cdot \mu_a}{\gamma}} \left( 1 - \frac{1}{R_{d1}} \right). \quad (7)$$

In the inequality, 7, the term  $\frac{\phi}{\rho}$  gives growth rate of trees multiplied by the average life span of trees with consideration of competition between with adult saguaros. The term  $\frac{k_1}{1 + \frac{\epsilon \cdot \mu_a}{\gamma}}$  can

be simplified to the form  $\frac{k_1 \gamma}{\gamma + \epsilon \mu_j}$ , which gives the proportion of the carrying capacity of saguaros that will be taken up by juveniles becoming adults. Furthermore, from Equation 6a, it is known that  $R_{d1}$  must be greater than one for the survival of saguaros without nurse trees. Therefore, the inequality expressed in Equation 7 means that trees will become extinct if the overall growth of

trees is less than that of saguaros. However, for the coexistence equilibrium to exist, the overall growth of the nurse trees is higher than that of the saguaros and  $R_{d2} > 1$ .

### 3.4 Equilibria at Buffelgrass Existence Equilibrium

Using the  $B_2^* = k_3 \left(1 - \frac{\mu_B}{\omega}\right)$  equilibrium value for  $B^*$  only slightly changes the equilibria expressions for the saguaro and nurse tree populations from the  $B_1^* = 0$  case. From the equilibrium expression for buffelgrass survival equilibrium, it can be seen that  $B_2^*$  is the equilibrium value of buffelgrass if and only if  $\omega > \mu_B$ .

It is worth noting that buffelgrass itself is not directly affected by the saguaros or nurse trees, so similarities to the previously found equilibria are expected. These new equilibria values are in the form  $E_5 = (0, 0, 0, B_2^*)$ ,  $E_6 = (0, 0, T^*, B_2^*)$ ,  $E_7 = (S_j^*, S_a^*, 0, B_2^*)$ , and  $E_8 = (S_j^*, S_a^*, T^*, B_2^*)$ . One way to find these new equilibrium values is to modify certain parameters to reduce the complexity of the equilibria. death rate for juvenile saguaros,  $\mu_j$ , which will now be referred to as  $\tilde{\mu}_j$ , can be defined; in order to eliminate the effects of buffelgrass, by letting

$$\tilde{\mu}_j = \mu_j + B\theta_j. \quad (8)$$

The substitution of the expression 8 for  $\mu_j$  will provide the same dynamics as the model without buffelgrass. Notice that the buffelgrass equation is independent of the three populations,  $S_j$ ,  $S_a$ , and  $T$ , which makes the substitution possible. Similarly, we can define the following three new parameters: the adult saguaro death rate,  $\tilde{\mu}_a = \mu_a + B\theta_a$ , the growth rate of the trees,  $\tilde{\phi} = 1 - \frac{\theta_T B}{\phi}$ , and an adjusted carrying capacity,  $k_4 = k_2 \tilde{\phi}$ . The new parameter  $k_4$  will have a different meaning than  $k_2$  which was originally used as the carrying capacity of nurse trees and saguaros in the competition term. In order to justify the use and substitution of  $k_4$ , it is important to analyze the presence of  $k_2$  in the model.

The only other time  $k_2$  is used, apart from the competition term in the tree differential equation, is in the term  $\frac{T\alpha_1 S_a}{k_2}$  which is a part of the adult saguaro differential equation. Multiplying the term,  $\frac{T\alpha_1 S_a}{k_2}$ , by  $\frac{\tilde{\phi}}{\phi}$  produces  $k_4$  in the denominator. However, the numerator is also changed into something that does not exactly match the original model:  $T S_a \alpha_1 \tilde{\phi}$ . Since  $\alpha_1$  only occurs here, it can also be replaced. The term  $\alpha_1$  is replaced by  $\tilde{\alpha}_1 = \tilde{\phi} \alpha_1$ . The substitution of  $k_4$  and  $\tilde{\alpha}_1$  produces:

$$\frac{T S_a \alpha_1}{k_2} = \frac{T S_a \tilde{\alpha}_1}{k_4}.$$

Substituting  $\tilde{\mu}_j$ ,  $\tilde{\mu}_a$ ,  $\tilde{\phi}$ ,  $k_4$ , and  $\tilde{\alpha}_1$  into the model reduces System 1, the model with the inclusion of buffelgrass at  $B_2^* = k_3 \left(1 - \frac{\mu_B}{\omega}\right)$  equilibrium, where  $\omega > \mu_B$ , to the following system:

$$\frac{dS_j}{dt} = r S_a \cdot \max \left\{ 0, \left(1 - \frac{\epsilon S_j + S_a}{k_1 + bT}\right) \right\} - \gamma S_j - \tilde{\mu}_j S_j, \quad (9a)$$

$$\frac{dS_a}{dt} = \gamma S_j - \frac{\tilde{\alpha}_1}{k_4} S_a T - \tilde{\mu}_a S_a, \quad (9b)$$

$$\text{and } \frac{dT}{dt} = \tilde{\phi} T \left(1 - \frac{T + \sigma S_a}{k_4}\right). \quad (9c)$$

Because this system is now similar to System 3, the demographic reproductive numbers can be redefined using the substituted parameter values.

$$R_{d3} = \frac{r}{\tilde{\mu}_a} \cdot \frac{\gamma}{\gamma + \tilde{\mu}_j} \quad (10a)$$

$$R_{d4} = \frac{r}{\tilde{\alpha}_1 + \tilde{\mu}_a} \cdot \frac{\gamma}{\gamma + \tilde{\mu}_j} \quad (10b)$$

Analysis of the equations in System 9 at equilibrium produce eight possible scenarios. The scenarios where buffelgrass is excluded are the same as the equilibria described in Section 3. With buffelgrass, there are additional cases. These include the case when saguaros die out, but trees are able to coexist with buffelgrass, the case when nurse trees die out, but saguaros coexist with buffelgrass, and the case when all three species are able to coexist. As in Section 3, there are two possible coexistence equilibria. However, after numerical analysis only one is shown to exist with the current parameter values.

The result of existence and stability analysis, given in Table 2, found that coexistence with buffelgrass is possible with nurse trees without saguaros if  $R_{d4} < 1$ , or each adult saguaro is producing less than one new adult saguaro in its lifetime, and that  $\omega > \mu_B$ , or that the buffelgrass growth rate is greater than the rate at which it is harvested. Furthermore, the coexistence of buffelgrass with saguaros with the exclusion of nurse trees can occur if  $R_{d3} > 1$ , meaning each adult saguaro produces more than one new adult, and  $\frac{\tilde{\phi}}{\rho} < \frac{k_1}{1 + \tilde{E}} \left(1 - \frac{1}{R_{d3}}\right)$ , which says that saguaros are able to grow and out-compete trees at a faster rate than trees are able to grow. For coexistence of all three species, the condition for saguaros to out-compete trees must not be true, and saguaros must reproduce at a high enough rate to propagate the population. However, saguaro equilibrium value must be small enough for  $S_a^* < \frac{\phi}{\rho}$ , or the saguaro population must be small enough to not out-compete nurse trees.

Equilibria and Stability			
	Equilibrium	Existence	Stability
$B_1^* = 0$	$E_1 = (0, 0, 0, 0)$	always	Unstable
	$E_2 = (0, 0, T_2^*, 0)$	always	$R_{d2} < 1$ and $\omega < \mu_B$
	$E_3 = (S_{j3}^*, S_{a3}^*, 0, 0)$	$R_{d1} > 1$	$\frac{\phi}{\rho} < \frac{k_1}{1 + \tilde{E}} \left(1 - \frac{1}{R_{d1}}\right)$ and $\omega < \mu_B$
	$E_4 = (S_{j4}^*, S_{a4}^*, T_4^*, 0)$	$S_a^* < \frac{\phi}{\rho}$ and $R_{d2} > 1$	Unstable(numerical)
$B_2^* = k_3 \left(1 - \frac{\mu_B}{\omega}\right)$	$E_5 = (0, 0, 0, B_2^*)$	always	unstable
	$E_6 = (0, 0, T_2^*, B_2^*)$	always	$R_{d4} < 1$ and $\omega > \mu_B$
	$E_7 = (S_{j7}^*, S_{a7}^*, 0, B_2^*)$	$R_{d3} > 1$	$\frac{\tilde{\phi}}{\rho} < \frac{k_1}{1 + \tilde{E}} \left(1 - \frac{1}{R_{d3}}\right)$ and $\omega > \mu_b$
	$E_8 = (S_{j8}^*, S_{a8}^*, T_8^*, B_2^*)$	$R_{d4} > 1$ and $\frac{\phi}{\rho} > \frac{k_1}{1 + \tilde{E}} \left(1 - \frac{1}{R_{d3}}\right)$	Stable (numerical)

Table 2: Provides the existence and stability criteria for the equilibria points of System 1, and 9.

## 4 Parameter Estimation

In this section, a review of literature was conducted in order to obtain values for parameters of interest. Although many of the exact values of the parameters were not able to be found, some of the parameters were estimated from the literature, and others were based on assumptions. These values given in Table 4 are used as the baseline parameters in model simulations.

- *Rate that seeds are germinated and survive to one year,  $r$ :*

According to the Western National Parks Association a saguaro can produce up to 375000 seeds per year [12]. Steenbergh and Lowe [13] estimated that around 0.1% of the seeds were able to establish and survive. Therefore there are only 375 seedlings per adult saguaro. Additionally, [13] mentions that the proportion of the germinated seeds that survive to be a year is only 0.0126. Therefore,  $r$  is computed to be 375 times 0.0126 = 4.725 juveniles/(adults\*time), which equals juveniles/time when multiplied by  $S_a$  in Equation 3a.

- *Proportion of space taken up by juvenile saguaros compared to adult saguaros,  $\epsilon$ :*  
Saguaro root systems are laterally extensive and shallow [1]. The root system of the saguaro can stretch out in all directions as long as the saguaro's height [14]. In our study juvenile saguaros measure up to 3.7 m, and adult saguaros measure from 3.71 m to 18 m. This means the root radius is up to 3.7 m for juveniles and between 3.71 m and 18 m for adults. Hence the average root radius of a juvenile is 1.85 m, and the average root radius of an adult is 5.5 m. Calculating the area for the roots for the juvenile and adult yields  $(1.85)^2\pi$  and  $(5.5)^2\pi$ , respectively from the area of a circle equation  $\pi r^2$ . To obtain the parameter value the juvenile radius area is divided by the adult radius area = 0.113.
- *Number of adult saguaros that can survive in a given space,  $k_1$ :*  
A census at the Ironwood Forest National Monument showed that there could be more than 250 saguaros per hectare [15]. For the simulation the value 250 will be used as their carrying capacity.
- *Average number of juveniles that survive under a nurse tree per tree,  $b$ :*  
From the total population of nurse trees, only trees older than 20 years old can be able to nurse a juvenile saguaro successfully [16]. Assuming the ages of the nurse tree population are evenly distributed, meaning there are equally as many trees at each age in their lifespan, then with an average life span of 100 years, 20% of the nurse tree population cannot host a juvenile saguaro, thus  $1 - 0.20 = 0.8$ . Additionally, this study assumes the average for a juvenile to survive under a nurse tree is 1. Hence, 0.8 is our  $b$  value.
- *Rate that juveniles become adults,  $\gamma$ :*  
According to information from the Saguaro National Park, the saguaro starts to produce flowers at the age of 35 [17], and this study considers the saguaro an adult once is able to reproduce. Hence our  $\gamma$  value is  $1/35 \text{ yr.}^{-1}$ .
- *Death rate of juveniles per year,  $\mu_j$ :*  
In Orum's study [8], it was found that 50% of the juvenile saguaro classes died over a 12-year span. Therefore, the  $\mu_j$  value is  $0.5/12 \text{ yr.}^{-1}$ .
- *Rate at which trees out-compete saguaros,  $\alpha_1$ :*  
In order to incorporate the competition between adult saguaros and nurse trees, it was necessary to consider the case where trees out-compete the saguaros. From the literature, it was found that as the saguaro grows older, it kills its nurse tree. Therefore, the probability that a tree out-competes the saguaro is very small. Hence it is assumed  $\alpha_1$  value is  $1 \times 10^{-6} \text{ yr.}^{-1}$ .
- *Average number of adult saguaros and nurse trees found in one hectare,  $k_2$ :*  
From the  $k_1$  parameter, it is known that there are 250 adult saguaros per hectare. During the literature review, ranges between 315 [15] and 1100 were found for palo verde trees [6]. The value of  $k_1$ , 250, was added to the two new values, which yields a range from 565 to 1350 for  $k_2$ . Although there is potential for variation, it was decided to create an average of these quantities to better represent this in the model. Thus 565 plus 1350 divided by 2 = 957.5 per hectare.
- *Death rate of adults per year,  $\mu_a$ :*  
A saguaro has a life span of 150 to 200 years [17]. For consistency, the adult class in the model can live from 115 to 165 years. The average of 115 and 165 is calculated, which is 140. Therefore the death rate of an adult saguaro is  $1/140 \text{ yr.}^{-1}$ .
- *Logistic growth term for palo verde population,  $\phi$ :*  
Pavek [6] found in her research that additions of palo verde are naturally very slow. Only two new trees have been registered in the past 30 years. Hence, 2 divided by 30 =  $0.07 \text{ yr.}^{-1}$  for the value of  $\phi$ .
- *Rate that trees die due to competition with saguaros,  $\rho$ :*  
Orum [8] found in his study that there was a high survival rate to freezes of saguaros under 80 years of age. This suggests that they are still protected by a nurse tree. Then, 80 minus 35=45 years is time the competition between adult saguaros and trees exists. So, the rate at which there is a competition is  $1/45$ . Furthermore, a nurse tree can live up to 100 years, then

1/100 is the natural death rate of the tree [18]. To calculate  $\rho$  the value of  $b$ , the average number of juveniles that survive under nurse trees, will also be needed. Therefore, we have 1/45 times 1/100 times 0.8 ( $yr \cdot indiv$ )<sup>-1</sup>.

- *Proportion of the carrying capacity,  $\sigma$ :*  
To calculate this unitless parameter value, from the logistic growth term in Equation 3c,  $\rho$  and  $k_2$  were multiplied and divided by  $\phi$ ,  $\sigma = \frac{k_2 \cdot \rho}{\phi}$ . Thus, the value of  $\sigma$  is 2.432.
- *Frequency of buffelgrass caused wildfires and their effects on juvenile saguaros,  $\theta_j$ :*  
In this model it was assumed the mortality rate of juvenile saguaros in a fire is 1 in the event of a fire. Buffelgrass can be 1.5 m tall [19]. The fire can spread from shrub to shrub if the distance between them is less than two times their height, then if buffelgrass is less than 3 m apart, then fire will spread [20]. Taking this into consideration, 10,000m<sup>2</sup> (1 hectare) divided by 9m<sup>2</sup> (space needed per shrub) equals 1111.111 shrubs. Hence, approximately 1,111 shrubs of buffelgrass is required for fire to spread in the given area. Additionally, fires in the Sonoran Desert were uncommon, only burning about once every 250 years [21]. Now, data shows that there have been an increase of 0.27% of burned land in 2000-2014 compared to 1984-1999 [22], which by subtracting by .0027 gives a frequency of about 0.997. Therefore, 1 divided by the product of 1111, 250 and 0.997 = 0.00000361.
- *Frequency of buffelgrass caused wildfires and their effects on adult saguaros,  $\theta_a$ :*  
In Esra Büyüktaktakin study, it was found that after a fire, 68% to 85% of saguaros die, with an average of 75% [23]. Doing similar calculations done for  $\theta_j$ , we have .75 divided by the product of 1111, 250 and 0.997 = 0.00000271.
- *Frequency of buffelgrass caused wildfires and their effects on trees,  $\theta_t$ :*  
In McLaughlin and Bowers study it was found that palo verde trees would have a 63% palo verde trees in an area where a fire has occurred die after the fire [24]. Because of this, we assume that the mortality rate due to fire is .63 yr<sup>-1</sup>. Doing similar calculations done for  $\theta_j$ , we have .63 divided by the product of 1111, 250 and 0.997 = 0.00000227.
- *Logistic growth term for buffelgrass population (birth-death),  $\omega$ :*  
According to the information from the National Park Service Buffelgrass fact sheet, buffelgrass has a increasing annual rate of 35% [10]. Hence, the value of  $\omega$  is 0.35.
- *Death by harvesting,  $\mu_B$ :*  
According to the information from the Saguaro National Park website, it takes three years of biannual visits to clear a plot of buffelgrass by harvesting [9]. Therefore  $\mu_B$  value is 1/3 yr<sup>-1</sup>.
- *Average number of buffelgrass found in an area (one hectare),  $k_3$ :*  
In Esra Büyüktaktakin study, it was estimated that there could be up to 6 plants of buffelgrass per m<sup>2</sup> [23]. Since this model is doing the study over one hectare, then we have 60,000 buffelgrass plants per hectare.

Parameter	Description	Units	Value	Reference
$r$	Germination rate of saguaros	$\frac{indv}{year}$	4.725	[12, 13]
$\epsilon$	Conversion of juveniles to adults in terms of space	unitless	0.113	[1, 14]
$k_1$	Adult saguaro carrying capacity	indv	250	[15]
$b$	Average juveniles under nurse tree	indv	0.8	[16]
$\gamma$	Saguaro maturation rate	$\frac{1}{year}$	$\frac{1}{35}$	[17]
$\mu_j$	Juvenile death rate	$\frac{1}{year}$	$\frac{0.5}{12}$	[8]
$\alpha_1$	Rate nurse trees out-compete saguaros	$\frac{1}{year}$	$1 \times 10^{-6}$	assumed
$k_2$	Approximate carrying capacity of adults and nurse trees	indv	957.5	[15, 6]
$\mu_a$	Death rate of adult saguaros	$\frac{1}{year}$	$\frac{1}{140}$	[17]
$\phi$	Growth rate of palo verdes	$\frac{1}{year}$	0.07	[6]
$\rho$	Rate adult saguaros out-compete trees	$\frac{1}{year \cdot indv}$	$\frac{0.8}{45 \cdot 100}$	[8, 18, 16]
$\sigma$	Proportion of the carrying capacity	unitless	$\frac{\rho \cdot k_2}{\phi} = 2.432$	[8, 18, 16, 15, 6]
$\theta_j$	Juvenile saguaro wildfire death rate	$\frac{1}{year \cdot grass}$	$3.61 \times 10^{-6}$	[19, 20, 21, 22]
$\theta_a$	Adult saguaro wildfire death rate	$\frac{1}{year \cdot grass}$	$2.71 \times 10^{-6}$	[23, 19, 20, 21, 22]
$\theta_t$	nurse trees wildfire death rate	$\frac{1}{year \cdot grass}$	$2.27 \times 10^{-6}$	[24, 19, 20, 21, 22]
$\omega$	Growth rate of buffelgrass	$\frac{1}{year}$	.35	[10]
$\mu_B$	Harvesting rate of buffelgrass	$\frac{1}{year}$	$\frac{1}{3}$	[9]
$k_3$	Carrying capacity of buffelgrass	indv	60,000	[23]

Table 4: Model Parameters

## 5 Population Dynamics between only Saguaros and Nurse Trees at Buffelgrass Extinction Equilibrium

In order to determine how an invasion of buffelgrass will affect the life cycle of saguaros and their nurse trees, it is necessary to first examine the dynamics of the saguaros and nurse trees without buffelgrass, that is at the  $B^* = 0$  equilibrium, where  $\omega < \mu_B$ . The dynamics seen in Figure 3 show that when left to their natural life cycle, saguaros and nurse trees will coexist. In the figure, the equilibrium population values are not used, so transitional dynamics can be seen. The juvenile saguaro population increases to a point where it can no longer be supported by the environment and then begins to decline. The adult population then increases as a result of the juveniles aging to  $S_a$ , or adulthood. The juvenile population has such a drastic increase because of the high germination rate. The subsequent peak in the adult population is smaller than that in the

juvenile population, because juvenile also have a higher mortality rate than adults. The juvenile population eventually decreases to zero because adults are taking up all the available space. Once the adult population declines to a certain level, there is now room for new juvenile saguaros, so the juvenile population is able to increase. Because of competition, as the adult saguaro population increases, the tree population decreases, but begins to increase once the adult saguaro population has decreased to a certain level. Although the tree population appears to die out, it does not. The minimum value for  $T$  in Figure 3 is actually about  $T = 3$ . Eventually, all three populations are able to coexist. This is because the parameter values used in this simulation satisfy the conditions for coexistence and stability given in the analysis section. The simulation is calculated over a span of 500 years in order to account for the long lifespans of palo verdes and saguaros, which are about 100 and 175, respectively.

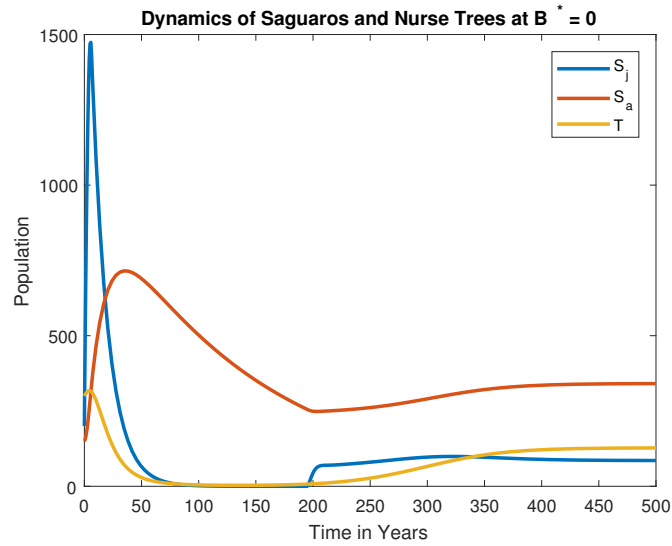


Figure 3: Dynamics of the system at  $B^* = 0$  with the baseline parameter values found in Table 4 and the initial conditions  $(S_j, S_a, T) = (200, 150, 300)$ , which are used throughout the simulations. The sudden increase around year 200 in the juvenile saguaro population is due to max function in Equation 1a.

In the sensitivity analysis in Section 7, the dynamics of the tree and saguaro populations without buffelgrass are studied with respect to changes to the logistic growth for the palo verde population ( $\phi$ ), the rate of tree death due to competition with saguaros ( $\rho$ ), the average number of juveniles that survive under a nurse tree ( $b$ ), and the rate that seeds are germinated and survive to one year ( $r$ ). However, the only parameters from this list that could reasonably be changed in the real-world are  $\phi$ , the growth rate of trees, and  $r$ , the growth rate of juvenile saguaros. Each of these rates could be increased by planting new trees or saguaros.



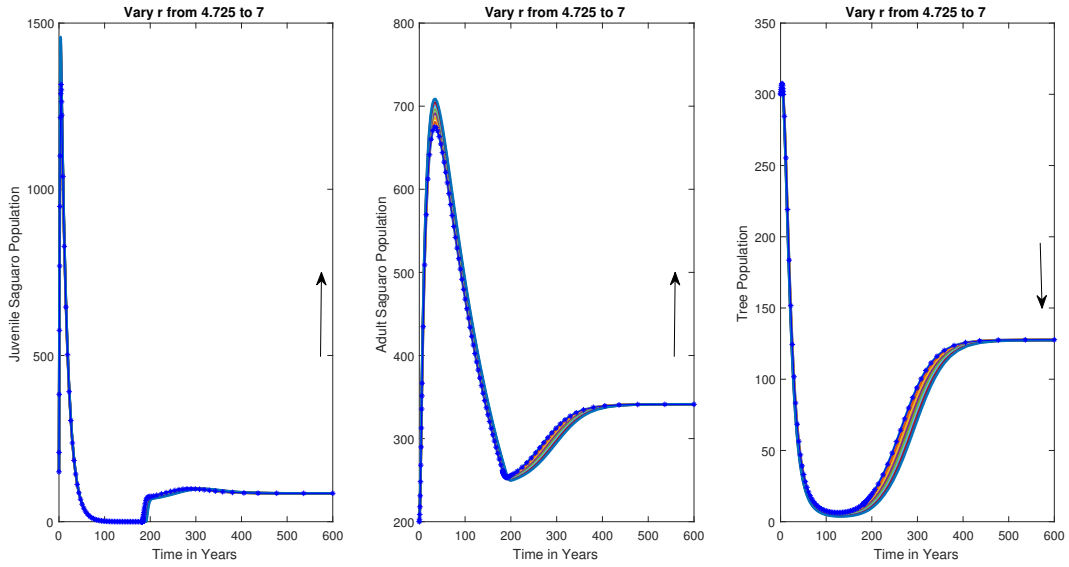


Figure 4: The dotted blue line represents the baseline case for the parameters, given in Table 4. The arrows represent the direction that values of the equilibrium populations are changing as  $r$  is decreased.

In Figure 4, as  $r$  is increased, the  $S_j$  and  $S_a$  populations at coexistence for equilibria are increased, but not by much. The value at equilibrium for the nurse tree population,  $T$ , is slightly decreased, because an increased  $S_a$  population increases the competition faced by trees. It can be inferred that trying to increase the saguaro population by increasing the growth rate is not an effective strategy. However, varying  $\phi$  has a greater effect.

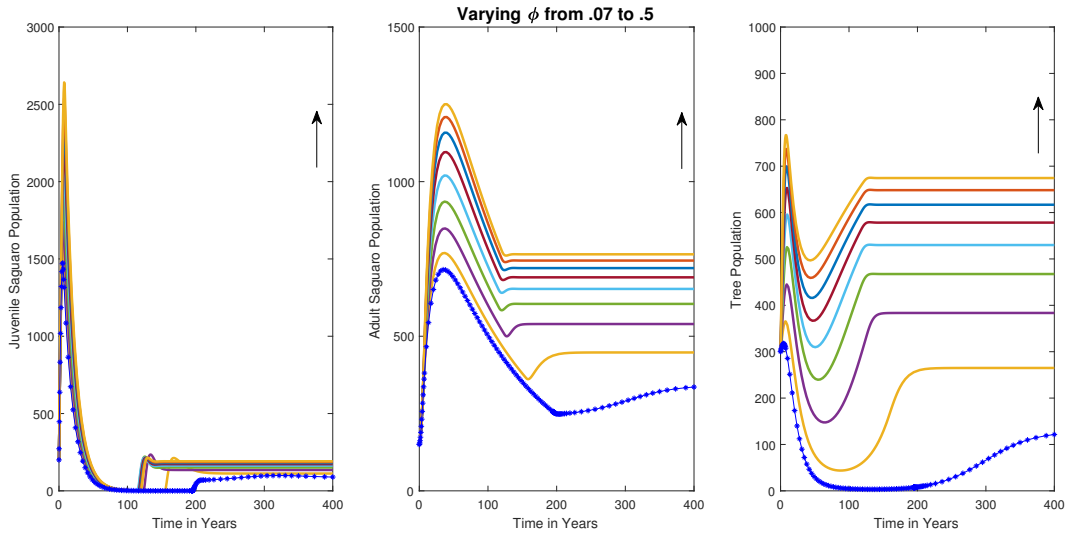


Figure 5: The dotted blue line represents the baseline case for the parameters, given in Table 4. As  $\phi$  is increased, the final values for the populations  $S_j$ ,  $S_a$ , and  $T$  also increase.

From Figure 5, it can be inferred that increasing  $\phi$  in order to increase the saguaro population would be an effective strategy. This could be achieved through volunteers planting trees. Changing  $\phi$  can also be thought of as having the same effect as changing  $b$ , because increasing  $\phi$  increases the nurse tree population, which increases the term  $bT$ . Since  $bT$  increases the carrying capacity

of juvenile saguaros, increasing this term results in a greater saguaro population.

## 6 Population Dynamics at Buffelgrass Existence Equilibrium

The effects of buffelgrass on the saguaro cacti and palo verde populations were incorporated in the  $\theta$  terms in the model of Section 2. These terms capture the death of saguaros by wildfire by averaging out the deaths over the frequency of wildfires to get a constant term.

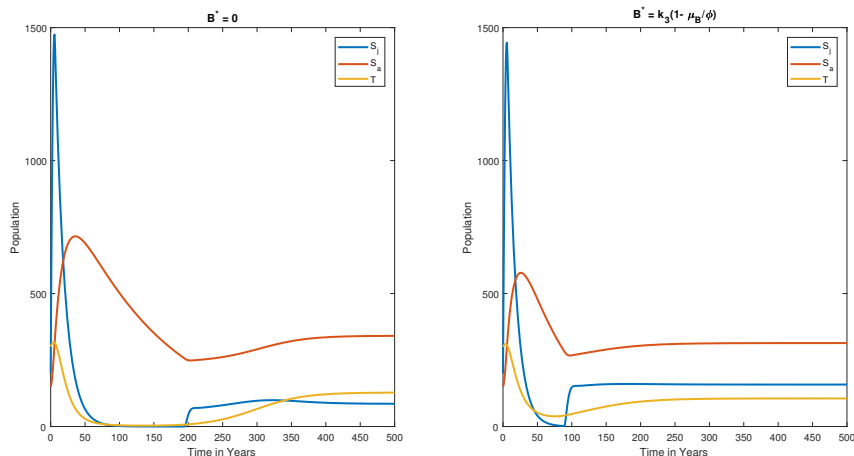


Figure 6: This figure compares the population dynamics of the saguaros and nurse trees at  $B_1^* = 0$  (left) and  $B_2^* = k_3 \left(1 - \frac{\mu_B}{\omega}\right)$  (right).

To show the dynamics of the populations, the buffelgrass population was taken at equilibrium,  $B_2^* = k_2 \left(1 - \frac{\mu_B}{\omega}\right) = 2857.14$ , with the baseline parameter values, including  $\omega > \mu_B$ . In Figure 6, the buffelgrass population is not shown because the population is much larger than the other species, and because its dynamics are not affected by the other species. With the inclusion of buffelgrass, there is not a great change to the equilibrium population values, which is due to the small  $\theta$  values at the baseline. However, the adult saguaro and tree populations do decrease and the juvenile population increases. Also, equilibrium of the three species is reached sooner. This is most likely because of the higher death rates for saguaros and trees.

### 6.1 Varying the Parameters Associated with Buffelgrass

It is known that natural fires in the Sonoran Desert used to happen about once every 250 years [21]. Natural wildfires occur randomly, and are caused by natural phenomena, such as lightning. In an undisturbed desert ecosystem, wildfires spread slowly, if at all, due to lack of fuel material, and therefore it is easier to contain and diminish destruction. As mentioned earlier, buffelgrass is an excellent fire fuel, and therefore, it allows fire to burn stronger and longer. The presence of buffelgrass in the desert ecosystem allows fire to easily spread among all native species. Therefore, it can be said that in a wildfire situation, buffelgrass acts as conductor of fire through an area. Buffelgrass becomes a greater threat to the ecosystem when the population is high and fire frequency increases due to human behaviors, such as leaving camp fires unattended or committing arson.

This study intends to see the effects of the increase of fire frequency with a high buffelgrass population on saguaros and their nurse trees. Hence, it was decided to vary the parameters values related to fire frequency,  $\theta$ 's, buffelgrass growth rate,  $\omega$ , and death of buffelgrass by harvesting,  $\mu_B$ . The following figures show the effects of increasing the  $\theta$  values by increasing the frequency of wildfires on the populations.

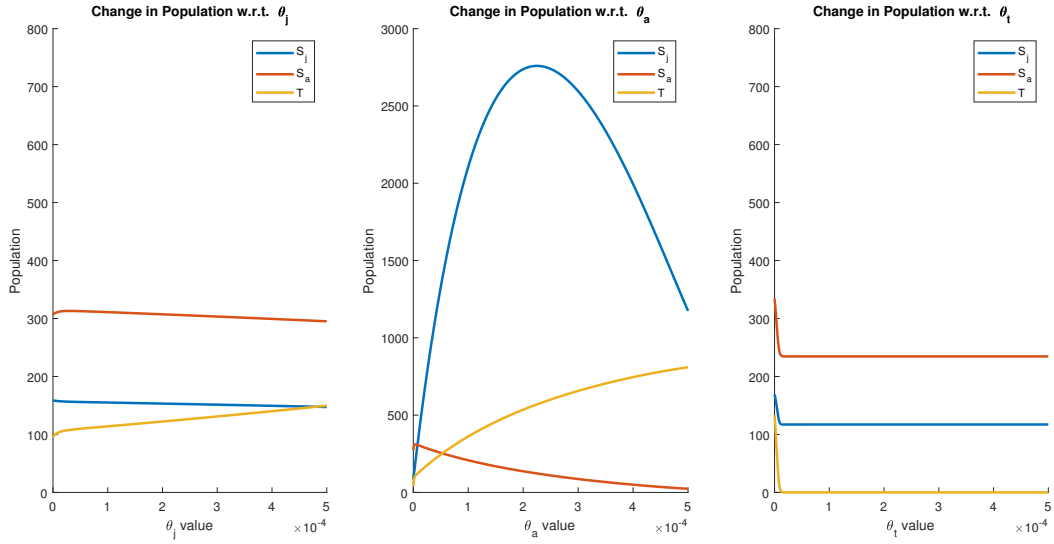


Figure 7: This figure shows the effects of varying each  $\theta$  on the saguaro and tree populations at time 400, when the populations have reached their equilibrium values. The y-axis gives the population values, and the x-axis gives the  $\theta$  values in  $(yr \cdot grass)^{-1}$ .

From the first graph in Figure 7, it can be seen that varying  $\theta_j$  does not result in much change in the equilibrium populations. Because the juvenile population is based on the adult population, increasing  $\theta_j$  by itself does not greatly affect any of the populations. If it is greatly increased,  $\theta_j$  will eventually cause the decline of the juvenile and adult saguaro populations and the increase in the palo verde population.

As the value of  $\theta_a$  is increased, the adult saguaro populations approach extinction. However, the juvenile population increases with  $\theta_a$  up to a point. This is because juvenile saguaros compete with adult saguaros over space, so when adults die, there is more space available for juveniles. When there is no longer enough adult saguaro to produce juveniles, the juvenile population also begins to decline. The tree population increases because of the lack of competition. In reality, this would not occur because the increased frequency of fires would also affect the tree population. As expected, in Figure 7, increasing the  $\theta_T$  value does not greatly affect the adult and juvenile saguaro populations. However, increasing  $\theta_T$  even by a small amount causes the palo verde population to become extinct. The slight decrease in the saguaro populations is because as the nurse tree population declines, fewer juveniles will be germinated and survive. This in turn causes a decrease in the adult population.

Comparing Figure 6b and Figure 7, it is reasonable to conclude that increasing the frequency of wildfires will drive both the saguaro and palo verde populations to extinction, if increased to a great enough frequency. Further evidence of these changes in the saguaro and nurse tree population is shown in Figure 8.

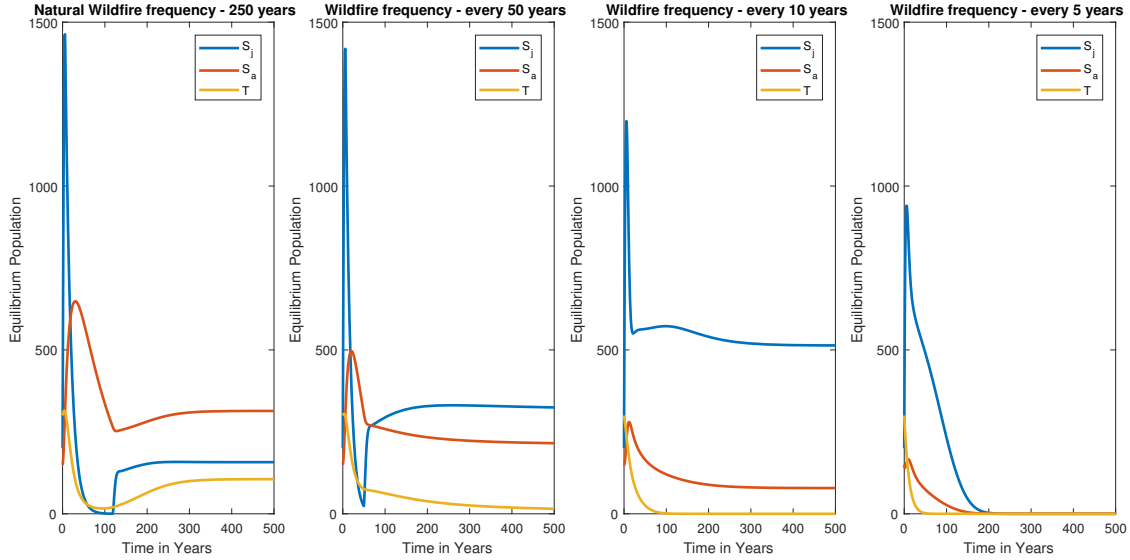


Figure 8: Here the wildfire frequency is increased and the resulting population dynamics of saguaros and nurse trees are shown.

Since the current wildfire frequency in the Saguaro National Park could not be found, the true values of the  $\theta$  terms are not known, and the values given in Table 4 may not be accurate. As mentioned previously, the frequency of wildfire can be increased by random events by human interventions, and be more destructive with the presence of buffelgrass. Therefore, in order to answer the question as to whether buffelgrass will cause the extinction of the saguaro and nurse tree populations, different wildfire frequencies were tested with the model equations in Figure 8. An interesting detail to notice is that in the second graph in Figure 8, the juvenile saguaro population surpasses that of the adult. This behavior coincides with the dynamics in Figure 1, which show the actual dynamics occurring in Saguaro National Park. Therefore, this result might imply that the actual wildfire frequency is closer to once every 50 years rather than once every 250 years, which is the historical occurrence. The reasoning for this is that buffelgrass propagates unnatural wildfires, such as those caused by human activity, which would otherwise not occur. The threshold wildfire frequency value for the juveniles surpassing the adults is 84 years. Furthermore, the results from this figure also show that increasing wildfire frequency to every 10 years would result in the extinction of nurse trees,  $(S_j^*, S_a^*, 0, B^*)$ , and increasing the frequency to every five years would eliminate saguaros,  $(0, 0, 0, B^*)$ . The threshold wildfire frequency for the extinction of nurse trees in an area is one wildfire every 24 years. The case where saguaros are eliminated by wildfires but trees are able to survive does not occur with the current parameter values for Equation 1c. However, if the growth rate of trees were to increase, this case may be found. Since buffelgrass causes the increased spread of fires, we can assume that reducing the amount of buffelgrass would allow the natural wildfire rate to hold.

The next step is to examine the effects of employing strategies to decrease the buffelgrass population. These strategies include reducing the growth rate, which could be done through chemical spraying, and increasing the harvesting term, by increasing the rate it takes to eliminate a patch of buffelgrass.

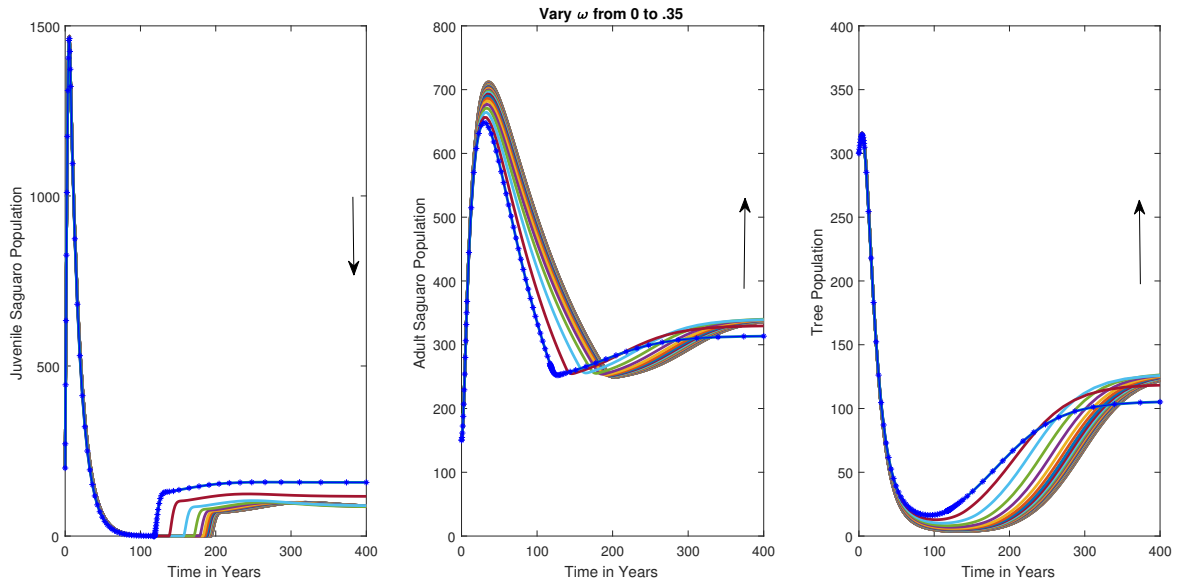


Figure 9: Effects of decreasing  $\omega$  from .35 to 0 on the population values of  $S_j$ ,  $S_a$ ,  $T$ . The blue dotted line shows the dynamics with the baseline parameter value of  $\omega = .35$ . The arrows show the effect of decreasing  $\omega$  on the equilibrium populations.

Figure 9 shows the changes in the juvenile and adult saguaro and tree populations from decreasing the buffelgrass growth rate,  $\omega$ . These changes include greater resulting populations for adult saguaros and trees. However, the resulting juvenile population is smaller, which is because more saguaros are able to age into adulthood, which decreases the available space for new juveniles. Although the equilibrium tree population increases, it takes longer for the tree population to grow back after the initial decrease due to competition with the growing adult saguaro population. This is because the peak value for the adult population increases with the decrease of  $\omega$  and slows the growth of trees through competition.

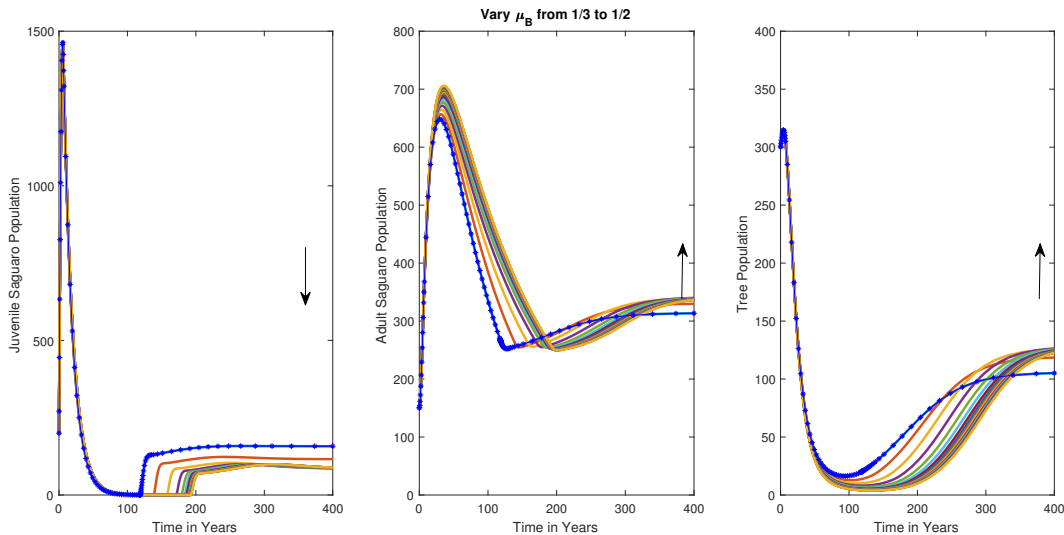


Figure 10: Effects of increasing  $\mu_B$  from  $\frac{1}{3}$  to  $\frac{1}{2}$  on the saguaro and tree population values. The dotted, blue line represents the dynamics with the baseline parameters,  $\mu_B = \frac{1}{3} yr^{-1}$ .

The results of Figure 10 are similar to those of Figure 9. In Figure 10, it can be seen that

increasing the harvesting rate can increase the adult saguaro and nurse tree populations, while decreasing the juvenile population at the final time in the simulation, because more saguaros are able to age into adulthood and therefore take up space that would otherwise be available for juveniles.

This study is looking at the impact of wildfires fueled by buffelgrass on the saguaro and nurse tree populations. From Figure 8 we can conclude the increase of the wildfires frequency can lead to the saguaro and nurse tree population extinction if the wildfire frequency increases to about every 5 years, which will lead to an alteration of the Sonoran Desert ecosystem. From Figures 9 and 10, it can be inferred that taking measures to reduce the growth rate and increase the harvesting rate of buffelgrass would result in an increase of the adult saguaro and tree populations, which would protect the Sonoran Desert ecosystem. Because these strategies have about the same effect on the equilibrium populations, it will be important to compare the implementation costs of each strategy to determine which is more efficient.

## 7 Sensitivity Analysis

The type of sensitivity analysis used for the model is a local sensitivity analysis, which quantifies the effects of slightly perturbing the value of a critical parameter on a quantity of interest. In this case the value of the critical parameter is changed by one percent and the quantities of interest are the equilibrium populations. However, these results are only valid for a small region around the baseline solution. When looking at the results in Tables 5 and 6, it is important to note that the sign of each sensitivity index gives the direction of the change in the quantity of interest, and the value gives the magnitude of the change in percentage. [25].

### 7.1 Sensitivity Analysis of Critical Parameters at Buffelgrass Extinction Equilibrium

In this section, sensitivity analysis is going to be performed on critical parameters of the basic model with buffelgrass at extinction equilibrium  $B^* = 0$ . The parameters being analyzed are the rate that seeds are germinated and survive to one year,  $r$ , the average number of juveniles that survive under a nurse tree per tree,  $b$ , and the logistic growth term for palo verde population,  $\phi$ , since they can be controlled.

Sensitivity Analysis	$r$	$b$	$\phi$
$S_j$	0.0013	0.1006	0.6534
$S_a$	0.0013	0.1006	0.6534
$T$	-0.0084	-0.6534	2.2520

Table 5: Sensitivity indices of the population values of  $S_j$ ,  $S_a$ , and  $T$  at equilibrium when changing the parameter values by 1% from their baseline value given in Table 4.

In Table 5 it can be seen that for all critical parameters,  $S_a$  and  $S_j$  have the same sensitivity index with respect to these parameters. This is because any change in the juvenile population will affect how many saguaros will reach maturity, or become adults. Furthermore, any change in the adult population will affect how many new juvenile saguaros are produced. Therefore affecting one population will affect the other by an equal amount at equilibrium. Furthermore, Table 5 shows that increasing  $r$ , the germination rate of juvenile saguaros, by 1%, will only slightly affect the saguaro and nurse tree populations, increasing the saguaros by 0.001% and decreasing the nurse trees by .0084% due to competition with the increased adult saguaro population. The parameter  $b$  has a greater effect on the equilibrium populations than  $r$  and increases the saguaro populations by 0.1006% when increased by 1%. This is because the carrying capacity of juveniles is increased by increasing  $b$ , which increases  $bT$ , resulting in more juveniles and thus more adults. The tree population is decreased by 0.6534% due to increased competition. The parameter  $\phi$  had the greatest effect on all of the populations. Increasing  $\phi$  by 1% allows for the tree population to grow by 2.2520%. This increase allows the juvenile population to grow through an increased carrying capacity and thus allows the adult population to grow. Therefore, increasing  $\phi$  is not only the

most efficient way to increase saguaro population in the absence of buffelgrass, but also promotes the growth of the tree population.

## 7.2 Sensitivity Analysis of Critical Parameters at Buffelgrass Existence Equilibrium

One of the goals of this study is to see the impact of wildfires and buffelgrass on the saguaro and nurse tree populations. Therefore, a local sensitivity analysis is performed on  $\theta_j$ ,  $\theta_a$ ,  $\theta_T$ ,  $\mu_B$ ,  $\omega$  and  $\phi$  parameters. This analysis will support the results of the simulations in Section 6.

Sensitivity Analysis	$\theta_j$	$\theta_a$	$\theta_T$	$\mu_B$	$\omega$	$\phi$
$S_j$	$-3.92 \times 10^{-4}$	0.4916	-0.0753	-8.3189	8.3232	0.7213
$S_a$	$-3.92 \times 10^{-4}$	-0.0111	-0.0753	1.7351	-1.7354	0.7213
$T$	0.0028	0.0803	-0.2980	4.2973	-4.2973	2.8558
$B$	N/A	N/A	N/A	-20	20	N/A

Table 6: Sensitivity indexes of the population values of  $S_j$ ,  $S_a$ ,  $T$ , and  $B$  after 400 years when changing the parameter values by 1% from their baseline value given in Table 4.

For the analysis in Table 6, the populations were used at their previously found coexistence equilibria values, that is  $S_j = 157.588$ ,  $S_a = 313.478$ ,  $T = 105.202$ , and  $B = 2857.14$ . After running the baseline equations to equilibria, the parameters were varied and then run again to measure changes. This analysis shows that when increasing  $\theta_j$  by 1% the saguaro population decreases by  $3.91 \times 10^{-4}\%$ , and the tree population increases by 0.0028% since there is less competition with adult saguaros. The increase of  $\theta_a$ , will directly decrease adult saguaro population by 0.01111% but will increase the juvenile saguaro population by 0.49% since it creates more available space for their establishment. The increase of  $\theta_a$  will also positively affect the tree population by increasing it by 0.08%, since the death of adult saguaros decreases the competition between them and the trees. On the other hand, the increase of  $\theta_T$ , will decrease all populations, the saguaro population by 0.07% and the tree population by 0.29%. Furthermore, it can be seen that the saguaro, nurse tree, and buffelgrass populations are most sensitive to changes in  $\mu_B$  and  $\omega$ . The increase of  $\mu_B$  would decrease the buffelgrass and juvenile saguaro populations by 20% and 8.32% respectively, and increase the adult saguaros and trees by 1.73% and 4.29% respectively. An increase in adult saguaros limits the space available for juvenile saguaro establishment, through competition for space. Finally, the increase of  $\omega$  will increase the buffelgrass and juvenile saguaros populations by 20% and 8.32% respectively, but decrease the adult saguaros and trees by 1.73% and 4.29%, respectively. Since there is more buffelgrass, there are fewer juvenile saguaros becoming adults and staying in the juvenile class, which declines the growth rate of the adult and tree population. The juveniles are also limited in capacity by the reduction in nurse trees. Therefore, from these results, the most efficient way to protect the saguaro and nurse tree populations would be to reduce the buffelgrass population by either decreasing  $\omega$  or increasing  $\mu_B$ .

## 8 Discussion

The saguaro cactus, a keystone species for the Sonoran Desert, has recently faced a decline in its population. Throughout the harsh summers, many species, such as the endangered honey bee or the antelope jack rabbit, rely on the fruits and flowers of the saguaro for food. Saguaros only produce these fruit and flowers during their two month seed germination period, which occurs yearly from June to August. Saguaros do not produce any fruit or flowers until roughly 35 years of age, at which point they becomes a fully reproductive adult. Unfortunately, this is because the saguaro's growth is very slow and they are susceptible to freezes during their first years, but can live up to two hundred years. The juvenile saguaro needs a nurse tree during its first thirty-five years to be able to survive to adulthood, and this creates commensalism between the juvenile and nurse tree. Additionally, because the root system of the saguaro is laterally extensive and shallow, a competition of space is created only between adult saguaros and nurse trees.

Although this is the natural life cycle of the saguaro, it can be altered with the presence of the non-native buffelgrass. Buffelgrass root systems expand vertically several meters deep into the soil, rather than horizontally and shallow, like most other native plants. This allows them to grow right next to other plants, including saguaro, nurse tree, or other buffelgrass. The deep root system allows it to quickly reemerge after a fire. Buffelgrass is characterized for being an excellent fire fuel that allows to fire to burn longer and propagate easily, and cause the death of native species. After the wildfire, buffelgrass can quickly regrow after a week and invade newly available spaces. This represents a danger to nurse trees, such as the palo verde, and saguaros, since there is no space for new establishments.

A mathematical stage structured model was built and analyzed to study the interactions between these saguaros, trees, and buffelgrass wildfires. The decision to classify between juvenile and adult saguaro cactus was motivated by the complexity and long life of the species. To better first understand the natural dynamics of the saguaros and its nurse trees, a simple model was studied and analyzed.

In order to maintain a stable population equilibrium, several conditions were found. The expected number of adult saguaro cacti produced by one adult saguaro in the presence of nurse trees must be greater than one for population maintenance among the cacti. However, perhaps the most important realization of the analysis with buffelgrass, is from Theorem 1, coexistence. Numerically, results show that the stability of saguaro cactus populations does exist with buffelgrass for the baseline set of parameter values. Ideally, buffelgrass should be reduced to increase the available space for cacti and nurse trees.

From the numerical simulations it was found that at the buffelgrass extinction equilibrium, the saguaro and nurse tree populations are able to coexist. In this case, the most efficient way to influence the production of more adult saguaros is to increase  $\phi$ , the growth rate of trees. From the numerical simulations at buffelgrass existence equilibrium, it can be seen that with the current wildfire frequency, given in Table 4, the saguaro and nurse tree populations are able to coexist with buffelgrass. However, if the wildfire frequency increases, saguaros and nurse trees would be put at risk. The best way to reduce this risk according to both, the simulation and sensitivity analysis, is to reduce the buffelgrass population by decreasing  $\omega$ , the growth rate of the buffelgrass population, and increasing  $\mu_B$ , the harvesting rate affecting the buffelgrass population.

From the results of the simulation, it can be inferred that the most efficient way to protect the saguaro population is to decrease the buffelgrass population through the application of herbicide, reducing the buffelgrass growth rate, or by hiring workers or recruiting more volunteers to pull up buffelgrass, increasing the harvesting rate.

Future work for this model should be the inclusion of optimal control strategies on reducing the buffelgrass and increasing saguaros as well as their nurse trees. The reduction of buffelgrass would help to maintain the saguaro cacti population by diminishing the spread of wildfires through the desert. However, controlling buffelgrass invasion requires resources that come with a cost. Through optimal control analysis, the results would shed some insight to which strategies are better than others to keep the cost low and make an impact on reducing buffelgrass. Additionally, the inclusion of commensalism and competition of the buffelgrass with the saguaro and nurse trees populations can be explored in the model. Further, the model could take into account a random increase of wildfires caused naturally or by human intervention. A method that can be used to explore this is through the use of stochasticity.

## 9 Acknowledgements

We would like to thank the Mathematical and Theoretical Biology Institute (MTBI) co-Directors Dr. Carlos Castillo-Chavez, and Dr. Anuj Mubayi for giving us the opportunity to participate in this research program. We would also like to thank associate director Sherry Woodley, coordinator Ciera Duran and management intern Sabrina Avila for their efforts in providing logistics for activities during MTBI. We also want to give special thanks to our mentors, Fan Yu, Juan Meléndez-Alvarez, Dr. Leon M Arriola, and Dr. Anuj Mubayi for their contributions through-



out this project. The research has been carried out at the MTBI which is a Research Experience for Undergraduate (REU) summer program at the Simon A. Levin Mathematical, Computational and Modeling Sciences Center (SAL MCMSC) at Arizona State University (ASU). This project has been partially supported by grants from the National Science Foundation (DMS1263374), the National Security Agency (H98230-15-1-0021), the Office of the President of ASU, and the Office of the Provost at ASU.

## References

- [1] T. D. Drezner, "The Keystone Saguaro *Carnegiea Gigantea*, Cactaceae: a review of its ecology, associations, reproduction, limits, and demographics,"
- [2] B. Riley, "Tourism to Saguaro National Park creates \$66.5 million in Economic Benefit for Tucson." Web, 2015.
- [3] T. Drezner and R. C. Balling, "Regeneration cycles of the keystone species *Carnegiea gigantea* are linked to worldwide volcanism," *Journal of Vegetation Science*, vol. 19, no. 5, p. 587–596, Apr. 2008.
- [4] E. A. Pierson and R. M. Turner, "An 85-Year Study of Saguaro (*Carnegiea Gigantea*) Demography," *Ecology*, vol. 79, no. 8, p. 2676–2693, Dec. 1998.
- [5] T. D. Drezner, "Plant facilitation in extreme environments: The non-random distribution of saguaro cacti (*Carnegiea gigantea*) under their nurse associates and the relationship to nurse architecture," *Journal of Arid Environments*, vol. 65, no. 1, p. 46–61, Apr. 2006.
- [6] D. S. Pavek, "Parkinsonia microphylla," *Fire Effects Information System, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory*, 1994.
- [7] M. J. Orum TV, Ferguson N, "Data from: Saguaro mortality and population regeneration in the cactus forest of Saguaro National Park: seventy-five years and counting," 2016.
- [8] T. V. Orum, N. Ferguson, and J. Mihail, "Saguaro (*Carnegiea gigantea*) Mortality and Population Regeneration in the Cactus Forest of Saguaro National Park: Seventy-Five Years and Counting," *PLOS ONE*, vol. 11, no. 8, p. e0160899, Aug. 2016.
- [9] "Buffelgrass - Saguaro National Park (U.S. National Park Service)." Online.
- [10] "Buffelgrass Fact Sheet." Online.
- [11] A. S. Hauser, "Pennisetum ciliare." Online, 2008.
- [12] J. E. Bowers, "Questions about the saguaro," 2003.
- [13] W. F. Steenbergh, C. H. Lowe, *et al.*, "Ecology of the saguaro: II, Reproduction, germination, establishment, growth, and survival of the young plant.," *Ecology of the Saguaro: II, Reproduction, Germination, Establishment, Growth, and Survival of the Young Plant.*, 1977.
- [14] S. N. P. U. N. P. Service, "Saguaro roots." Online.
- [15] A.-S. D. Museum, "Biological Survey of Ironwood Forest National Monument." Online.
- [16] Y. Bashan, B. Salazar, M. E. Puente, M. Bacilio, and R. Linderman, "Enhanced establishment and growth of giant cardon cactus in an eroded field in the Sonoran Desert using native legume trees as nurse plants aided by plant growth-promoting microorganisms and compost," *Biology and Fertility of Soils*, vol. 45, pp. 585–594, Jul 2009.
- [17] S. N. P. U. N. P. Service, "How saguaros grow." Online.
- [18] A.-S. D. Museum, "Plant Fact Sheet: Foothill Palo Verde." Online.
- [19] S. Kaufman and W. Kaufman, *Invasive Plants: A Guide to Identification and the Impacts and Control of Common North American Species*. Stackpole Books, 2007.
- [20] C. D. of Forestry and F. Protection, "Maintain defensible space-prepare for wildfire." Online.

- [21] S. N. Park, “Buffelgrass management.” Online.
- [22] U. S. E. P. Agency, “Climate change indicators: Wildfires.” Online.
- [23] I. E. Büyüktaktakin, Z. Feng, A. D. Olsson, G. Frisvold, and F. Szidarovszky, “Invasive species control optimization as a dynamic spatial process: an application to buffelgrass (*Pennisetum ciliare*) in Arizona,” *Invasive Plant Science and Management*, vol. 7, no. 1, pp. 132–146, 2014.
- [24] S. P. McLaughlin and J. E. Bowers, “Effects of Wildfire on A Sonoran Desert Plant Community,” *Ecology*, vol. 63, no. 1, pp. 246–248, 1982.
- [25] C. A. Manore, K. S. Hickmann, S. Xu, H. J. Wearing, and J. M. Hyman, “Comparing dengue and chikungunya emergence and endemic transmission in a. aegypti and a. albopictus,” *Journal of Theoretical Biology*, vol. 356, pp. 174–191, 2014.
- [26] M. S. Keasey, “The saguaro book,” 1981.

## 10 Appendix

### 10.1 Jacobian of Model Equations with Buffelgrass

The general Jacobian of the model equations after the inclusion of buffelgrass is given below.

$$\begin{pmatrix} -\frac{r \cdot \epsilon \cdot S_a^*}{k_1 + bT^*} - (\mu_j + \gamma + \theta_j B) & r \left(1 - \frac{\epsilon S_j^* + 2S_a^*}{k_1 + bT^*}\right) & rbS_a^* \frac{\epsilon S_j^* + S_a^*}{(k_1 + bT^*)^2} & -\theta_j S_j \\ \gamma & -(\mu_a + \theta_a B) - \alpha_1 \frac{T^*}{k_2} & -\alpha_1 \frac{S_a^*}{k_2} & -\theta_a S_a \\ 0 & -\phi \cdot \sigma \frac{T^*}{k_2} & \phi \left(1 - \frac{2T^* + \sigma S_a^*}{k_2}\right) - \theta_t B & -\theta_T T \\ 0 & 0 & 0 & -\mu_B + \omega \left(1 - \frac{B}{k_3}\right) - \frac{B\omega}{k_3} \end{pmatrix} \quad (11)$$

### 10.2 Numerical Simulations of Coexistence Conditions and Stability

Using the parameter values given in Table 4, the coexistence of the saguaro and nurse tree population can be verified with and without the inclusion of buffelgrass.

#### 10.2.1 Coexistence at Buffelgrass Extinction Equilibrium

In order to verify that saguaros and nurse trees coexist without buffelgrass, it is necessary to prove that the conditions described in Section 3 hold true for the estimated parameter values. The conditions for having at least one positive root are as follows:

$$\frac{\phi}{\rho} > \frac{k_1}{1 + E} \left(1 - \frac{1}{R_{d1}}\right), \quad (12a)$$

$$\text{and } R_{d2} > 1; \quad (12b)$$

with the parameter values given in Table 4, these conditions are satisfied. That is, since these conditions are shown to be true, the model will have at least one coexistence equilibrium. Furthermore, once the possible equilibrium values are found, the condition

$$S_a^* < \frac{\phi}{\rho} \quad (13)$$

must be satisfied for each in order for two coexistence equilibria to exist.

The equilibrium population values of the trees and juvenile saguaros depend on the quadratic equation for the value of  $S_a$ . Numerically solving this quadratic gives two possible equilibrium populations for the adult saguaro population,  $S_{a1} = 341.225$  and  $S_{a2} = 3.97549 \times 10^8$ . Since only the equilibrium point,  $S_a = 341.225$  satisfies Equation 13, there is only one coexistence equilibrium.

For the existing equilibrium population of  $S_a$ , the other population values are  $S_j^* = 85.3079$  and  $T^* = 127.726$ .

The stability of the existing coexistence equilibrium can be shown at least for our given parameter values from Table 4 by substituting the equilibrium population values into the Jacobian of the model equations from Equation 11. Since not all of eigenvalues have a negative real part, the equilibrium point is not stable for this particular set of parameter values. This just means that if buffelgrass is introduced into the population it will not die out.

### 10.2.2 Coexistence at Buffelgrass Existence Equilibrium

To verify the coexistence of the saguaro populations, nurse trees, and buffelgrass we need to check that the conditions mentioned in Section 3 hold true for the estimated parameter values. The conditions for the existence of two roots are the following,

$$\frac{\tilde{\phi}}{\rho} > \frac{k_1}{1 + \tilde{E}} \left( 1 - \frac{1}{R_{d3}} \right) \quad \text{and} \quad R_{d4} > 1$$

With the baseline parameter values given in Table 4, and the new parameters for the buffelgrass model from the Appendix A Section 2, these conditions are satisfied. Since these conditions are shown to be true, the model will have two possible coexistence equilibria. The equilibria population values of the trees, juvenile saguaros, and buffelgrass depend on the quadratic equation for the value of  $S_a^*$ , and existence depends on the inequality  $S_a^* < \frac{\tilde{\phi}}{\rho}$ . Solving the quadratic for  $S_a^*$  gives two possible equilibrium populations for the adult saguaro population,  $S_{a1} = 313.478$  and  $S_{a2} = 5.95358 \times 10^9$ . However, only one of these values satisfies  $S_a^* < \frac{\tilde{\phi}}{\rho}$ ,  $S_a = 341.225$ . For the existing equilibrium population of  $S_a$ , the other population values are  $S_j = 157.588$ ,  $T = 105.202$ , and  $B = 2857.14$ .

The stability of the coexistence equilibrium can be shown numerically for the given parameter values by substituting the baseline parameters from Table 4, the new parameters for buffelgrass model, and the equilibrium population values into the Jacobian of the model equations from Equation 11 in Appendix. Since the real part of each eigenvalue is negative, the equilibrium point is locally asymptotically stable, for the values of Table 14.

### 10.3 Adding Seasonality with Buffelgrass at Extinction Equilibrium

To incorporate the seasonal dynamics of the saguaro populations, the reproduction rate,  $r$ , is changed, and the death terms for the saguaro populations  $\mu_j$  and  $\mu_a$  are to be functions of time. In the literature, it was found that saguaros only reproduce for a two month period of the year from May to June, June to July, or July to August. The particular two month period depends on their location [26].

For the reproduction rate, a sinusoidal function is created to force the expected behavior of the growth rate, that is given by:

$$r_{new}(t) = (2 \cdot r_{avg}) \cdot \cos^{14} \left( 3t + \frac{\pi}{6} \right) \quad (14)$$

In the Equation 14,  $3t + \frac{\pi}{6}$  is used to center the function over the middle of the year so that births only occur between May and August. This is also the reason  $\cos^{14}$  is used, to force the rate to be centered over the middle of the year. The amplitude is the average growth rate, or  $r_{avg}$ , given on the y axis of Figure 11.

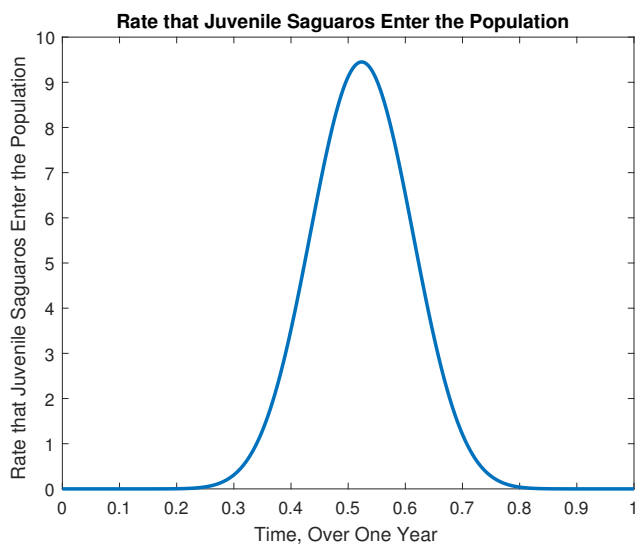


Figure 11

For the death rate of the adult and juvenile saguaros, respectively, we have,

$$\mu_{a \text{ new}} = \mu_{a \text{ avg}} \cdot \cos^{14}(3.15t) + \mu_{a \text{ natural}},$$

and

$$\mu_{j \text{ new}} = \mu_{j \text{ avg}} \cdot \cos^{14}(3.15t) + \mu_{j \text{ avg}}.$$

Similarly to the growth rate equation, the  $\cos^{14}(3.15t)$  term is used to force the death rate to increase in the winter months, when saguaros in both age groups are susceptible to freezing temperatures. For the adults, the amplitude is the average death rate due to freezing and the cosine function is added to the rate that saguaros reach their natural lifespan. For the juvenile saguaros, the minimum of the function is the average death rate, which doubles in winter months.

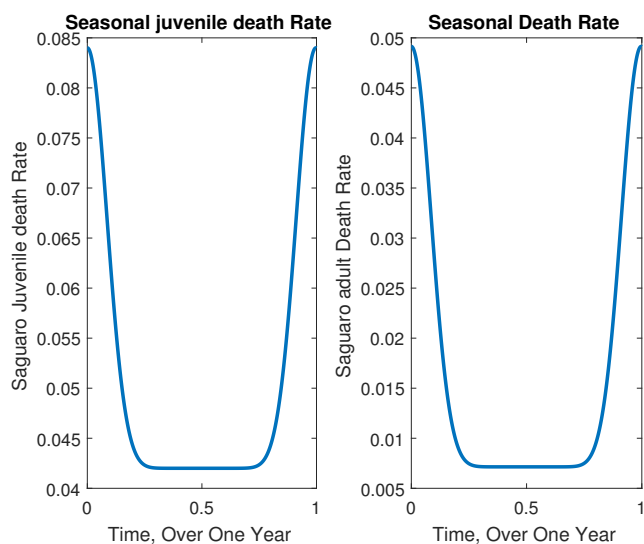


Figure 12: Death rate of adult and juvenile saguaros over one year.

The resulting changes in the model can be observed in Figure 13.

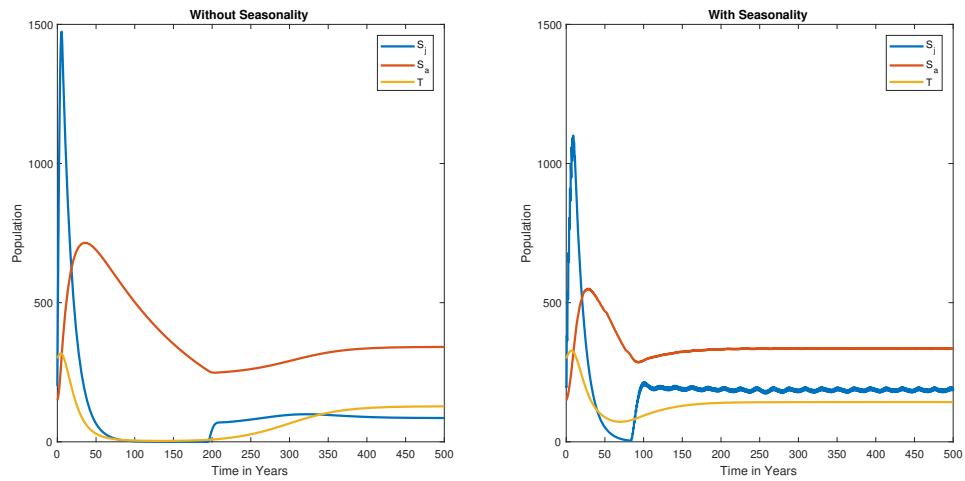


Figure 13: Difference in the systems with and without seasonality using the baseline parameter and same initial population values as Figure 3.

Figure 13 shows the change to seasonal recruitment and death rates causes saguaro populations to reach equilibrium sooner and limits their peak population values, which is due to decreasing the germination rate by only making germination possible at certain times of the year. The equilibrium populations for juveniles and trees are increased, but the equilibrium adult saguaro population is decreased. This is because the death rates of the saguaro populations are increased during the winter. This does not result in a smaller juvenile population, because less adults means more room for juveniles to grow. The increased tree population is also due to the decreased adult saguaro population, and also allows more juveniles to grow.