Modelling biological control strategies for water hyacinth

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Abstract

The water hyacinth, *Eichhornia crassipes*, is currently regarded as the world's, as well as South Africa's, worst aquatic weed. One of the more successful methods of controlling this weed is biological control. Natural enemies are sought in the weed's native land, put through quarantine and then released in the new habitat where they feed on the weed, contributing to the suppression of populations. The direct release of biological control agents (BCAs) after quarantine is known as *classical biological control.* Another biological control method, which makes use of *mass rearing* technology once BCAs have been cleared from quarantine, has evolved. BCAs can be reared in very large numbers before they are released. In addition, this method also makes more frequent re-releases possible, speeding up biological control. In this study, a stage-structured plant-herbivore model is developed to mathematically describe the water hyacinth's population growth as well as its interaction with populations of the various life stages of the *Neochetina eichhorniae* weevil as BCA. The model is used to evaluate the cost-effectiveness of mass rearing programs in biological control versus classical biological control in order to determine whether the faster decrease in water loss is worth the expense pertaining to mass rearing programs. The model also provides guidance towards the optimal magnitude and frequency of BCA releases.

Uittreksel

Die waterhiasint, *Eichhornia crassipes*, word tans beskou as die wêreld, sowel as Suid-Afrika, se ergste wateronkruid. Een van die meer suksesvolle metodes om hierdie onkruid te beheer, is biologiese beheer. Natuurlike vyande word in die onkruid se land van oorsprong gesoek, deur kwarantyn geplaas en dan in die nuwe habitat vrygelaat, waar hulle op die onkruid voed en bydra tot die onderdrukking van die bevolkings. Die direkte vrylating van biologiese beheeragente ná kwarantyn staan bekend as *klassieke biologiese beheer*. Nog 'n biologiese beheermetode het ontwikkel, wat gebruik maak van massakweektegnologie nadat biologiese beheeragente uit kwarantyn ontslaan is. Biologiese beheeragente kan in baie groot getalle gekweek word voordat hulle vrygelaat word. Hierdie metode maak ook meer gereelde hervrylatings moontlik, wat biologiese beheer dus versnel. In hierdie studie word 'n plant-herbivoormodel wat volgens fases gestruktureer is, ontwikkel om die waterhiasint se bevolkingsaanwas en sy interaksie met bevolkings van die verskillende lewenstadiums van die *Neochetina eichhorniae*-kewer as biologiese beheeragent wiskundig te beskryf. Die model word gebruik om die koste-effektiwiteit van massakweekprogramme in biologiese beheer teenoor klassieke biologiese beheer te evalueer, met die doel om te bepaal of die vinniger afname in waterverlies die koste wat met massakweekprogramme gepaard gaan, werd is. Die model verskaf ook leiding met betrekking tot die optimale omvang en frekwensie van biologiese beheeragentvrystellings.

Table of Contents

List of Figures

List of Tables

CHAPTER 1

Introduction

The Amazonian water hyacinth, *Eichhornia crassipes*, has since the 1880s spread its roots across the USA and eventually the world, where it is now notorious for being the world's, as well as South Africa's, worst aquatic weed. Initially distributed for its ornamental value, water hyacinth now rules water masses in tropical and warm regions of the world by forming dense impenetrable layers across the surfaces, as illustrated in Figure 1.1. Man and animal suffer severely under its reign. Natural habitat is abducted. Travelling on water and fishing are hampered. Water sports areas are limited. Irrigation systems are blocked. Hydro-electric turbine intakes are obstructed. Water loss rates drastically increase due to the higher evapotranspiration rate of water hyacinth, leading to higher water supply costs. Health risks arise with the plants providing breeding grounds for mosquitoes and other disease carriers. Communities relying on invaded water bodies for transport and basic needs are devastatingly affected [9, 17].

Figure 1.1: *Water hyacinth blankets the upper reach of the Shuikou hydropower station on the Minjiang River in East China, August 2, 2011* [12].

Several initiatives to counter act this invasive alien plant species' growth have been investigated since the early 1900s. Chemical, mechanical and manual control methods proved itself both very expensive and ineffective, especially for large infested water bodies. These concerns motivated a more serious consideration of the use of biological control methods [9].

1.1 Background

Figure 1.2: *Water hyacinth flower.*

Water hyacinth is a water plant that originates from the Amazon in South America. Floating on water surfaces or anchoring itself with long, feather-like roots, it exists in still or slow-moving fresh water and presents beautiful light blue or violet flowers. The upper petal has a characteristic dark blue patch with a yellow centre. Flowers grow together in flower spikes in clusters of 8 - 10 flowers, with each flower measuring about 5 cm in diameter. Adult plants are normally 10 - 20 cm high, but can extend to 1 meter when growing together in dense mats. The leaves are rounded and shiny, dark-green in colour, with distinctive upright or bulbous petioles [8, 17].

Water hyacinth reproduces by budding or the spreading of seeds. Budding entails the process of growing long shoots or the breaking off of parts of the plant that develop into new plants. The plant also produces thousands of seeds several times a year after flowering. Seeds can produce flowers as early as 10 - 15 weeks after it started to grow in warm, shallow water or moist silt. Wind, water streams, boats, birds and other animals may unintentionally assist in spreading the plant into other areas. Water hyacinth has an exponentially high growth rate, especially under ideal conditions, such as tropical weather, warm temperatures and water with high nutrient levels (particularly nitrogen and phosphorous). It can double its size in the matter of a week. Seeds can still reproduce after 15 - 20 years of remaining in water sediments. These qualities make it extremely difficult to control this determined water hyacinth species [8, 17].

1.1.1 History of water hyacinth control globally

Research over past decades has investigated possible uses of the plant such as a fertilizer, fodder, paper and fibre source, or for mineral nutrient removal from polluted water. Eradicating the weed therefore involves a potential conflict of interests. However, these uses seldom develop into sustainable activities and the cost of water hyacinth to communities far outweighs any benefits [9].

One of the more successful methods of control is biological control. Natural enemies are sought in the weed's native land, put through quarantine and then released in the new habitat where they attack the weed by feeding on it, thereby contributing to the suppression of the plant population. In its natural habitat, water hyacinth is attacked by a large number of arthropods. Study of the ecology of some of these as possible biological control agents began in Argentina in 1961. Some were found unable to survive on any organism other than water hyacinth, while others may also survive on some additional plant species. The first natural enemies were released as biological control agents (BCAs) in the USA in early 1970s. Since then several agents have been released in 33 countries [9].

The way that the weed and its enemy influence each other resembles predator-prey interaction, where the weed plays the role of the prey and its enemy the predator. As the population of the weed increases, the population of the enemies also increases as they have more to feed on. After a while, the weed's population will begin to decrease as a result of all its enemies' feeding. This will in turn lead to a decrease in the population levels of the enemy as the availability of food is reduced. With less enemies on attack, the weed has a chance to expand its population again and the cycle repeats itself [4].

Biological control outranks other methods by offering a more sustainable, environment-friendly, long-termed, more affordable solution to the problem, even for large or inaccessible areas [7].

1.1.2 History of water hyacinth control in South Africa

In South Africa, water hyacinth was first documented in 1908 on the Cape Flats and was introduced into KwaZulu-Natal at about the same time, supposedly as an ornamental aquatic plant for garden ponds and aquaria. Since then it has spread to water bodies all over the country. A warning of what was likely to happen with water hyacinth was printed as early as 1913 [8].

Since the 1970s South African control options have largely focussed on the use of herbicides, consisting of target-specific chemical pesticides used to kill or control unwanted plants [15]. Opposed to this, biological and integrated control have received much less effort and investment, despite the fact that these methods proved highly successful in other parts of Africa and the world. Integrated control involves the use of two or more methods to achieve optimum control. Available control methods include mechanical control, physical removal, application of herbicides and the importation and release of biological control agents [9].

A biological control programme was implemented in 1973, but was discontinued in 1975 because of interference from uncoordinated herbicide control operations. Legislation, in the form of the Conservation of Agricultural Resources Act in 1983, has declared the water hyacinth an aquatic weed that must be controlled. Control is aimed at managing infestations to acceptable levels of about 10% cover rather than targeting it for complete eradication. Under this legal obligation, biocontrol was resumed after the Department of Water Affairs and Forestry (DWAF) instigated a country-wide integrated management plan to control the weed in 1985/1986. This still largely involved the use of herbicides, with limited attention to biocontrol [22]. Currently, the main focus of integrated control in South Africa is a combination of biological and herbicidal control. With the exception of cables spanned across rivers to collect the weed, no large scale mechanical control is practised at this stage [9].

The biological control of water hyacinth in South Africa relies on six established agents, the largest number in all countries involved in such programmes against water hyacinth. The most popular agents are the *Neochetina* weevils (see Figure 1.3). After years of thorough research, these agents can now be easily and relatively cheaply distributed worldwide [9].

Figure 1.3: *The* Neochetina eichhorniae *adult weevil.*

The Working for Water funded mass rearing centre for weed biological control agents is based at the South African Sugarcane Research Institute (SASRI) in Mount Edgecombe in KwaZulu-Natal [17]. SASRI, with its specialized entomological skills, has proven to be highly efficient in the mass production of weed biocontrol agents. Aquatic weed BCAs are reared on their host plants in portable pools and the terrestrial agents in portable greenhouses and old water settling tanks converted into shade houses. Mass rearing and re-releases are aimed at establishing the full suite of natural enemies at all sites throughout the country, to ensure that inappropriate release methods used previously were not the cause of non-establishment [7].

Figure 1.4: *New Year's Dam, South Africa, where* N. eichhorniae *was released in 1990 and by 2000 had reduced the infestation to 10% cover. In 1997 (left), the dam was more then 90% covered by water hyacinth. In 2003 (right), water hyacinth covered less than 10% of the dam* [10].

Biological control in South Africa has been effective in certain areas such as the New Year's Dam in the Eastern Cape (Figure 1.4), but remains hampered by certain restrictions [7]. Firstly, *unsuitable climatic conditions* like cold winters and frequent frost may restrict some of the species to become abundant and control the weed. Successful biological control of water hyacinth elsewhere in the world highly correlates with tropical or subtropical climates. Secondly, *high nitrogen and phosphorus levels* in infested waters allow the weed to thrive and reproduce rapidly. BCAs are often unable to suppress the resulting sudden and massive growth of the host plant. Measures to limit the plant growth rate, such as the upgrading of waste-water treatment works and investigation into industrial effluent (and therefore nutrient control), is an ongoing process. Finally, *flooding, herbicide application and mechanical removal programmes* regularly remove the natural enemy populations as well as the water hyacinth infestations, limiting the success of biological control. When cleared or treated water bodies are re-infested after these removals, the enemies are absent, resulting in rapid and abundant growth of the weed [7, 22].

The sound and cost-effective management of the water hyacinth weed also remains a challenge in South Africa.

1.2 Problem description

Over the years, different biological control methods have been developed. *Classical biological control* consists of three steps:

1. Finding an appropriate natural enemy in the weed's land of origin.
2. Putting the BCAs through studies under quarantine to determine which plant species could be damaged by the agents, making them candidates to be released only if they do not pose a threat to other organisms [14].
3. With the necessary consent, releasing the BCAs that survived quarantine directly in the new habitat [9].

This process consists of a once off release of BCAs and yields a relatively small amount of agents to be released at any one time. Even though successful biological control of water hyacinth has been achieved, this method takes a long time to be effective.

Another biological control approach has evolved. This approach involves the same first two steps as classical biological control, however, once BCAs have been cleared from quarantine, they are taken to a *mass rearing* facility. With the use of mass rearing technology, the BCAs can be reared in very large numbers before they are released. In addition to this, this method also makes more frequent re-releases possible. As a result, *more* BCAs may be *frequently* released to speed up biological control [1].

The BCAs should be managed in such a way that water hyacinth may be combatted in the most effective way. At the moment, institutions are just releasing as many BCAs as possible at a time. The cost of rearing these agents makes it worth the while to investigate the releasing process in order to determine whether there exists a release strategy that would yield optimum results [1].

In this study, mathematical modelling will be used to compare the classical approach to the mass rearing approach in terms of cost-effectiveness, determining whether the faster decrease in water loss is worth the expenses pertaining to mass rearing programs.

1.3 Scope and objectives

The scope of the research will only consider biological control of water hyacinth in South Africa. This narrows the temperature range that will be taken into account down to the applicable possible temperatures in this country.

Biological control of water hyacinth in South Africa currently relies on two weevil species (*N. bruchi* and *N. eichhorniae*), the water hyacinth bug, a pyralid moth, a galumnid mite and a leaf sap sucker [17]. The scope is limited to the *N. eichhorniae* weevil species and how it can be optimally utilised as BCA in South Africa.

The mean-field approximation is assumed throughout the study. This entails the assumption that all the individuals are evenly spread out over a specified area and can all reach another point within this area in the same amount of time. This is acceptable due to the fact that a small enough unit of area will be considered.

When considering the cost of water loss, the benefit that land owners or farmers may have from more available water will not be taken into account, only the price of water.

The primary objectives of this study are:

1. Perform a literature study of the different life cycles of the water hyacinth and the *N. eichhorniae* weevil.

2. Perform a literature survey of mathematical models previously formulated to describe the interaction between the two species.

3. Construct a model to mathematically describe the water hyacinth population growth and its interaction with the populations of the various life stages of the *N. eichhorniae* weevil as BCA.

4. Use the model to evaluate the cost-effectiveness of mass rearing programs in biological control versus classical biological control as well as to provide guidance towards the optimal magnitude and frequency of BCA releases.

5. Expand on the scope of the model and provide ideas for possible future studies.

CHAPTER 2

Literature review

This chapter consists of two main sections, namely the biological and mathematical background applicable to this study. The life cycles of both the water hyacinth and the *N. eichhorniae* weevil are discussed in §2.1. The mathematical models formulated to model the interaction between the two species are discussed in §2.2.

2.1 Biological background

In order to model biological control strategies for water hyacinth, it is necessary to investigate the life-cycles of the plant and its enemies as well as the way they influence each other.

2.1.1 Origin and distribution of water hyacinth

In 1823, the German naturalist C. von Martius discovered the species while carrying out floral surveys in Brazil. He named it *Pontederia crassipes.* Sixty years later, it was included in the *Eichhornia* genus. The reason for the world-wide distribution of this weed is generally accepted to be due to its ornamental value or as feed while totally ignorant of the plant's invasive capabilities and the enormous negative ecological impact it would have on fresh water ecosystems. The native range of *E. crassipes* is spread throughout South America and parts of central America [8].

In North America, water hyacinth is believed to have been introduced in 1884 at the Cotton States Exposition in New Orleans, Louisiana. Since its introduction to Louisiana, it has spread to about 50% of the states in the USA [8].

Asia was invaded towards the end of the 19^{th} century via Japan and Indonesia where the weed grew naturally in rice fields and as an ornamental plant in botanical gardens. In India it first appeared in Bengal at the beginning of 1890. It has also established in Taiwan and China as early as 1901 as a good fodder plant [8].

Water hyacinth was first noticed in Australia in Brisbane, Sydney and Grafton in the 1890s and has since spread to all mainland states. In 1962, it expanded its territory to Papua New Guinea. New Zealand, Bangladesh and many islands in the Pacific Ocean [8].

Europe has been affected by water hyacinth through Portugal since 1939. JF Potter commented in *The Environmentalist* that water hyacinth has also been observed in the wild in Britain and quoted: "Invasive species, particularly those associated with aquatic habitats, are out competing many of Britain's native plants and the law is doing nothing to stop them…" [13].

In recent times, the following factors have assisted in allowing the weed to disperse:

- A lack of enforcement of relevant legislation or in some cases no relevant legislation,
- the lack of general public awareness, and
- the lack of political will-power to step in.

Africa has been particularly affected by the introduction and spread of water hyacinth [8].

2.1.2 Life cycle of water hyacinth

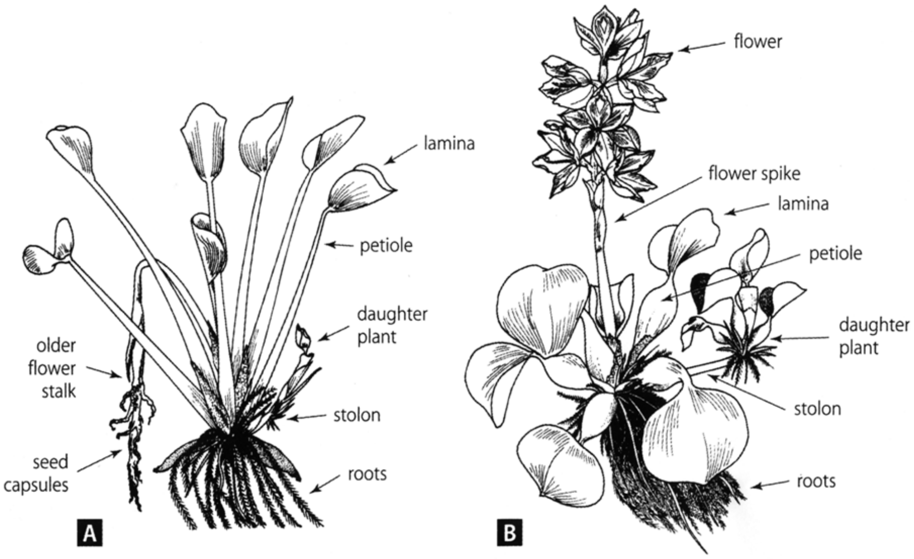

Figure 2.1: *Water hyacinth plants with (A) slender petioles and (B) bulbous petioles* [9].

Water hyacinth, growing in ideal conditions, has an incredible mechanism to outgrow any native species occurring in the system. It can reproduce in two ways: vegetatively and sexually.

- The main method of reproduction is *vegetatively*. The "mother" plant produces new plants from stolons (see Figure 2.1). Winds, currents and wave actions help to spread the plant to other areas. From 10 adult plants, about 655 360 daughter plants can be produced in a single growing season. Thus it has the capacity to increase sevenfold in 50 days, doubling its size in as little as a week. The edge of the surface mat extends by 60cm per month. Two plants can multiply to 1 200 plants in 120 days. The surface area increases by an average of 8% per day and the surface mat can double every 6.2 days [8].

- *Sexual* reproduction is known to be limited. The ovary of one plant may produce up to 500 ovules, with an average of 44.2 and a maximum of 50 seeds per capsule/ovule. Research indicates that an average seed germination rate of as high as 87.5% is possible. More than 90 000 capsules have been observed in an area of one hectare. This equates to 45 million seeds per hectare. Seeds are produced several times a year following flowering. Pollination by insects rarely occurs, but when the plant starts to wilt, self-pollination is common. Water hyacinth seeds may remain dormant for up to 20 years until the correct climatic conditions arise for it to germinate. Seeds germinate in warm, shallow water or on moist sediments. Flowering may occur 10 - 15 weeks thereafter. Plants may flower throughout the year if the climate and environmental conditions are favourable [8, 17].

The presence of nitrogen and phosphorus wastage in water bodies encourage an even faster growth of the plant.

2.1.3 Life cycle of the mottled water hyacinth weevil (*N. eichhorniae*)

A generalised life cycle of the *N. eichhorniae* weevil may be seen in Figure 2.2. A more detailed discussion of the weevil's various life stages follows:

Eggs: Slender, soft, single eggs are laid under the epidermal layers of the leaves. Under temperatures of 25°C, females lay between 5 and 7 eggs per day. A female can lay a total of approximately 300 eggs in her lifetime. Eggs need high temperatures to develop normally and will not hatch at temperatures under 15°C.

Larvae: Larvae develop through three instars. Newly hatched, they tunnel through the lower parts of the petioles and find themselves in the crown of the plant where they dig small pockets and feed on new buds. As the plant grows, the more matured instar larvae, now established in the older outer leaves, sometimes make their way back to younger leaves where their feeding causes severe damage. The development rates depend highly on the quality of the plant and the temperature.

Pupae: Fully grown larvae exit the crown and make their way down to the roots where they pupate under water. They build a cocoon out of pieces of root hair and attach it to larger established roots. They can remain in the cocoon for several months.

Adults: Adults are nocturnal and hide themselves during the day near the crown of the plant to protect themselves against severe heat which may reduce egg production and even cause death. They start feeding on the outside of the plant within 24 hours of its appearance whereafter the production of eggs commences about 6 days later. The male and female ratio is generally close to 1, although in South Africa females seem to dominate on healthy plants while there is an excess of males on unhealthy plants.

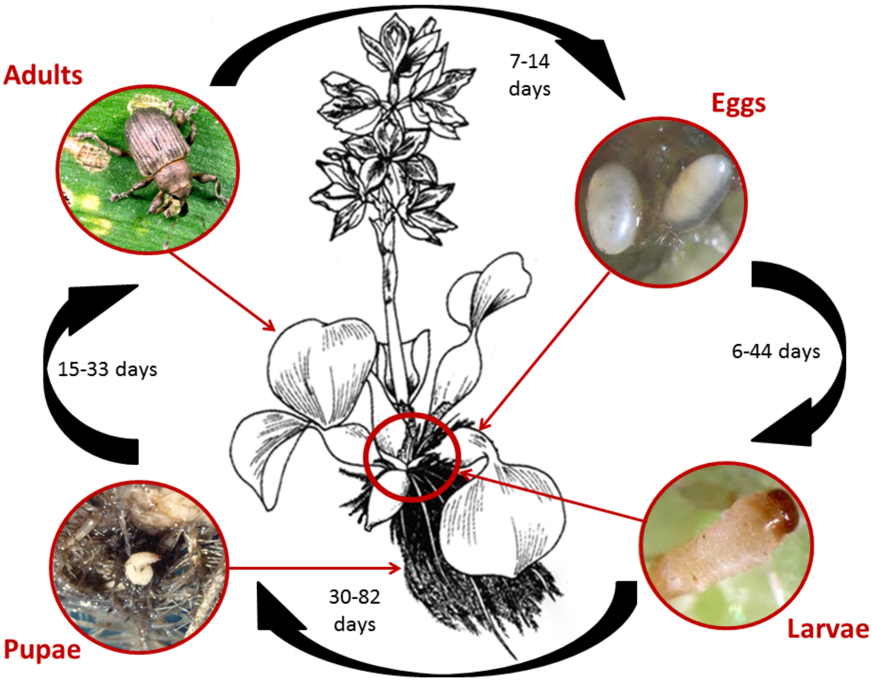

Figure 2.2: *Life cycle and development duration for each stage of the* N. eichhorniae *weevil and its occurrence on different organs of the water hyacinth.*

2.1.4 Impact of weevils on water hyacinth

Figure 2.3: *Leaf feeding scars caused by* N. eichhorniae *adults.*

Both the *N. eichhorniae* larvae and adults feed on the plant. Adult beatles feed externally on the epidermal layers of the leaves leaving behind its trademark of small, semi circular scars, as may be seen in Figure 2.3.

Heavy feeding by adults on the lamina causes leaves to dry out and curl. The larvae's tunnelling into the petioles and the crown of the plant causes the petioles to become thin and fragile and plants to become waterlogged until they eventually sink and die. In the long-term, the weevils' influence results in a reduction of production of flowers, leaves and daughter plants. Dense mats of water hyacinth start to break up, with patches of water becoming visible between the plants. New areas of growth and small plants are affected first, leaving behind a stand of plants with more uniform size and structure. As the sizes of the mats decrease over time, it becomes easier to eliminate them. The speed and efficiency with which control is achieved depends, amongst other factors, on the number of insects released and their distribution through the infested areas [9, 17].

N. eichhorniae is the most popular of the introduced BCAs, although its effectiveness is reduced by floods, physical removal of plants and herbicide sprays [17].

2.2 Mathematical modelling

The increasing use of mathematical models in population biology, whether dealing with a human population, a population of an endangered species, bacterial or viral growth, has helped in understanding the dynamic processes involved in the field and in making practical recommendations. The study of population change has a very long history. In 1202 an exercise in an arithmetic book written by Leonardo of Pisa involved building a mathematical model for a growing rabbit population. Many subsequent examples followed in later decades, for example, the well known Lotka-Volterra equations for describing predator-prey interactions in ecology[1] [16]. Mathematical models have also been applied to competition interactions, renewable resource management, evolution of pesticide resistant strains, ecological and genetically engineered control of pests, multi-species societies and plant-herbivore interactions, to name but a few [11].

When species interact, the population dynamics of each species is affected. Two-species systems are considered in this study. More specifically, plant-herbivore interactions which resemble predator-prey interactions to a certain extent, however, with one species being static, are considered.

2.2.1 Differential equations and predator-prey systems

Differential equations relate unknown functions of variables with their derivatives. These equations may be used when the relationship between the varying quantities of the solutions (expressed as the set of functions that satisfies the equations) and their rates of change over time (expressed as the functions' derivatives) are known or assumed [23]. Differential equations thus

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[1] Ecology refers to the study of the interrelationship between species and their environment.

come in handy where changes are noticed in real-world problems and predictions about future behaviour on the basis of how current values change are required [16].

Predator-prey systems take the form of a pair of linked differential equations. Consider the situation where one species, the prey, has an unrestricted supply of food and the other species, the predator, feeds on the prey. An example of this is where rabbits represent the prey and foxes the predators. This will yield a model of two dependent variables where both are functions of time. Let $R(t)$ be the number of rabbits (prey) and $F(t)$ the number of foxes (predators) at time t. In the absence of predators, the abundant supply of food will support exponential growth of the prey, that is,

$$\frac{dR(t)}{dt} = kR(t),$$

where k is a positive constant. In the absence of prey, the predator population will decline at a rate proportional to itself, that is,

$$\frac{dF(t)}{dt} = -rF(t),$$

where r is a positive constant. In the case where both species are present, the primary cause of death among the prey is being eaten by a predator, while the birth and survival rates of the predators depend on the availability of food, that is, the prey. It is assumed that the two species encounter each other at a rate that is proportional to both populations, that is, proportional to the product $R(t)F(t)$. The more there are of either population, the more encounters there are likely to be. The system of two differential equations governing this scenario is given by

$$\frac{dR(t)}{dt} = kR(t) - aR(t)F(t) \quad \text{and} \tag{2.1}$$

$$\frac{dF(t)}{dt} = -rF(t) + bR(t)F(t), \tag{2.2}$$

where a and b are also positive constants. The term $-aR(t)F(t)$ decreases the natural growth rate of the prey and the term $bR(t)F(t)$ increases the natural growth rate of the predators [11, 16].

Equations (2.1) and (2.2) are known as the *predator-prey equations* or the *Lotka-Volterra equations*. A solution of this system of equations is a pair of functions $R(t)$ and $F(t)$ that describe the populations of prey and predators as functions of time. Because $R(t)$ and $F(t)$ occur in both equations, the system is coupled and the equations have to be solved simultaneously [16].

2.2.2 A logistic growth model for water hyacinth populations

Wilson *et al.* have modelled water hyacinth population growth (excluding weevil interaction) using a logistic model

$$\frac{dP}{dt} = rP\left(1 - \frac{P}{K}\right), \tag{2.3}$$

where P denotes the biomass density of water hyacinth plant material (kg/m^2), r the intrinsic growth rate of the plant per day and K the carrying capacity (kg/m^2) [25].

At low plant densities, the population will increase at its intrinsic growth rate, r. As the density of plants approaches the carrying capacity, K, the rate of increase in water hyacinth population tends linearly to zero (see Figure 2.4). If the density is above the carrying capacity, the population will decrease to K [25].

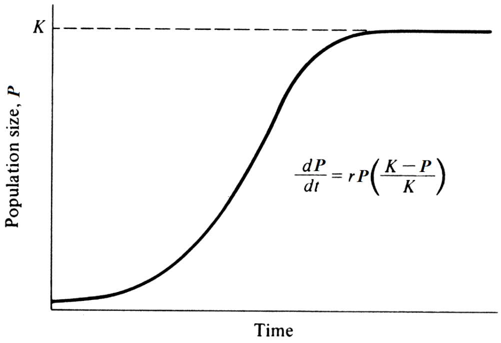


Figure 2.4: *Water hyacinth population (biomass) plotted against time.*

2.2.3 Modelling water hyacinth and weevil interaction

Wilson *et al.* also presented the following plant–herbivore model to investigate the introduction of the *N. eichhorniae* weevil as BCA to water hyacinth:

$$\frac{dP}{dt} = rP\left(1-\frac{P}{K}\right) - c_1A\left(1-e^{-d_1P}\right) \tag{2.4}$$

$$\frac{dA}{dt} = A\left(-a+c_2\left(1-e^{-d_2P}\right)\right), \tag{2.5}$$

where the first term of equation (2.4) represents the logistic growth of the plant as discussed in §2.2.2, the second term of equation (2.4) represents the plant's interaction with the weevil and equation (2.5) represents the population growth of the weevil, dependant on the density of the plant. Here, A denotes the weevil population, $-a+c_2$ the maximum rate of *increase* for the weevil population when there are many plants (e^{-d_2P} is approximately zero) and a the maximum rate of *decline* for the weevil population, when there are few plants (e^{-d_2P} is approximately 1) [26]. These interactions are shown in Figure 2.5.

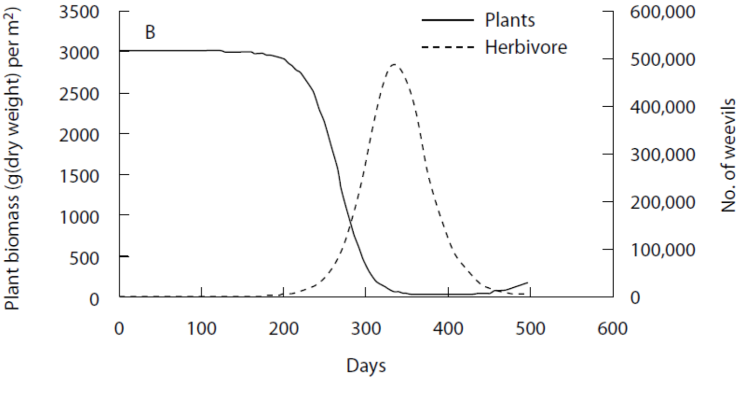


Figure 2.5: *Plant-herbivore model output* [26].

This model does not include the different stages of the weevil's life cycle. It is assumed that all weevils have the same effect on the plant while in reality late larval stages are the most damaging. A time delay to the growth of the weevil was added to account for this. This model also excluded the effect that different temperatures have on population growth [26].

2.2.4 Stage-structured population model of *N. eichhorniae*

Kendall Hauptfleisch, a MSc student at the University of the Witwatersrand, presented a stage-structured population model of *N. eichhorniae*. This model excludes any interaction with water hyacinth. The larval and adult weevil population growth under cold and warm temperatures were tested and yielded the outcomes as illustrated in Figure 2.6 [6]. It may be seen that the population densities at the warm site are much higher than the population densities at the cold site. At both sites, the population density of larvae are significantly higher than the population density of adult weevils.

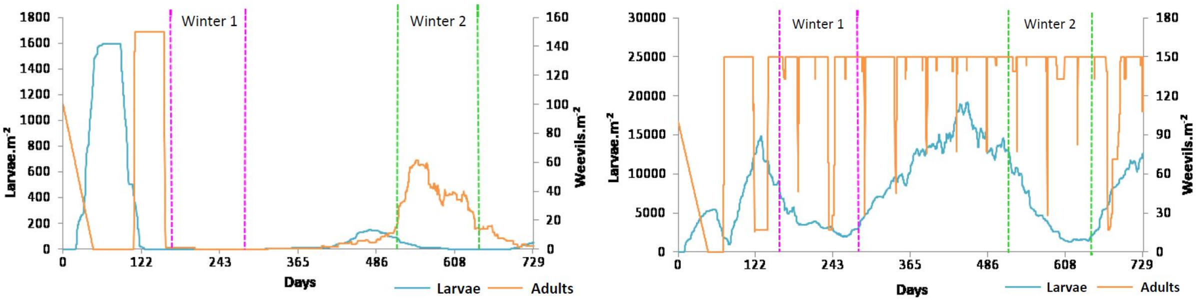


Figure 2.6: *Cold site (Delta Park) and warm site (Mbozambo Swamp)* [6].

The weevils do not have a stable stage-structure in the field. There appears to be systematic variation in the proportion of larvae to adults. Because the larvae and adults have different effects on the plant, changes in the stage-structure of the weevil population will cause changes in the average herbivory pressure per weevil. If the different herbivory effects are included (i.e. damage is caused predominately by older larvae), the model needs to explicitly express some form of age or stage-structure [24].

CHAPTER 3

Methodology

A stage-structured plant-herbivore model, formulated as coupled delay-differential equations, is used to govern the water hyacinth and weevil system. A description of the stage-structured nature of the model is given in §3.1, whereafter the mathematical description of the model and cost function are given in §3.2 and §3.3, respectively. The assumptions made as well as the parametrisation of the model are then discussed in §3.4 and §3.5. The chapter concludes with a model verification and a model validation in §3.6 and §3.7.

3.1 Stage-structure

For the purpose of this study, stage-structure will only be added to the weevil population and not the water hyacinth population. The water hyacinth will be considered only at its mature stage to evaluate the influence that the weevils will have on an established water hyacinth population, investing a water body to its carrying capacity.

The weevil population is represented by five development stages: eggs, young larvae, old larvae, pupae and adults. All individuals within each of these stages may be regarded as functionally identical by having the same per capita vital rates. By adding the stage-structure, the model takes more detail of the life-history of the weevils into account, making it a more realistic representation. In particular, the density-dependent mortality in the larval stage of the weevil population may be modelled explicitly.

Individuals enter a stage by developing from the previous stage or by reproduction from the mature stage. Individuals leave a stage through death or, for immature stages, through maturation (see Figure 3.1).

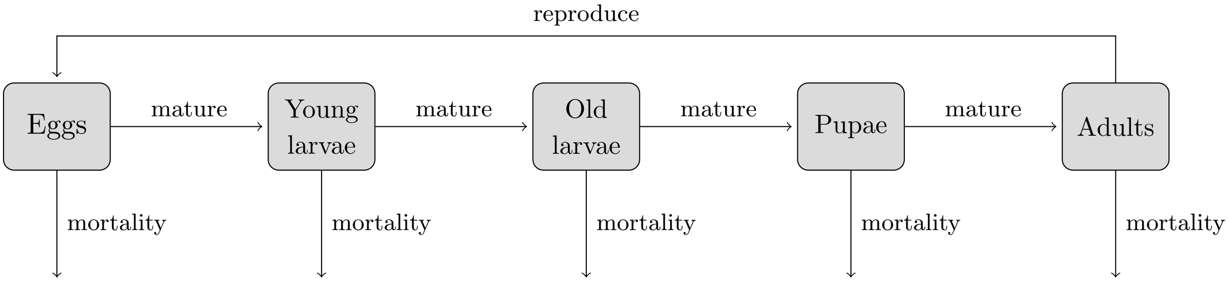


Figure 3.1: *Diagram of the* N. eichhorniae *weevil's life cycle.*

3.2 Model structure and notation

The number of equations is limited to the number of stages that have density-dependent processes (mortality, feeding or fecundity). The two larval stages and the adult state will therefore be sufficient to represent the weevil population. Let $W(t)$ denote the biomass density of water hyacinth material at time t (kg/m^2) and $L_1(t), L_2(t)$ and $A(t)$ denote the densities of young larvae, old larvae and adult weevils per m^2 at time t, respectively.

The rate of change in the water hyacinth and weevil populations may be represented by

$$\frac{dW(t)}{dt} = r(\theta)W(t)\left(1-\frac{W(t)}{K}\right) - c_{L_2}(\theta)L_2(t)\left(\frac{W(t)}{W(t)+h}\right), \tag{3.1}$$

$$\frac{dL_1(t)}{dt} = q(\theta)A(t-t_E(\theta))\sigma_E(\theta) - \mu_{L_1}(\theta)L_1(t) - j\frac{L_1(t)}{W(t)}L_1(t) - L_1(t-t_{L_1}(\theta))\sigma_{L_1}(\theta), \tag{3.2}$$

$$\frac{dL_2(t)}{dt} = L_1(t-t_{L_1}(\theta))\sigma_{L_1}(\theta) - \mu_{L_2}(\theta)L_2(t) - L_2(t-t_{L_2}(\theta))\sigma_{L_2}(\theta) \text{ and} \tag{3.3}$$

$$\frac{dA(t)}{dt} = L_2(t-t_{L_2}(\theta))\sigma_{L_2}(\theta)\sigma_P(\theta) - \mu_A A(t) + RX(t), \tag{3.4}$$

where θ denotes the temperature in °C, $r(\theta)$ the intrinsic growth rate of the plant per day and K the carrying capacity (kg/m^2) of the water resource. Furthermore, $c_{L_2}(\theta)$ denotes the rate of damage caused by the older larvae and h the plant density at which herbivore feeding is reduced by half. In (3.2), $q(\theta)A(t-t_E)$ represents the number of eggs laid t_E days ago, where $q(\theta)$ denotes the rate of oviposition of viable eggs, $t_i(\theta)$ the duration in days of stage i of the weevils, $\sigma_i(\theta)$ the maturation rate per day for stage i and $\mu_i(\theta)$ the density independent mortality rate per day for stage i. Also in (3.2), j denotes the density-dependent scaling parameter that is equal to the number of kilogrammes of plant material per young larva at which the young larva population growth rate is zero, assuming density only affects the survival of young larvae. Finally, R denotes the fixed amount of new adult weevils released per m^2 at any time and

$$X(t) = \begin{cases} 1 & \text{if adults are released at time } t \\ 0 & \text{otherwise.} \end{cases}$$

For the classical approach, $X(t)$ will be equal to 1 only at time $t=0$.

Intrinsic growth rate of water hyacinth

The growth rate of water hyacinth, $r(\theta)$, is given by

$$r(\theta) = r_{max}f(n,p)g(\theta), \tag{3.5}$$

where r_{max} denotes the maximum growth rate of the plant per day (worst case scenario), n and p denote the concentration of nitrogen and phosphorus in the water (mg/l) and θ the temperature (°C). Wilson *et al.* proposed that the growth rate of water hyacinth increases linearly with temperature up to an optimum (θ_h^{opt}) and decreases linearly with temperatures above that [25]. The temperature function, $g(\theta)$, is given by

$$g(\theta) = \begin{cases} 0 & \text{if} \quad \infty < \theta \leq \theta_h^{min} \\ \frac{\theta-\theta_h^{min}}{\theta_h^{opt}-\theta_h^{min}} & \text{if} \quad \theta_h^{min} < \theta \leq \theta_h^{opt} \\ \frac{\theta_h^{max}-\theta}{\theta_h^{max}-\theta_h^{opt}} & \text{if} \quad \theta_h^{opt} < \theta < \infty. \end{cases} \tag{3.6}$$

No growth at temperatures below the minimum temperature will therefore occur. However, it is assumed that plant growth will be affected negatively at temperatures higher than the maximum temperature.

The function of nitrogen and phosphorus concentration in the water, $f(n,p)$, is given by

$$f(n,p) = \begin{cases} \frac{p}{p+h_p} & \text{if} \quad \frac{n}{p} > \frac{h_n}{h_p} \\ \frac{n}{n+h_n} & \text{if} \quad \frac{n}{p} \leq \frac{h_n}{h_p}, \end{cases} \tag{3.7}$$

where h_n and h_p (mg/l) are the half-saturation coefficients for nitrogen and phosphorus, respectively.

Wilson *et al.* [25] showed that under constant experimental conditions, water hyacinth follows logistic growth, with $r_{max} = 0.11$/day and $K = 70$ kg/m^2.

The nitrate-nitrogen concentration is set to $n = 1.4$ mg/l and the phosphate concentration to $p = 0.3$ mg/l. This is the same levels that Tucker and DeBusk used in an experiment on the growth of water hyacinth in Florida over 1 year [21].

In line with what Wilson *et al.* [25] did, h_n is set equal to 0.2 and h_p to $h_n/7$. Substituting these values together with the fixed nitrogen and phosphorus levels into equation (3.7) yields a constant function of nitrogen and phosphorus concentration in the water of $f(n,p) = 0.875$.

The water hyacinth daily growth rate, $r(\theta)$, measured at different temperatures, is given in Figure 3.2.

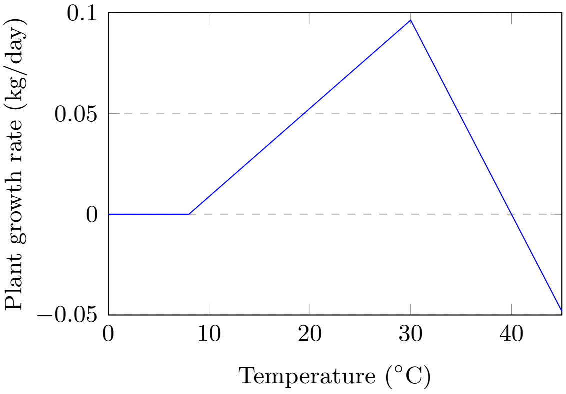


Figure 3.2: *Water hyacinth growth rate per day, $r(\theta)$, measured at different temperatures and assuming parameter values given in Table 3.2.*

Development duration of life stages of weevil

Time lags are used to account for the time it takes for the weevil to develop from one stage in its life cycle to the next. At time $t = 0$, following adult releases of weevils, there are only adult weevils present in the system, with the number in all other stages equal to 0. It is assumed that the adults immediately start laying eggs, leading to young larvae entering the system after $t_E(\theta)$ days. Old larvae are expected to start appearing $t_{L_1}(\theta)$ days after this. The development rate per day of each stage increases linearly with temperature up to an optimum (θ_i^{opt}) and decreases linearly with temperatures above that. This rate, $\alpha_i(\theta)$, with $i = E, L_1, L_2$ or P, is given by

$$\alpha_i(\theta) = \alpha_i^{max} h_i(\theta), \tag{3.8}$$

where α_i^{max} denotes the maximum development rate per day of stage i of the weevil's life cycle ($i = E, L_1, L_2$ or P) and $h_i(\theta)$ its temperature function given by

$$h_i(\theta) = \begin{cases} \frac{\theta - \theta_i^{min}}{\theta_i^{opt} - \theta_i^{min}} & \text{if} \quad \theta_i^{min} < \theta \leq \theta_i^{opt} \\ \frac{\theta_i^{max} - \theta}{\theta_i^{max} - \theta_i^{opt}} & \text{if} \quad \theta_i^{opt} < \theta < \theta_i^{max} \\ 0 & \text{otherwise.} \end{cases} \tag{3.9}$$

The daily development rate for each stage will thus increase linearly from the minimum temperature (θ_i^{min}) up to the optimum temperature (θ_i^{opt}), and decrease linearly for temperatures above that up to the maximum temperature (θ_i^{max}). The development rate of each stage will be zero for all temperatures below θ_i^{min} and above θ_i^{max}.

The development duration of each stage in days, $t_i(\theta)$, with $i = E, L_1, L_2$ or P, is then given by

$$t_i(\theta) = \begin{cases} \frac{1}{\alpha_i(\theta)} & \text{if} \quad \frac{1}{\alpha_i(\theta)} < t_i^{max} \quad \text{and} \quad \alpha_i(\theta) > 0 \\ t_i^{max} & \text{if} \quad \frac{1}{\alpha_i(\theta)} \geq t_i^{max} \quad \text{and} \quad \alpha_i(\theta) > 0 \\ \infty & \text{if} \quad \alpha_i(\theta) = 0. \end{cases} \tag{3.10}$$

The development duration of each stage at different temperatures is given in Table 3.1. The parameter values given in Table 3.2 were used to calculate the development duration per stage.

	Development duration (in days)			
Temperature (°C)	Eggs (t_E)	Young larvae (t_{L_1})	Old larvae (t_{L_2})	Pupae (t_P)
16	44	47	35	33
20	24	47	25.87	29.85
25	12	28.85	14.42	19.90
30	8	20	10	14.93
35	16	40	20	29.85
39	44	47	35	33

Table 3.1: *Development duration (in days) per life stage of the weevil, measured at different temperatures.*

Oviposition rate

The oviposition rate of viable eggs, $q(\theta)$, is given by

$$q(\theta) = q_{max} h_q(\theta), \tag{3.11}$$

where q_{max} is the maximum number of eggs laid per adult per day. The effect of temperature on the oviposition rate appears to be similar to the effect of temperature on the development rates. The applicable temperature function, $h_q(\theta)$, is therefore similar to the temperature function of equation (3.9), but using the minimum (θ_q^{min}), optimum (θ_q^{opt}) and maximum temperatures (θ_q^{max}) for oviposition. The relationship between the oviposition rate and temperature is illustrated in Figure 3.3.

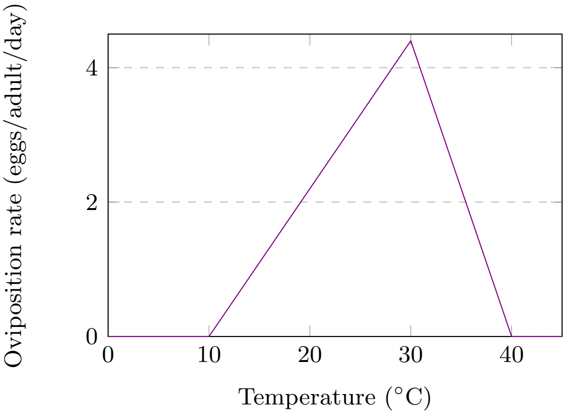


Figure 3.3: *The weevil oviposition rate (eggs/adult/day), measured at different temperatures.*

Rate of damage caused by older larvae

The rate of damage caused by older larvae, $c_{L_2}(\theta)$, is affected by temperature in the same way as the oviposition rate and development rate. It is given by

$$c_{L_2}(\theta) = c_{L_2}^{max} h_{c_{L_2}}(\theta), \tag{3.12}$$

where $c_{L_2}^{max}$ is the maximum rate of damage caused by older larvae and $h_{c_{L_2}}(\theta)$ is similar to the temperature function of oviposition, $h_q(\theta)$, using the same minimum, optimum and maximum temperatures as oviposition.

Stage-specific maturation rates

The maturation rate per day, $\sigma_i(\theta)$, for stage i ($i = E, L_1, L_2$ or P) of the weevil's life cycle, is given by

$$\sigma_i(\theta) = \frac{1}{t_i(\theta)}. \tag{3.13}$$

Stage-specific mortality rates

The density independent mortality rate per day, $\mu_i(\theta)$, for stage i ($i = L_1$ or L_2) of the weevil's life cycle, is given by

$$\mu_i(\theta) = \frac{1 - \beta_i(\theta)}{t_i(\theta)}. \tag{3.14}$$

In (3.14), $\beta_i(\theta)$ denotes the probability of surviving through stage i ($i = L_1$ or L_2), given by

$$\beta_i(\theta) = \beta_i^{max} h_i(\theta), \tag{3.15}$$

where β_i^{max} denotes the maximum probability of surviving through stage i. The temperature function, $h_i(\theta)$, is given by equation (3.9). The surviving probabilities at different temperatures are shown in Figure 3.4. The parameter values given in Table 3.2 were used to calculate the surviving probabilities and mortality rates.

The applicable stage-specific mortality rates per day, averaged over a range of temperatures (15°C - 40°C), equate to μ_{L_1}=0.01904 and μ_{L_2}=0.02594 for young and old larvae, respectively.

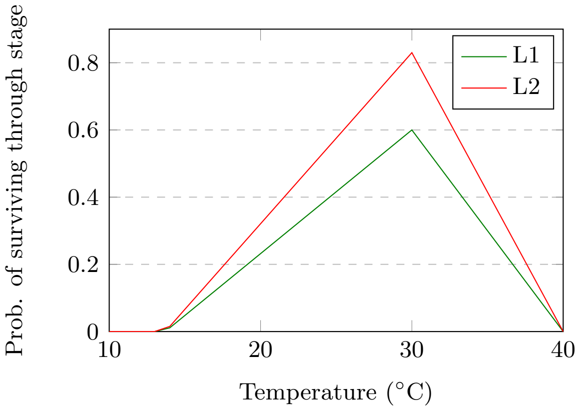


Figure 3.4: *Probability of surviving through life stages of weevil, measured at different temperatures.*

3.3 Cost function

In order to compare the cost-effectiveness of the classical biological control approach and the mass rearing approach, a cost function is constructed. The function adds the costs pertaining to the mass rearing of weevils and the cost of water loss, in terms of water evaporation, together. The cost of water loss will decrease as water hyacinth densities are reduced by the BCAs, since the evapotranspiration rate of water hyacinth is up to 3.7 times the evaporation rate of open water surfaces [20]. The cost function will be used to analyse whether the amount of money saved due to a faster decrease in loss of water per day as a result of more frequent weevil releases from mass rearing facilities, is worth the cost of rearing these weevils. The total cost, C, is given by

$$\begin{aligned} C &= \sum_t [\text{cost of weevils released per day}] + \sum_t [\text{cost of water loss per day}] \\ &= \sum_t [c_{we} R X(t)] + \sum_t [c_{wa} \mathrm{A}(e_h(W(t)) - e_n)] \,, \end{aligned}$$

where c_{we} denotes the cost of rearing a weevil at the mass rearing facilities, c_{wa} the cost of water per litre, A the area in m^2 of the water body under consideration, $e_h(W(t))$ the evapotranspiration rate of water hyacinth and e_n the normal evaporation rate of water.

The relationship between the plant evapotranspiration rate and the density of the plant is assumed to be as illustrated in Figure 3.5. When the plant density is equal to 0 kg/m^2, the evapotranspiration rate of the plant is equal to the evaporation rate of water. At low plant densities, the evapotranspiration rate will increase fast. The rate of increase in the evapotranspiration rate will decrease as the plant approaches the carrying capacity, where the evapotranspiration rate of the plant is 3.7 times the normal evaporation rate of water.

The cost of rearing a weevil, c_{we}, at the mass rearing facilities at SASRI is set equal to R5,50 per weevil [1], while the cost of water, c_{wa}, is set equal to R0,0044/ℓ [19]. The normal evaporation rate of water, e_n, is assumed to be 8.309 ℓ/m^2 [3], while the evapotranspiration rate of water hyacinth at time t is assumed to be given by $e_h(W(t)) = 8.309 + 5.263 \ln(W(t) + 1)$.

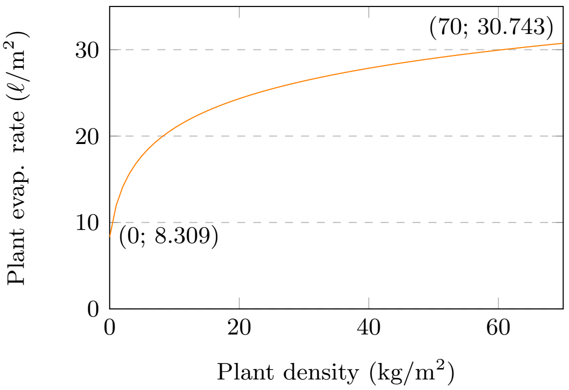


Figure 3.5: *Plant evapotranspiration rate for different plant densities.*

3.4 Assumptions

Several factors affecting the growth of the water hyacinth are not included in the model as it is difficult to quantify. These factors include frost, diseases, saltiness of water, wind, humidity, water currents, floods, light and carbon dioxide concentration [8, 24].

Constant nitrogen and phosphorus levels are assumed. This holds for both the classical biological control model and the model incorporating mass rearing and frequent releases.

While both the *Neochetina* larvae and adults feed on water hyacinth, it is assumed that only the larvae (especially the late larvae instars) cause damage to the plant. In addition to the removal of biomass, tunnelling of larvae can cause nutrient deficiency as well as provide a route of entry for disease-causing micro-organisms. The movement of larvae between leaves and the crown of the plant may also lead to flooding of old larval tunnels and a reduction in plant buoyancy [24].

As adults can remove over 50% of the laminar area, it is possible that adult feeding significantly reduces the plant's rate of photosynthesis. Moreover, adults prefer to feed on the youngest leaves and so any damage may disrupt leaf development. Still, this does not directly affect the rhizome or the meristem, both of which can be damaged by larval feeding. Moreover, there is only a very weak association between adult feeding and pathogen entry. In most cases adult damage is thought to be negligible compared to larval damage [24].

Other aspects of the weevil life are unlikely to cause much damage. Oviposition scars may provide a route for pathogen entry, but the risk from this should be much less than the tunnelling scars caused by mobile larvae. Pre-pupae are not particularly destructive, as only a few root hairs are required to create the pupal cocoons [24].

According to Wilson [24] most of the density dependent mortality appear to occur before the larvae damage the plant. Therefore only the young larvae, L_1, suffer density dependent mortality. It is assumed that the older larvae, L_2, and adults are not affected by density dependent mortality due to their relative mobility.

3.5 Parameterisation

The parameter values and ranges given in Table 3.2 are also assumed in the model.

Parameter	Description	Estimated Value (Range)	Units
h	plant density at which herbivore feeding is reduced by half	0.2	kg/m^2
$c_{L_2}^{max}$	maximum rate of damage caused by older larvae assuming this is the only stage causing damage to the plant	0.0951	kg/larva/day
j	density dependent mortality scaling parameter	0.0054	kg/young larva
q_{max}	maximum oviposition rate of viable eggs	4.4	eggs/adult/day
θ_h^{min}	minimum temperature for water hyacinth growth	8	°C
θ_h^{opt}	optimum temperature for water hyacinth growth	30	°C
θ_h^{max}	maximum temperature for water hyacinth growth	40	°C
θ_q^{min}	minimum temperature for oviposition	10	°C
θ_q^{opt}	optimum temperature for oviposition	30	°C
θ_q^{max}	maximum temperature for oviposition	40	°C
θ_E^{min}	minimum temperature for egg development	15	°C
θ_E^{opt}	optimum temperature for egg development	30	°C
θ_E^{max}	maximum temperature for egg development	40	°C
θ_{L_1,L_2}^{min}	minimum temperature for young & old larvae development	13.7	°C
θ_{L_1,L_2}^{opt}	optimum temperature for young & old larvae development	30	°C
θ_{L_1,L_2}^{max}	maximum temperature for young & old larvae development	40	°C
α_E^{max}	maximum development rate per day for eggs	0.125	-
$\alpha_{L_1}^{max}$	maximum development rate per day for young larvae	0.05	-
$\alpha_{L_2}^{max}$	maximum development rate per day for old larvae	0.1	-
α_P^{max}	maximum development rate per day for pupae	0.067	-
$t_E(\theta)$	duration from oviposition to hatching of eggs	(6-44)	days
$t_{L_1}(\theta)$	duration of young larval stage	(20-47)	days
$t_{L_2}(\theta)$	duration of older larval stage	(10-35)	days
$t_P(\theta)$	duration of pupae stage	(15-33)	days
t_E^{max}	maximum duration from oviposition to hatching of eggs	44	days
$t_{L_1}^{max}$	maximum duration of young larval stage	47	days
$t_{L_2}^{max}$	maximum duration of older larval stage	35	days
t_P^{max}	maximum duration of pupae stage	33	days
$\beta_{L_1}^{max}$	maximum probability of surviving the young larval stage	0.6	-
$\beta_{L_2}^{max}$	maximum probability of surviving the older larval stage	0.83	-
μ_A	density independent mortality rate per day for the adults	0.02	-

Table 3.2: *Model parameters and their corresponding units and values assumed in this study.*

3.6 Model verification

The model was implemented in MATLAB 8.0 (R2012b) where the coupled delay differential equations (DDEs) were solved using the built in function `dde23` [18]. In order to verify the model, a series of tests were performed to determine whether changes in certain parameters and variables yield the expected outcome.

With an increase in the number of adult weevils released in a water hyacinth infested area, the weed is driven to extinction faster, as expected (see Table 3.3).

Number of adults released	Days until extinction of plant
20	55.08
30	50.45
50	46.24
100	42.22

Table 3.3: *The time it takes for varying amounts of adult weevils released per m^2 at time $t = 0$ to achieve control at a temperature of 30 °C.*

The weed is driven to extinction faster at temperatures close to the optimum temperature for weevil development (30°C) and slower at temperatures below and above that, as expected. In fact, the weevils will not manage to drive the weed to extinction at very low or very high temperatures (see Table 3.4), which is also expected, since weevil development is severely restricted at these extreme temperatures.

Temperature (°C)	Days until extinction of plant
15	∞
22	115.56
25	73.41
30	46.24
32	61.49
34	92.56
35	∞

Table 3.4: *The time is takes for 50 adult weevils released at time* $t = 0$ *to achieve control at varying temperatures.*

As one would expect, the model illustrates a faster control of the weed as the rate of damage caused by the weevil is increased, and slower control, up to the point of no control, as the rate of damage is decreased (see Table 3.5).

$c_{L_2}^{max}$	Days until extinction of plant
0.02	∞
0.03	61.05
0.05	52.20
0.0951	**46.24**
0.15	43.94
0.20	41.88

Table 3.5: *The influence that a change in the maximum rate of damage caused by older larvae has on the time until extinction of the plant after a release of 50 adult weevils at time* $t = 0$ *at a temperature of 30 °C. The parameter value used in the model is* $c_{L_2}^{max} = 0.0951$.

3.7 Model validation

It is difficult to validate the model output with what happens in real life as the detailed impact of biological control agents released in infested water bodies has not been thoroughly recorded.

The Engelhard Dam in the Kruger National Park is an example of where biological control of water hyacinth has been successful. The dam has a length of 12.36 kilometres which accumulates to a total surface area of approximately 3 000 m^2 [5]. Engelhard dam was covered with water hyacinth prior to the releases of 20 000 adult hyacinth BCAs, namely *Neochetina bruchi* and *Eccritotarsus catarinensis*, on 27 October 2008. After 72 days, on 7 January 2009, openings in the water hyacinth mat indicated the impact of the BCAs on the plant [2]. It is unknown whether the area was eventually completely cleared from water hyacinth or not.

A simulation of a once off release of 13 *N. eichhorniae* adult weevils per m^2 in a water body infested with water hyacinth at its carrying capacity (70 kg/m^2) was performed. The temperature was set equal to 29°C, corresponding to the average temperature in the Kruger National Park over the time period of October to January. Simulation results indicate that control of water hyacinth may be achieved after 74.21 days, with the weed eliminated after this time period, as illustrated in Figure 3.6.

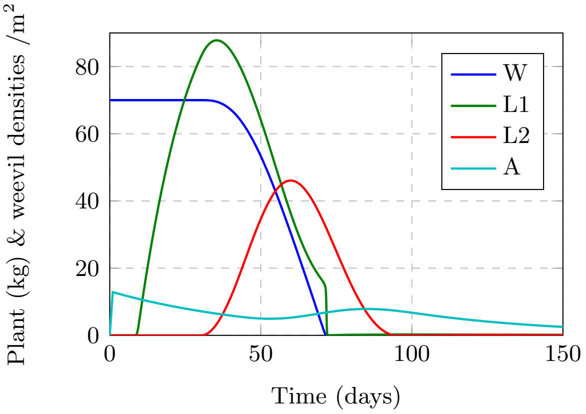


Figure 3.6: *Populations per* m^2 *after a once off release of 13 adult weevils per* m^2 *at time* $t = 0$.

Since the surface area of the Engelhard Dam on which the BCAs were released is unknown and different BCAs were released, it is difficult to compare the model output to this real life scenario. It may still be noted that the model indicates that with 13 *N. eichhorniae* adult weevils per m^2, uniformly spread across the area, a total of 20 000 weevils may clear an area of approximately 1 540 m^2 in 74.21 days. It is important to note that the model assumes a uniform spread of weevils across the entire area, which is not what happens in actual releases. In real life, the adult weevils are typically only released by hand at the edges of the infested water body. This is expected to result in slower suppression of water hyacinth populations.

CHAPTER 4

Results

In this chapter, different release strategies and the cost-effectiveness of the classical biological control approach versus the mass rearing approach are investigated and reported on in §4.1. A sensitivity analysis is also performed in §4.2 in order to ascertain how robust the model output is to changes in parameter values.

4.1 Release strategies

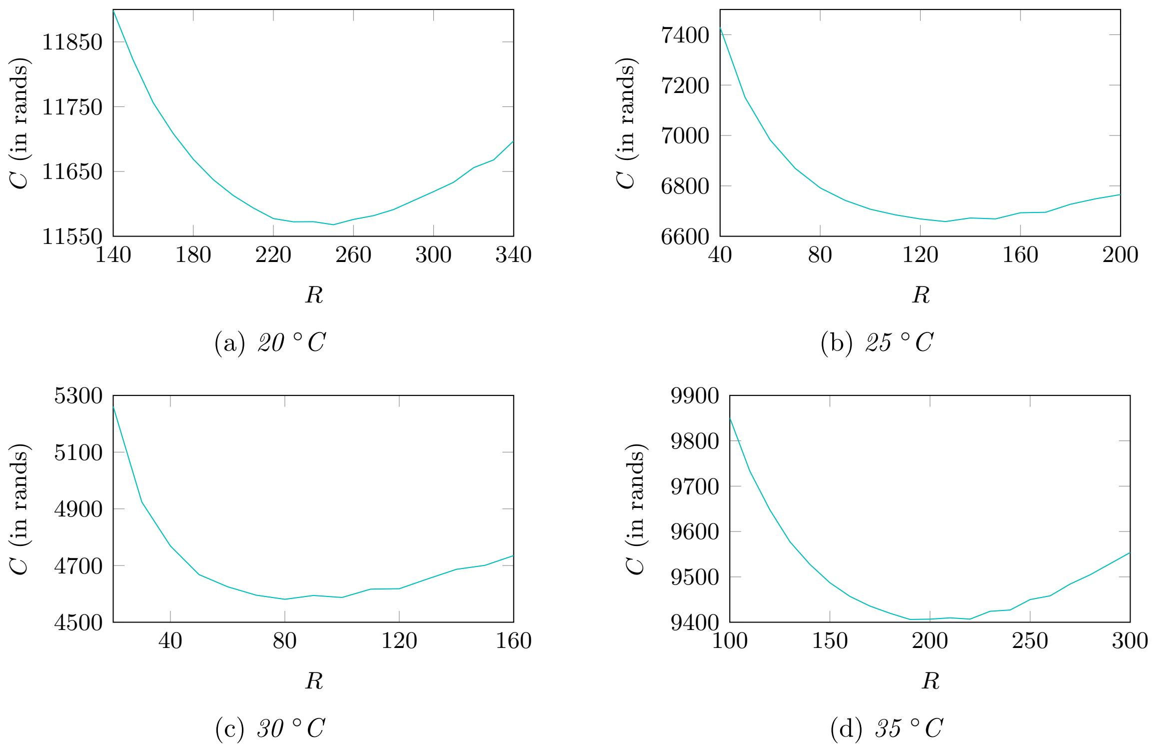
Release strategies for the classical as well as the mass rearing biological control approach are evaluated at different temperatures. The total cost, C, of once off releases are also compared to the total cost of more frequent releases made possible by mass rearing.

4.1.1 Classical biological control approach

Simulations were performed to obtain the total cost, C, for different numbers of adults released, R, at time $t = 0$ in an area of 1 000 m^2 over a period of 300 days. The optimal magnitude of adult releases is defined as the magnitude which yields the lowest total cost. These simulations were performed at temperatures of 20°C, 25°C, 30°C and 35°C to provide guidance towards the optimal magnitude of releases at cold sites, medium temperature sites, ideal temperature sites and warm sites, respectively (see Figure 4.1). Table 4.1 summarises the optimal release strategies for classical biological control. At temperatures below and above the ideal temperature, more adult weevils will be required. It is thus recommended to release BCAs during the time of the year when temperatures are expected to be 30°C on average to minimise the total cost. In reality, more weevils than the optimal magnitude may have to be released to allow for slower weevil development at temperatures varying around the average temperature. The model predicts the minimum total cost during cooler times of the year to be more than double the minimum total cost under ideal climate conditions. The population sizes after once off releases of the optimal magnitudes are given in Figure 4.2, where the control of the weed may clearly be seen.

	Temperature (°C)			
	20	25	30	35
Optimal magnitude (adults/m^2)	250	130	80	190
Total cost	R11 568	R6 659	R4 581	R9 407
Days until extinction	107.48	62.67	43.48	88.41

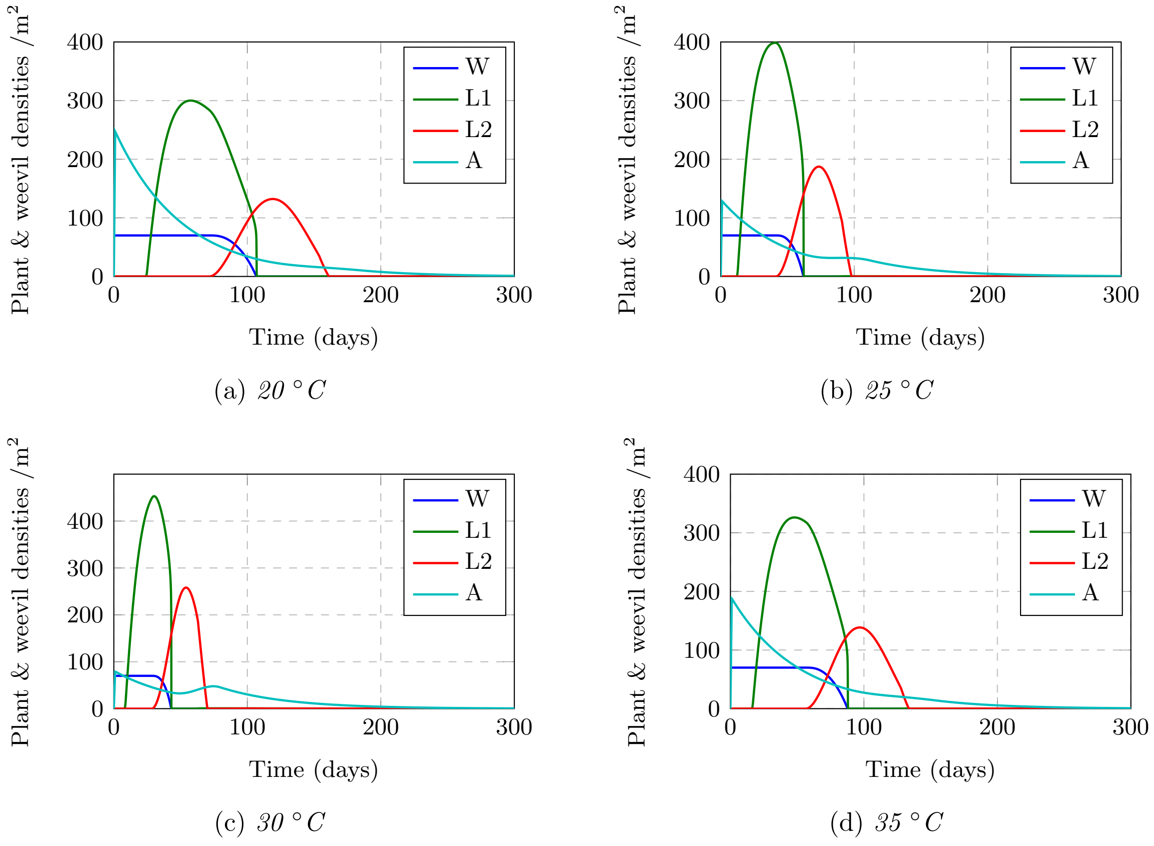
Table 4.1: *Optimal release magnitudes for different temperatures.*



(a) *20 °C* (b) *25 °C*

(c) *30 °C* (d) *35 °C*

Figure 4.1: *The total cost, C, for different numbers of adult weevils released at time $t = 0$, measured at different temperatures.*



(a) *20 °C* (b) *25 °C*

(c) *30 °C* (d) *35 °C*

Figure 4.2: *The populations per m^2 after once off releases of the optimal magnitudes at time* $t = 0$.

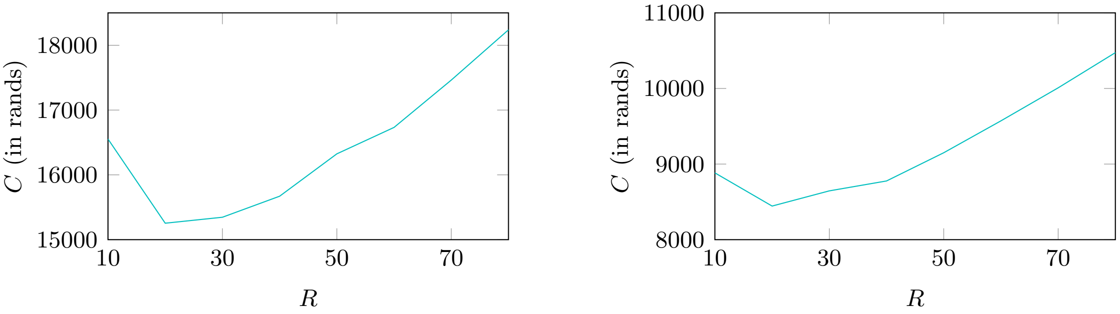
4.1.2 Mass rearing biological control approach

In order to compare the classical approach with the mass rearing approach, the magnitude of adult weevil releases, yielding the minimum total cost for different frequencies of releases at different temperatures, was determined by means of repeated simulation runs. Simulations were performed for an area of 1 000 m^2 over a period of 300 days at different temperatures. In Figure 4.3, the total cost, C, for different numbers of adult weevils released once a week at different temperatures may be seen. The total cost evaluations for the other frequencies are illustrated in Figures A.1 – A.4. The results are summarised in Table 4.2. It may be seen that the total cost is always lower at temperatures close to 30°C and higher at temperatures above and below the optimal temperature.

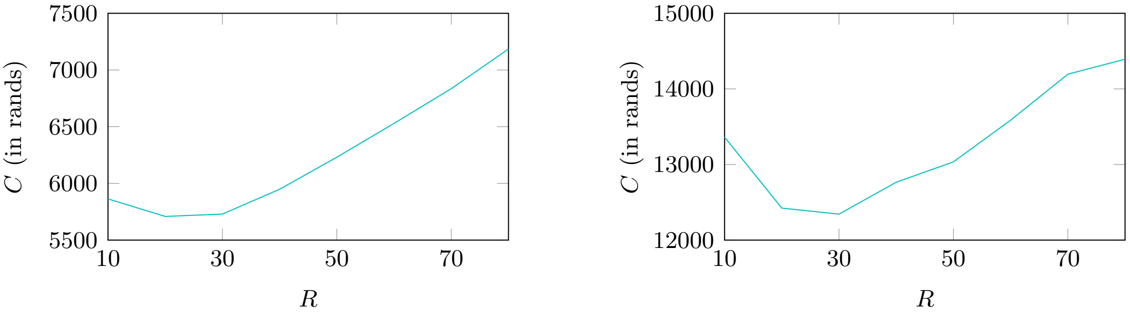
It is suggested that the optimal frequency for temperatures ranging between 20°C and 35°C will be a release *every fifth week*. The model output suggests that it is more cost-effective to release weevils less often. The populations after once a week releases of the optimal magnitudes are given in Figure 4.4. The weekly increase in the adult populations due to frequent releases and the extinction of the weed may clearly be seen.

		Temperature (°C)			
Frequency of releases		20	25	30	35
Every week	Optimal magnitude (adults/m^2)	20	20	20	30
	Total cost	R15 254	R8 445	R5 709	R12 344
	Days until extinction	139.05	76.51	50.70	104.74
	Total number released (adults)	400	220	160	450
Every second week	Optimal magnitude (adults/m^2)	60	60	30	40
	Total cost	R14 853	R8 175	R5 395	R11 987
	Days until extinction	126.02	68.76	49.93	109.29
	Total number released (adults)	540	300	120	320
Every third week	Optimal magnitude (adults/m^2)	80	50	40	70
	Total cost	R14 429	R7 929	R5 209	R11 556
	Days until extinction	125.21	72.55	47.91	102.90
	Total number released (adults)	480	200	120	350
Every fourth week	Optimal magnitude (adults/m^2)	80	60	50	80
	Total cost	R14 266	R7 643	R4 943	R11 358
	Days until extinction	128.95	70.69	46.21	102.71
	Total number released (adults)	400	180	100	320
Every fifth week	Optimal magnitude (adults/m^2)	100	80	50	100
	Total cost	R13 969	R7 232	R4 943	R10 941
	Days until extinction	125.76	67.08	46.20	99.52
	Total number released (adults)	400	160	100	300

Table 4.2: *The optimal adult release magnitudes for frequent releases at different temperatures.*

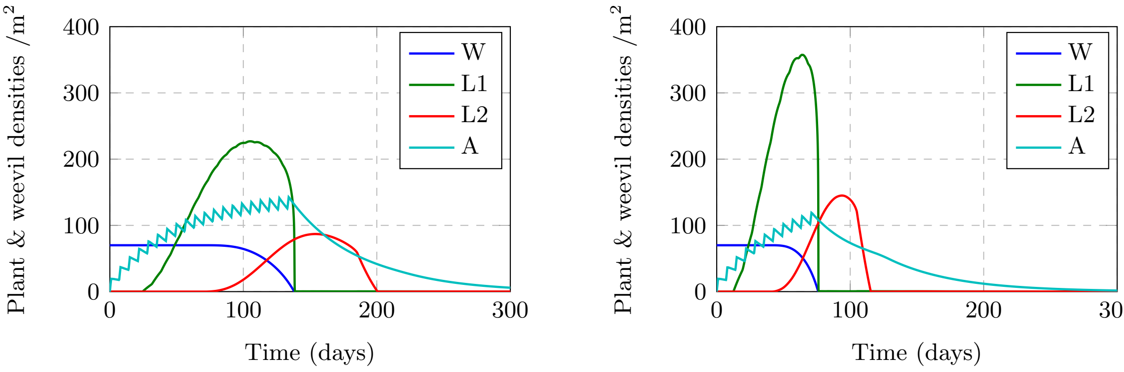


(a) *20 °C* (b) *25 °C*

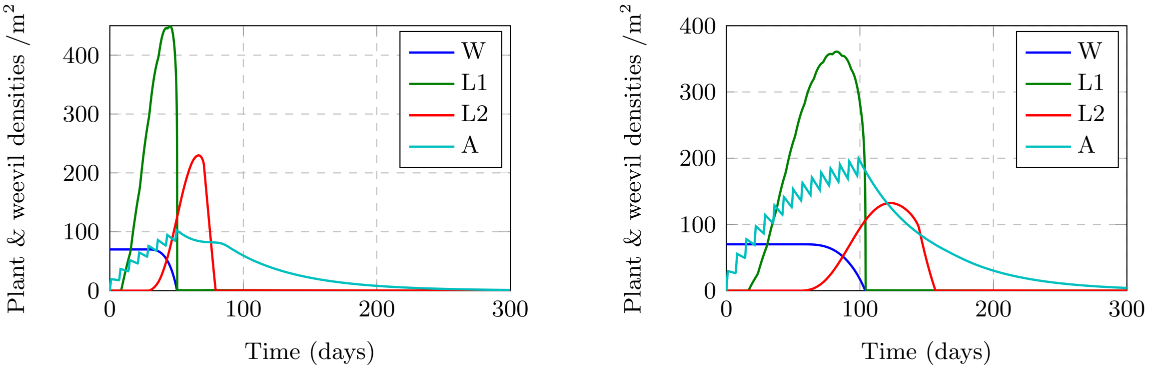


(c) *30 °C* (d) *35 °C*

Figure 4.3: *The total cost, C, for different numbers of adult weevils released once a week, measured at different temperatures.*



(a) *20 °C* (b) *25 °C*

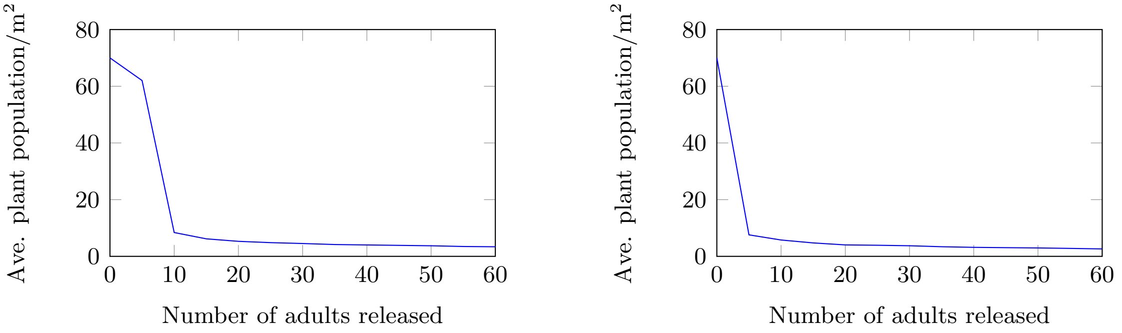


(c) *30 °C* (d) *35 °C*

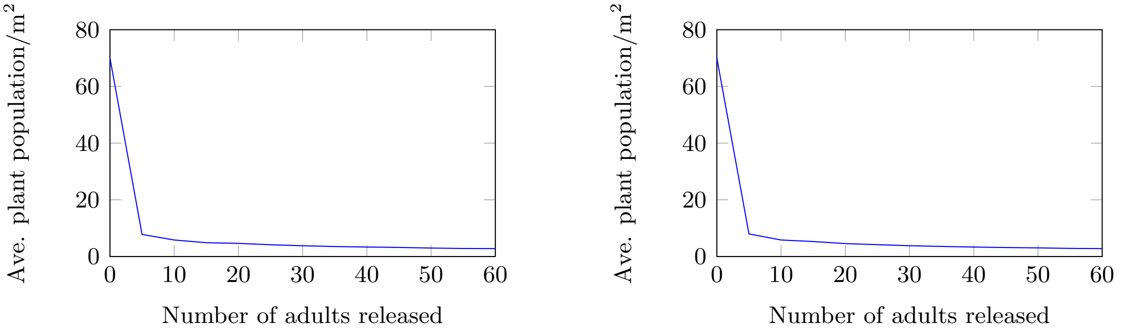
Figure 4.4: *The populations per m^2 after once a week releases of the optimal magnitudes.*

4.1.3 The classical versus the mass rearing approach

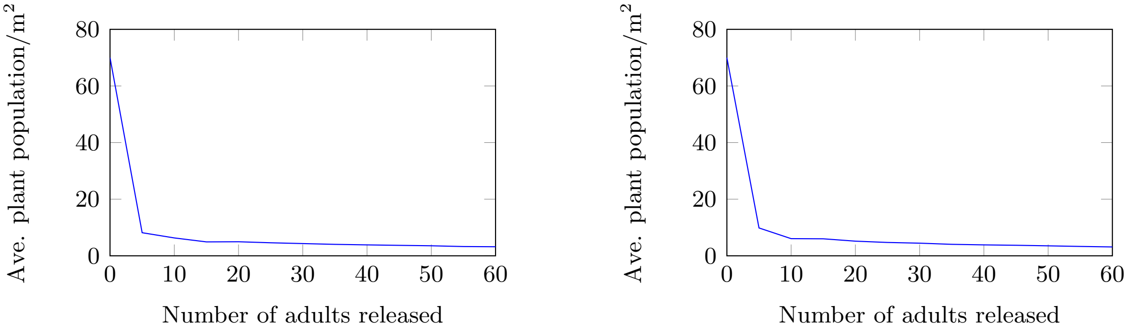
The average plant population sizes over 300 days for different numbers of adults released, as well as for different frequencies of releases, measured at a temperature of 30°C, are given in Figure 4.5. A once off release of adult weevils at time $t = 0$ was compared to different frequency releases of one week, two weeks, three weeks, four weeks and five weeks. From Figure 4.5 it may be seen that there was only a small difference between the average plant population size for a once off release and more frequent releases at very small numbers of adult releases (between 1 and 10). For larger numbers of adult releases, there was no significant difference in the average plant population sizes. Large numbers of adult releases, regardless of the frequency, all succeed in suppressing the weed to very low average densities. For all numbers of adult releases, there are no significant difference in average plant population densities for one, two, three, four or five week releases.



(a) *Once off release* (b) *Every week releases*



(c) *Every second week releases* (d) *Every third week releases*



(e) *Every fourth week releases* (f) *Every fifth week releases*

Figure 4.5: *Average plant population sizes per* m^2 *over 300 days for different release strategies, measured at a temperature of 30 °C. The release strategies considered consist of different numbers of (a) once off adult releases per* m^2 *at time* $t = 0$, *(b) releases every week, (c) every second week, (d) third week, (e) fourth week and (f) fifth week.*

More simulations were performed to compare different release strategies in terms of the number of days until the extinction of the plant at a temperature of 30°C. Once again, a once of release of adult weevils at time $t = 0$ was compared with more frequent releases. From Figure 4.6 it is clear that a once off release will only achieve control of the plant if 15 or more adult weevils are released per m^2. It may also be seen that more frequent releases yield faster control, especially for releases (5 to 10 adult weevils per m^2). For 20 adults and more, the frequency did not have a significant effect on the days until the extinction of the plant.

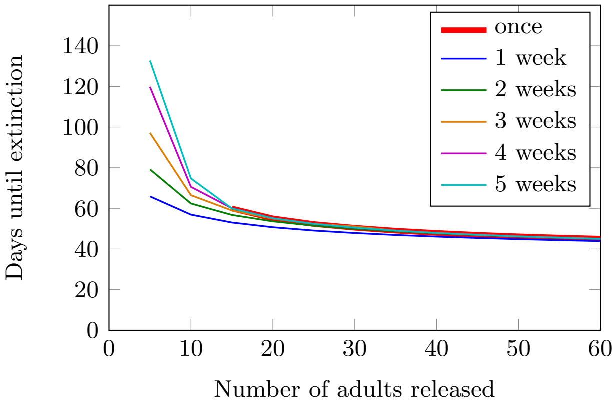


Figure 4.6: *Number of days until extinction of the plant for different release strategies, measured at a temperature of 30 °C.*

The total cost, C, of the optimal magnitude of once off weevil releases was compared to the total cost of the optimal magnitude of different frequency releases at different temperatures (see Figure 4.7). The magnitudes and total costs given in Tables 4.1 and 4.2 were used. The model output shows that, in the short term, the classical approach of once off releases is more cost-effective at all the temperatures than more frequent releases. It is therefore suggested that, under the assumptions of this study, the faster decrease in water loss because of more frequent releases is not worth the costs pertaining to the mass rearing of weevils. It is assumed that weevils are uniformly distributed throughout an area, where in a real life scenario, they are only released at the edge of an infested water body and take time to spread out through the whole area. This assumption leads to faster control of water hyacinth than in reality. More frequent releases may have a big influence on achieving control of water hyacinth if spatial dynamics are included in the model.

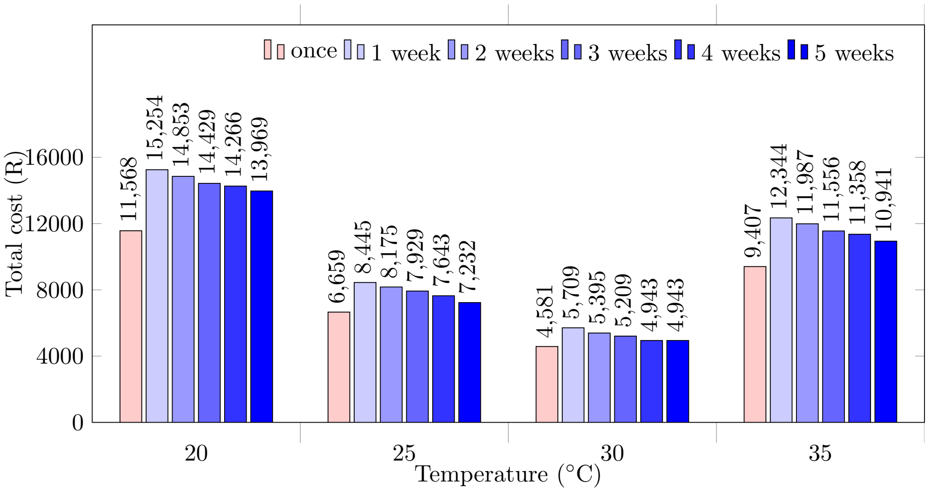


Figure 4.7: *Total cost evaluation of once off releases compared to more frequent releases, measured at different temperatures.*

With the classical approach, after the weed has been driven to extinction, the plant often starts to grow again after a period of time and then there are no weevils left to stop the weed from flourishing. The simulation model demonstrates similar behaviour in the plant population. An example of this is illustrated in Figure 4.8, where 10 adult weevils per m^2 were released at time $t = 0$ at a constant temperature of 30°C. The weed did not go completely extinct, but remained in the system at a very low density and then started to actively grow again after approximately one year and 7 months (580 days). The total cost of this scenario will be infinitely high as the cumulative cost of water loss will keep on increasing. The weevils will have to be imported again for a re-release in the area and the costs associated with this is also a factor to keep in mind when considering the long term implications of classic biological control. In the short term, mass rearing programmes are perhaps more expensive, but in the long run, the costs involved in the classical approach may be more than the model predicts.

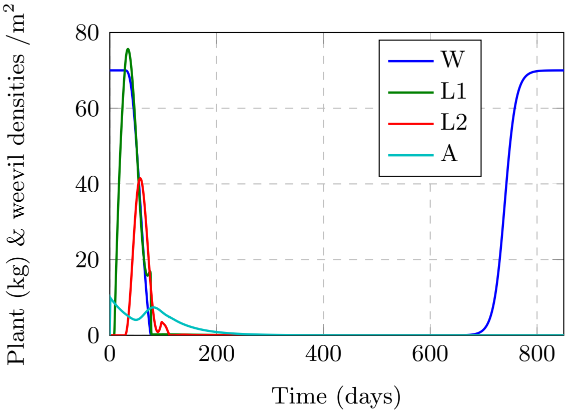


Figure 4.8: *Populations per m^2 after a once off release of 10 adult weevils per m^2 at time $t = 0$ at a constant temperature of 30 °C.*

4.2 Sensitivity analysis

Some of the parameter values in the model, i.e. the density dependent scaling parameters, j and h, as well as the rate of damage caused by older larvae, $c_{L_2}^{max}$, were assumed based on laboratory experiments or experiments performed in different parts of the world under different conditions. This data may differ from data in actual field behaviour in South Africa. For some of the parameter values, i.e. the relationship between plant density and the plant's evapotranspiration rate, no experimental values were available and certain values and relationships had to be assumed. In order to test whether the model output is reliable, single input parameters were varied while keeping all other parameters constant.

Sensitivity analyses of the total cost, C, the number of days until the extinction of the plant and the average plant population size per m^2, $W(t)$, respectively, were performed (see Figures 4.9 – 4.11). Single input parameters were varied for a simulation of a once off release of 20 adults at time $t = 0$ at a temperature of 30°C in an area of 1 000 m^2 considered over a period of 300 days.

From Figure 4.9 it may be seen that the total cost, C, is most sensitive to changes in the maximum daily development rates of eggs and young larvae, α_E^{max} and α_{L1}^{max}, the cost of water, c_{wa}, and the evaporation rate of water, e_n. In order to minimise total cost, weevils should be released during the time of the year when the climate is optimal (30°C) for maximum weevil development. As the cost of water increases, the total cost of biological control will also increase and the method of control should be re-evaluated to see if it is still cost-effective. The total cost does not seem to be too sensitive to changes in the maximum rate of damage caused by older larvae, $c_{L_2}^{max}$. In the case that the model underestimates the damage caused by the weevils, the total cost will not be influenced that much.

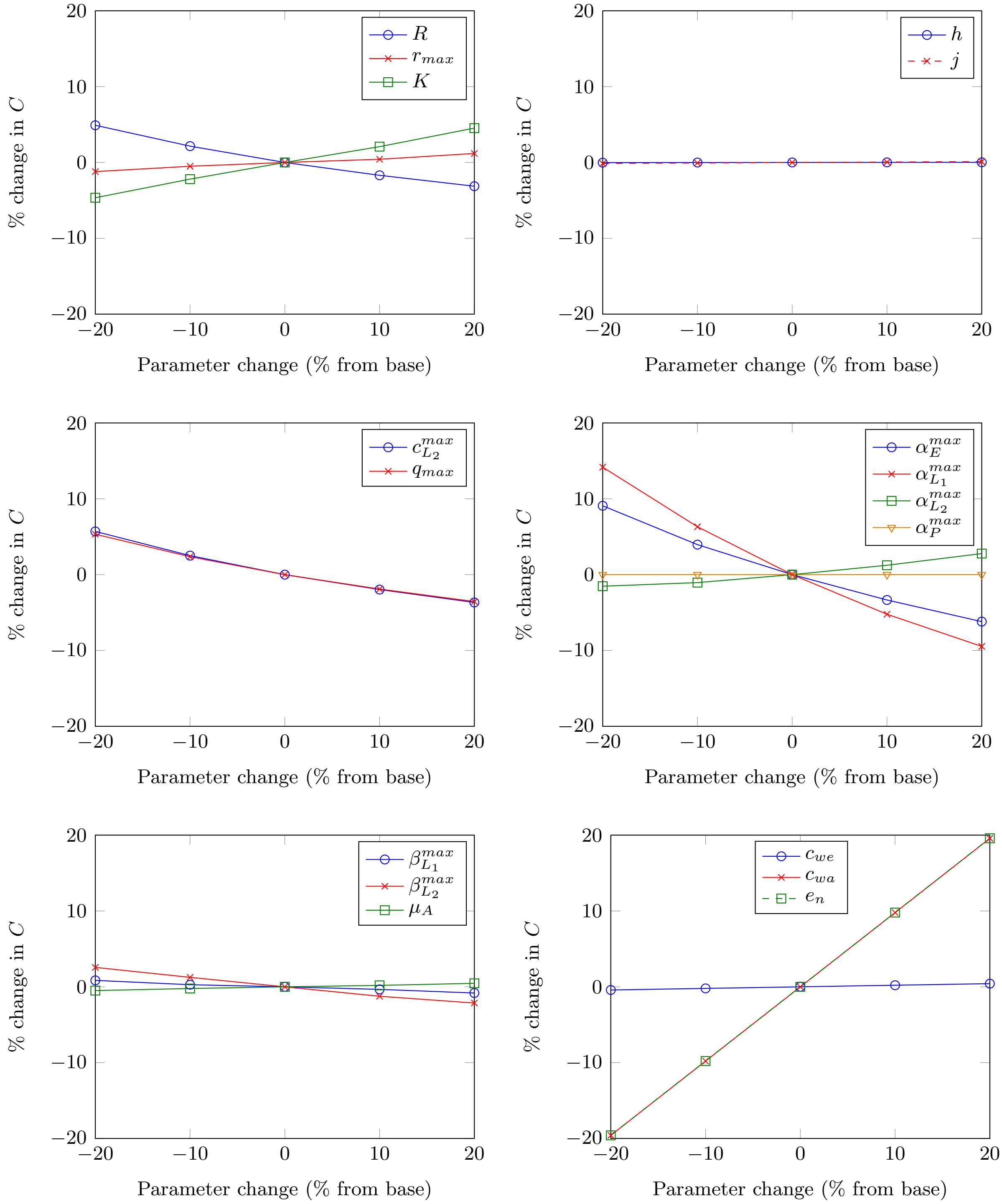


Figure 4.9: *The sensitivity of the total cost, C, with respect to percentage changes in various parameters.*

From Figure 4.10 it may be seen that the time until the extinction of the plant is also most sensitive to changes in the maximum daily development rates of eggs and young larvae, α_E^{max} and α_{L1}^{max}. The sensitivity of the time until the extinction of the plant is closely correlated with the sensitivity of total cost, except when it comes to the cost and evaporation parameters. In order to minimise the time until the extinction of the plant, weevils should be released during the time of the year when the climate is optimal (30°C) for the development of weevil eggs and young larvae.

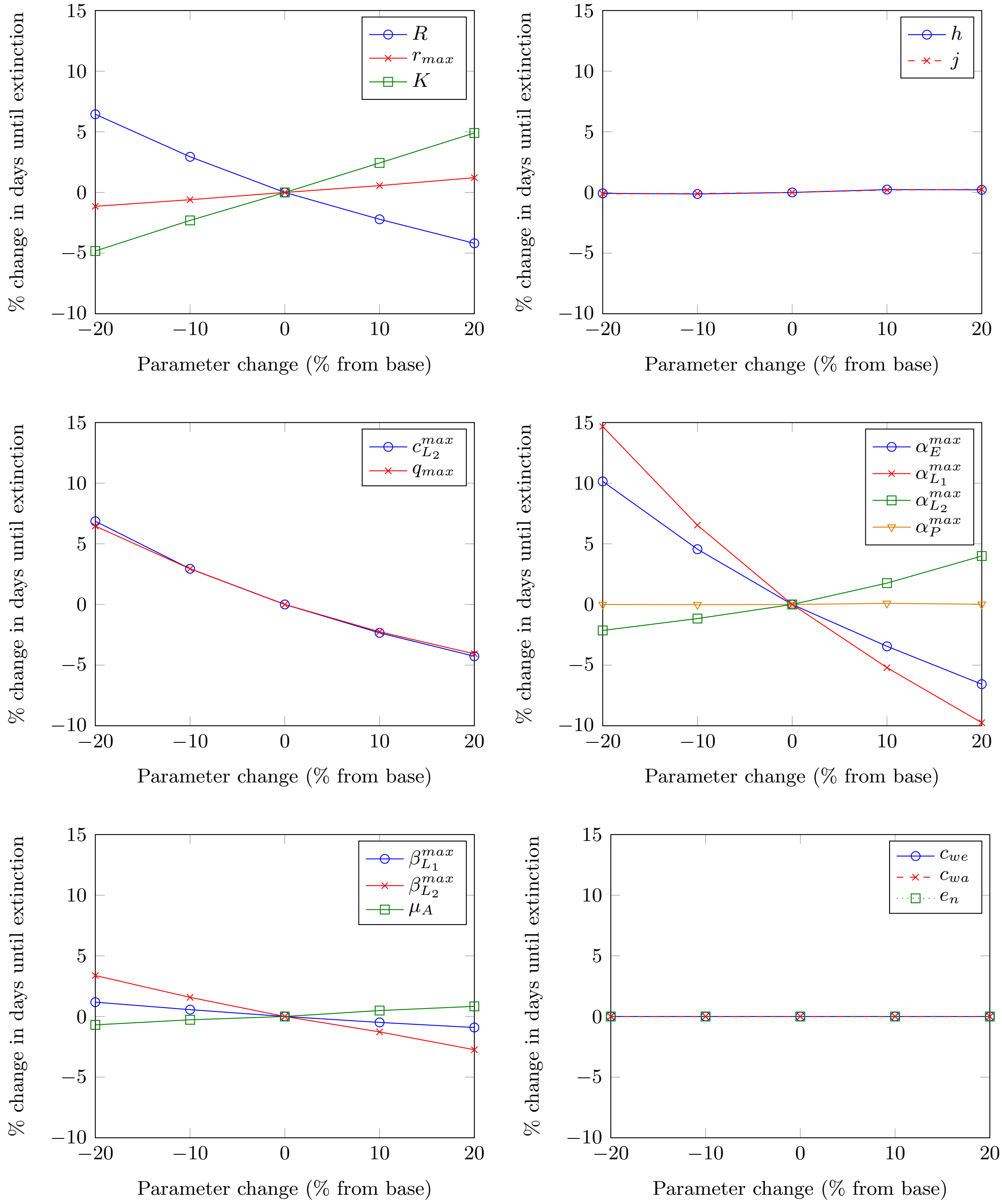


Figure 4.10: *The sensitivity of the number of days until the extinction of the plant with respect to percentage changes in various parameters.*

In Figure 4.11 it may be seen that the average plant population size per m^2, $W(t)$, is most sensitive to changes in the number of adults released, R, the carrying capacity of the water, K, the maximum oviposition rate of weevils, q_{max}, the maximum daily development rate for eggs, α_E^{max}, and the mortality rate for adult weevils, μ_A. The average plant population density is more sensitive when the number of adults released is decreased than when it is increased.

To minimise the average plant population density in the case where weevils possibly struggle to adapt in a new habitat or a disaster hits and a lot of them die (larger adult mortality, μ_A, which consequently decrease R), the number of adult weevils released should therefore be slightly larger than the optimal number. Furthermore, weevils should be released during ideal climate conditions (30°C) in order to maximise the oviposition rate as well as the egg development rate.

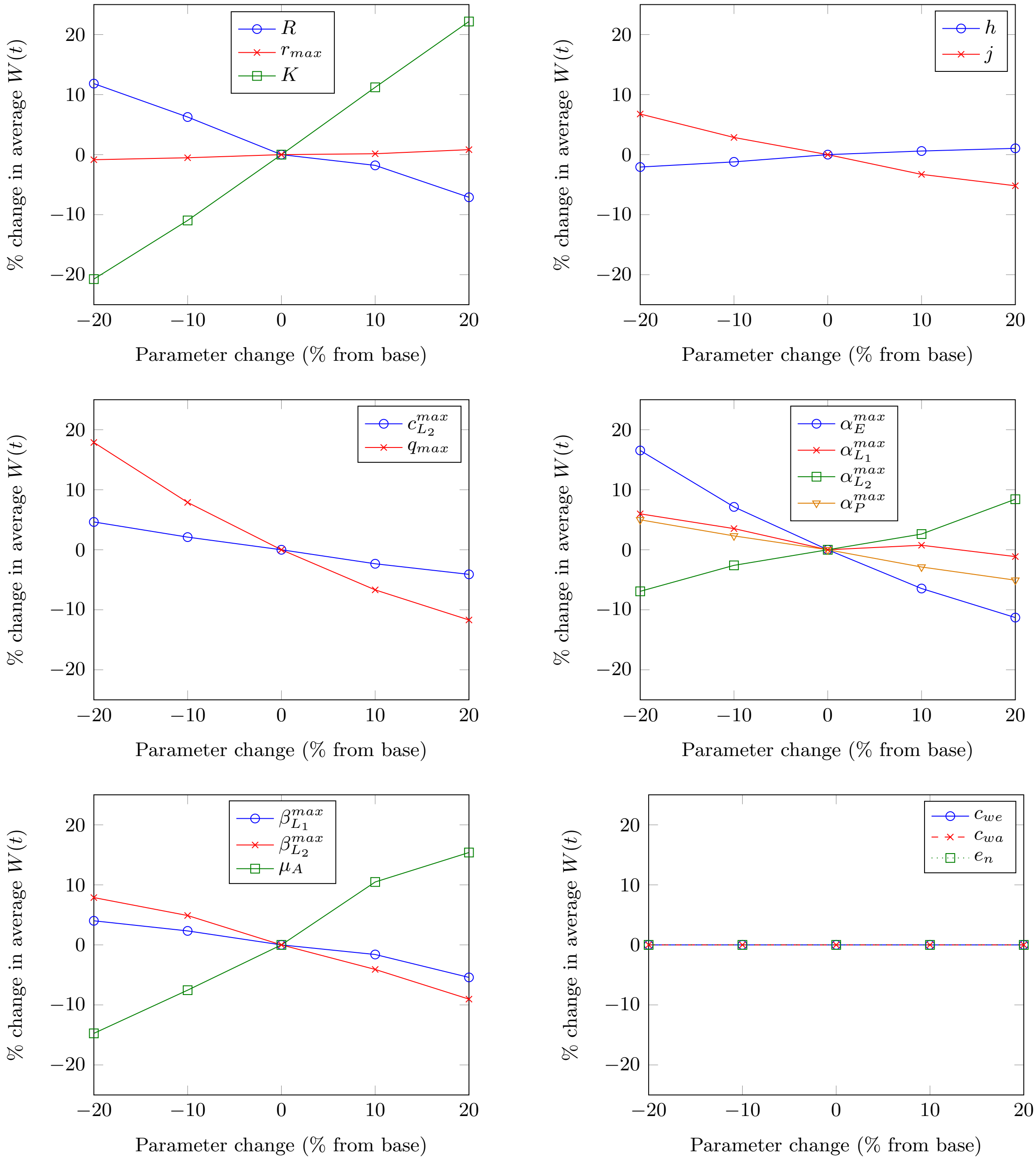


Figure 4.11: *The sensitivity of the average plant population size, $W(t)$, with respect to percentage changes in various parameters.*

CHAPTER 5

Conclusion

The chapter consists of a brief summary of the study in §5.1, recommendations in §5.2 and concludes with suggestions for future work in §5.3.

5.1 Summary

In Chapter 2, the background of the water hyacinth and the problems it poses to society were investigated, followed by a study of biological control as a method of controlling this weed. The life cycles of the water hyacinth and the *N. eichhorniae* weevil as biological control agent were studied, as well as mathematical models formulated to model the interaction between the two species. Thereafter, a plant-herbivore model, where stage-structure has been added to the weevil population, formulated as coupled delay-differential equations, was presented in Chapter 3 to govern the water hyacinth and weevil system. A cost function was constructed with which to compare the cost-effectiveness of the classical biological control approach and the mass rearing approach. The function adds the costs pertaining to the mass rearing of weevils and the cost of water loss, in terms of water evaporation, together. The assumptions of the study and a description of the parameters incorporated into the model were also given. In Chapter 4, the optimal magnitudes of adult releases (in terms of minimising total cost) for different frequencies of releases were obtained by means of repeated simulation runs of the model. This was then used to evaluate the cost-effectiveness of the classical biological control approach to the mass rearing approach. Finally, a sensitivity analysis was performed in order to ascertain the robustness of the model output, that is, total cost, days until extinction of the plant and average plant population size, with respect to changes in certain parameter values.

5.2 Recommendations

The model output indicates that more frequent releases yield higher total costs than once off releases at the range of temperatures tested. The results suggest that, in the short term, the classical biological control approach of a once off release at time $t = 0$ will be more cost-effective. In the long term, the weed often begins to grow again after an initial suppression with the classical approach. This will result in total costs sky-rocketing due to the increase in water loss because of the high evapotranspiration rate of the water hyacinth and the importation of weevils for re-releases. In this case, mass rearing programmes may be most advantageous.

The fact that the mean-field approximation is assumed throughout this study may have an influence on the conclusion that the classical approach will be more cost-effective. It is assumed that weevils are uniformly distributed throughout an area, where in a real life scenario, they are only released at the edge of an infested water body and take time to spread out through the entire area, if they even succeed in this. This assumption may indicate faster control of water hyacinth than in reality. More frequent releases could have a more significant influence on achieving cost-effective control of water hyacinth if spatial dynamics are included in the model.

When considering the different frequencies of releases with the mass rearing approach, the model output suggested that releasing weevils every 5 weeks will be the most cost-effective frequency. It is therefore deemed more cost-effective to release weevils less often.

The sensitivity analyses pointed out that the model output is very sensitive to changes in the maximum development rate of the egg and young larval stages of the weevil's life cycle. It would therefore be more advantageous to release weevils for biological control during the time of the year when average temperatures are expected to be close to 30°C, which is the optimal temperature for weevil development. This will minimise the total cost and the time until the extinction of the plant. The model output also proved to be more sensitive to a decrease in the number of adults released than an increase. It is therefore suggested to rather release slightly larger numbers of adult weevils than too little. If too little weevils are released, it may cause high increases in the total cost, the number of days until the extinction of the plant as well as the average plant population size.

5.3 Future work

There are a few areas where the scope of the model may be expanded in possible future studies.

Spatial dynamics

In future, spatial dynamics may be added to the model in order to give a more realistic representation of the impact of the *N. eichhorniae* weevil on water hyacinth. Spatial dynamics are expected to have a significant influence on the time until the extinction of the plant. Frequent releases may have a much bigger impact in contributing to decrease the time until the extinction of the plant and in this way decreasing the total cost.

Fluctuating temperatures

The model may be expanded to incorporate fluctuating temperatures over a period of time and not just one average temperature for a whole period. It is unrealistic to assume a constant temperature over a period of time. Even if it is the average temperature, fluctuating temperatures could have a big influence on the model output.

Data

If more thorough field behaviour data can be obtained, the model may be compared to real life scenarios in more depth. Knowledge about the area covered during the release of BCAs and the exact magnitudes and frequencies of releases may contribute to a more in-depth validation of the model.

The collection of more thorough field data or data from laboratory experiments may assist to more accurately estimate some of the parameters assumed in the model, i.e. the density dependent scaling parameters, j and h, as well as the rate of damage caused by older larvae.

Costs and benefits

In the future, there may be expanded on the cost of water loss. In this study, only the cost of water itself was considered and not the benefits that the availability of more water may provide to farmers or surrounding communities.

The re-importation costs of weevils after an initial release of weevils was unsuccessful using classical biological control may also be incorporated in the model in future. In the long run, re-importation costs may play a big role in the cost-effectiveness of the classical biological control approach.

Frequency of releases

In this study, only release frequencies of one to five weeks were considered. Future studies may consider expanding on the range of the frequencies of releases and investigating whether less frequent releases may yield more cost-effective control.

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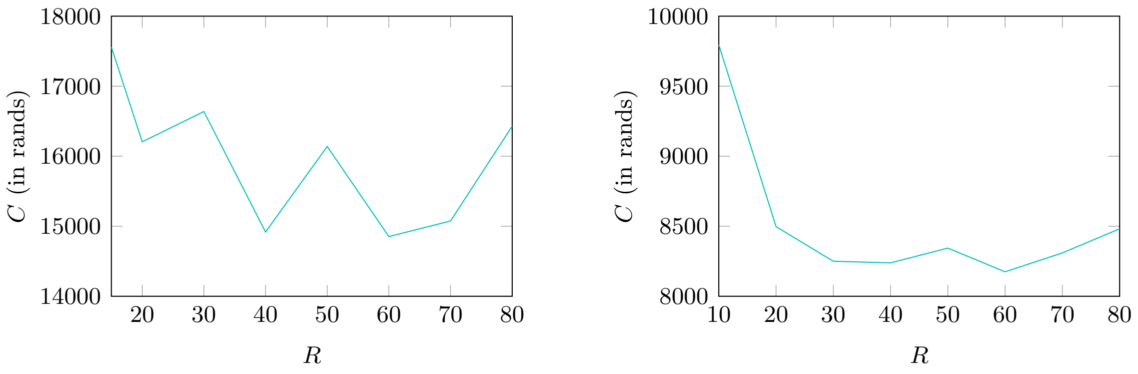
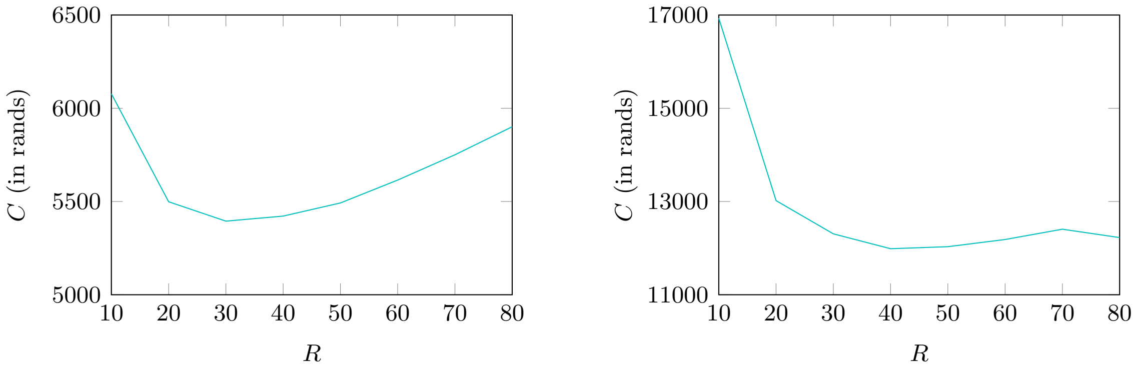
APPENDIX A

Results

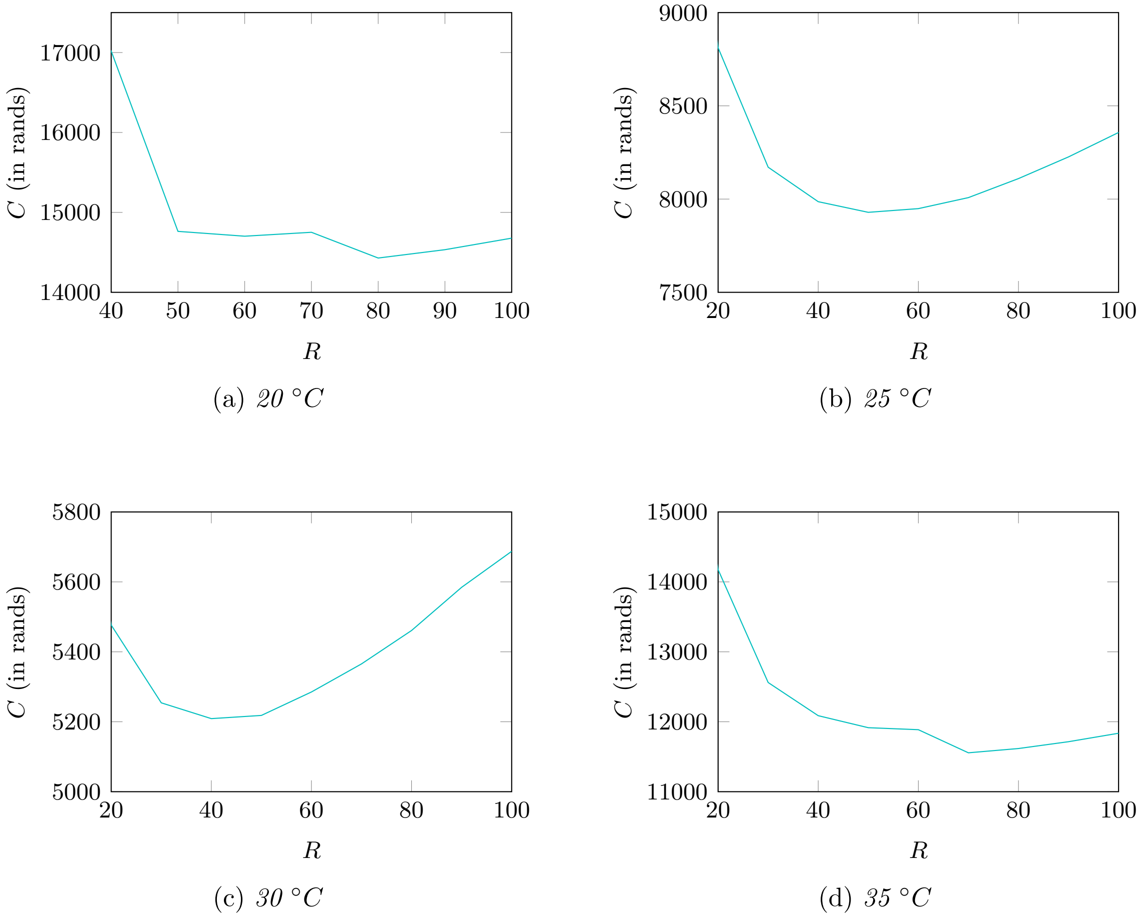


(a) *20 °C* (b) *25 °C*



(c) *30 °C* (d) *35 °C*

Figure A.1: *The total cost, C, for different numbers of adult weevils released once every second week, measured at different temperatures.*



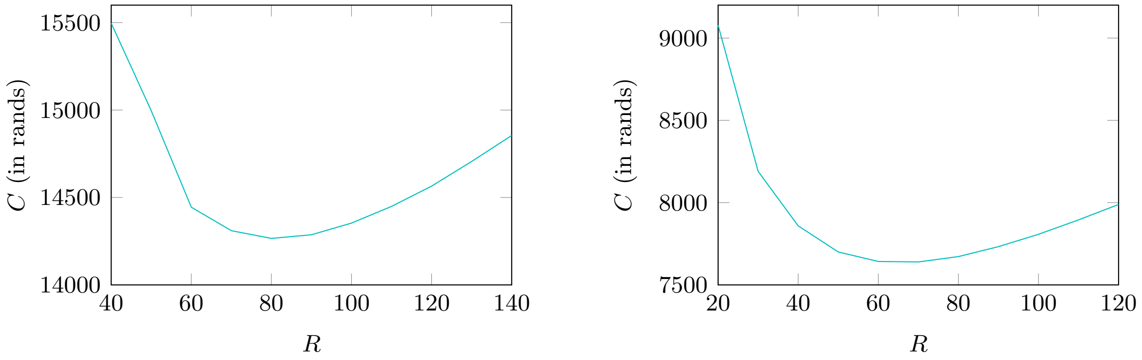
(a) *20 °C*

(b) *25 °C*

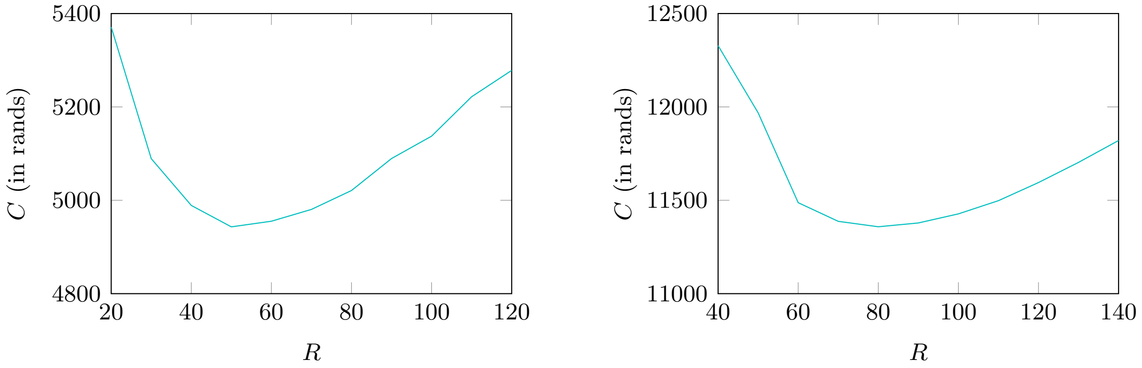
(c) *30 °C*

(d) *35 °C*

Figure A.2: *The total cost, C, for different numbers of adult weevils released once every third week, measured at different temperatures.*

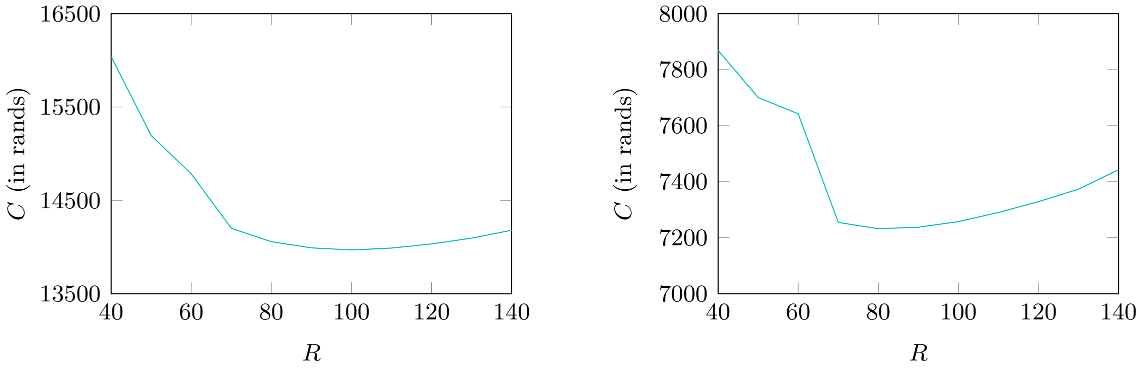


(a) *20 °C* (b) *25 °C*

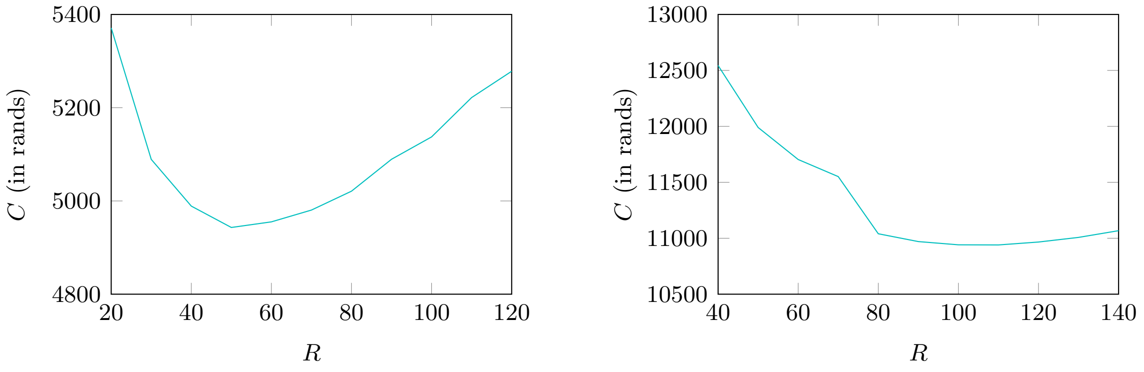


(c) *30 °C* (d) *35 °C*

Figure A.3: *The total cost, C, for different numbers of adult weevils released once every fourth week, measured at different temperatures.*



(a) *20 °C* (b) *25 °C*



(c) *30 °C* (d) *35 °C*

Figure A.4: *The total cost, C, for different numbers of adult weevils released once every fifth week, measured at different temperatures.*