Modelling the effect of two biocontrol agents on the invasive alien tree *Acacia cyclops*—Flowering, seed production and agent survival

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ABSTRACT

Invasive alien plants play an important role in our changing world and have a considerable negative impact on ecosystems in many parts of the world. One effective control strategy involves the use of biocontrol agents which either damage the invasive alien plant itself or reduce the production of seeds. In this paper, we focus on seed-attacking biocontrol agents. To be able to predict the impact of biocontrol agents on the seed production pattern provides a way of comparing the impact of different biocontrol agents before they have actually been released. This becomes complex in systems where more than one biocontrol agent is present and where both depend on the same resource. In this paper, we examine a system consisting of two seed-attacking biocontrol agents (a midge and a weevil) and one invasive alien plant (*Acacia cyclops*). We used a non-spatial but temporal model to predict the impact of these biocontrol agents on flowering and seed set. We used a global sensitivity analysis (i.e. analysing the impact of several parameter simultaneously) to evaluate the impact of selected parameters which were considered uncertain but important. We could show that the system, even without biocontrol agents, fluctuates for most parameter sets between years, and that the fluctuations increased after the release of the biocontrol agents, although the number of seeds produced was, on average, substantially smaller. We found that the two biocontrol agents could usually not coexist, highlighting that special care needs to be taken in selecting each additional biocontrol agent to avoid driving an already established biocontrol agent to extinction. These observations make a strong case for long-term monitoring after the release of biocontrol agent.

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1. Introduction

Invasive alien plants (IAPs) are an important threat to biodiversity in many ecosystems around the world. Although some IAPs have positive effects on individual native species or provide beneficial services (albeit in many cases only temporary), their impacts are very often detrimental to individual native species and biodiversity, ecosystem functioning and ecosystem services (Pyšek and Richardson, 2010). The effective management of IAPs requires the allocation of substantial resources. The usefulness of mechanical and chemical control measures are often limited by the inaccessibility of the IAPs and difficulties associated with finding isolated populations. Increasingly, the use of conventional control methods (mechanical and chemical clearing) is being integrated with the use of biological control agents (hereafter biocontrol agents or BCAs). These are organisms which have a negative effect on the health and/or reproduction of the IAPs. BCAs are nowadays introduced after detailed studies of host specificity to damage IAPs.

Utilised agents include a wide range of organisms, from pathogens to insects and, in the past, even mammals. The aim is either to kill or weaken the IAP or affect its reproductive success by targeting particularly important life-history stages. In this paper, we deal only with seed-attacking BCAs which are widely used, particularly in South Africa, in the control of woody invasive plants (Moran et al., 2005).

Many BCAs can disperse without human intervention, some even over long distances, and can therefore reach and affect IAPs in remote areas. Despite this very useful property of BCAs and their documented effectiveness in many cases, the actual dynamics of interactions between BCAs and IAPs are rather poorly understood. Most studies focus at the level of IAP populations and do not contain spatial aspects. Some simulation studies (e.g. Le Maitre et al., 2008) have focused on spatial dynamics but only at fine spatial scales (e.g., 1 km²) and use simplistic assumptions regarding key processes (e.g. fixed fire intervals and burning of the whole landscape). Even with these simplifications, an important understanding concerning spread pattern has emerged and it has been shown that seed-attacking BCAs can have a dramatic impact on IAP populations, affecting not only seed availability, but also reducing spread. Besides including a spatial aspect, Le Maitre et al. (2008) is one of

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very few simulation studies to examine a system involving more than one BCA.

Predicting the impact of even a single BCA is complex if there are feedbacks in the system. The system becomes much more complex if more than one BCA is present, especially where each BCA targets a different life stage of the IAP. Intuitively, if a single BCA is effective, a second one should increase the impact on the host. However, this need not be the case (e.g. Denoth et al., 2002), especially when the two BCAs compete for the same resource at different times (e.g. reproductive entities like flowers and seeds). Such systems are likely to include complex feedback loops, i.e. an agent which reduces seed set by destroying flowers would directly reduce the amount of seed available to a seed-feeding agent, but it also releases the IAP from the energetic demands of maturing seeds. These systems are further complicated when the BCAs have different life cycles and generation lengths. The effect of releasing a second BCA could range between efficacy and persistence of both agents and the hoped-for additive effects of having two agents, to regular and/or irregular fluctuations of one or both BCAs and even the possible extinction of one (e.g. (Denoth et al., 2002)).

A complex system involving one IAP and two BCAs, targeting the same resource at different stages of the reproductive cycle involving flowers and seeds, can be found in South Africa's Cape Floristic Region (CFR). The IAP, *Acacia cyclops*, is one of 14 invasive Australian *Acacia* species in South Africa that are the subject of a range of management actions (van Wilgen et al., 2011). This species is one of the most widespread and damaging invasive alien trees in the CFR where it smothers fynbos vegetation and has a range of impacts over tens of thousands of hectares (Richardson and van Wilgen, 2004). It produces large numbers of seeds (annual seed rain of up to 3000 seeds per m², Milton and Hall (1981) cited in Holmes and Newton (2004)), which take more than a year to develop from flowering to seed release, that may be stored in the soil and germinate after fire (Richardson and Kluge, 2008). However, the majority of seed produced germinate within a year of maturing, and do not remain dormant in the soil (Richardson and Kluge, 2008). As part of the integrated control of this IAP, a seed-attacking weevil (*Melanterius servulus* Pascoe (Coleoptera: Curculionidae)), was released in 1994 at 15 sites (Dennill et al., 1999) and subsequently redistributed to numerous sites throughout the range of *A. cyclops* in South Africa. The levels of damage inflicted by the weevil were substantial but considerable quantities of seed still remained in the system.

Subsequently, in 2001, a gall-forming midge which oviposits in flowers and consequently reduces seed set (*Dasineura dielsi* Rübsaamen (Diptera: Cecidomyiidae)), was established on *A. cyclops* at a single locality from which it rapidly spread throughout the invaded range of *A. cyclops* (Adair, 2005). In contrast to the adult weevil, which lives several years, the adult midge only lives a few days, but the larvae have a diapause which can last up to two years.

Monitoring at sites throughout the range of *A. cyclops* stands, subsequent to the establishment of *D. dielsi*, indicated that relatively synchronous fluctuations of flower production, and subsequent galling and seed production, occurs (Kleinjan, Impson, Hoffmann and Post, unpublished data). No analogous data for the years prior to the establishment of *D. dielsi* is available, although fluctuations are indicated by anecdotal observations (Impson et al., 2004, Impson, personal communication). Climatic fluctuations cannot be the only reason for the fluctuations, as these would not only be synchronous within a population, but also between nearby populations, which is not always the case.

In this paper, we discuss the possibility that fluctuations are caused by feedbacks inherent to the system and do not require any external non-annual fluctuating input. We also hypothesise that even without the presence of the BCAs these fluctuations will be present, although they may be amplified with BCAs present.

To address the questions of these temporal within-stand dynamics, we developed a non-spatial but temporally-explicit simulation model in R (R Development Core Team, 2011) which simulates the system of the IAP and the two BCAs over 1-day time steps in one stand. For the purpose of this model overall flower production within a year is considered to be constant between years, but does follow within a single year a given distribution. Climatic conditions are expected to influence the flowering and seed production patterns but are not included in the model. A limiting “resource” which includes certain aspects of climatic conditions integrated over one year was incorporated in the model. This limiting “resource” can be of any type, e.g. climatic (rain, sun), soil nutrients (nitrogen, phosphorous etc.), or space. This “resource” can also be seen as a measure of stress, whereby increased stress reduces the availability of the “resource” to the IAP. As the “resource” is such an abstract measure, we varied its value for different simulations over a wide range, from nearly zero to large (the point at which the “resource” no longer limits the IAP).

Knowledge about the BCAs (also to a lesser degree the IAP) is sparse regarding parameters governing population dynamics (e.g. generation times, number of eggs laid per female, survival rate from egg to adult BCA). In addition, what data are available, are mainly from lab studies, with often limited transferability to field situations. Consequently, ranges of parameter values were evaluated.

We conducted simulations with BCAs and without BCAs based on the same parameter sets and compared the results of the two. This approach enabled us to investigate the following questions, which will provide insight into the functioning of this type of systems as well as provide information to guide further introductions and selections of BCAs:

1. How likely is it that the system fluctuated before the introduction of the BCAs?
2. What is the impact of the introduction of the BCAs on the existence and strength and pattern of fluctuations?
3. How likely is co-existence of the two BCAs?
4. Which parameters of the BCAs are important for predicting the mean flower and seed production?
5. Given the highly simplified nature of the model, how applicable are the results to real life?

2. Methods

2.1. Simulation model

2.1.1. Model overview

Although the model is not an individual based model, the description follows the ODD protocol (“Overview, Design concepts, and Details”) set out by Grimm et al. (2006), which provides a standardised framework for describing individual based models.

2.1.1.1. Purpose. The purpose of this simulation model is to simulate the dynamics of different stages of an *A. cyclops* population (the IAP) and its associated BCAs, namely a seed-attacking weevil (*M. servulus*) and a gall-forming midge (*D. dielsi*). The aim of the model is to investigate the flower and seed production pattern in relation to the BCAs and the sensitivity to changes in selected input parameters. The model is temporally but not spatially explicit. It is deterministic, except in the determination of the actual number of the daily new flowers and green pods and the time from oviposition to emergence of the midge. As the emergence follows a given probability density function which is defined as a parameter, it is not possible to distribute a fixed number to follow this distribution without introducing a bias. To avoid this bias, it was decided

Fig. 1. Pictures showing *Acacia cyclops* seed production without biocontrol agents (1a); the weevil *Melanterius servulus* (1b) and destroyed seeds in a pod (1c); the midge *Dasineura dielsi* (1d) and resulting gallset (1e). ©Fiona Impson and John Hoffmann.

to distribute the number randomly following the given probability density function.

The model is implemented in R (R Development Core Team, 2011) using the packages *simecol* (Petzoldt and Rinke, 2007) and *date* (Therneau et al., 2009) for the simulations, *lhs* (Carnell, 2009), *tgp* (Gramacy and Taddy, 2010) and *RSQLite* (James, 2010) for the analysis, as well as *xtable* (Dahl, 2009) for the output of the formatted tables.

Fig. 1.

2.1.1.2. State variables and scales. The model consists of nine different stages: “*acaciaFlower*” (flower of the IAP), “*acaciaPod*” (pod of the IAP), “*acaciaSeed*” (seeds of IAP), “*acaciaWeevil*” (IAP entities oviposited on by weevil), “*acaciaMidge*” (IAP entities oviposited on by midge), “*weevilLarva*” (larva of the weevil), “*weevilAdult*” (adult weevil), “*midgeGall*” (gall of the midge), and “*midgeAdult*” (adult midge). These are subdivided into sub-stages (referred to as states) based on the time in days of the individual entity in a certain stage (see Fig. 2). The states to be analysed are the number of flowers present per day (from now on referred to as “flower”) and number of seeds produced per day (from now on referred to as “seeds”) of the simulation. As the flowers stay more than one day on the plant the sum of the flowers is *not* the number of flowers actually produced. The sum of the number of seeds produced is the actual number of seeds as the seeds are removed from the model at the beginning of a new day. It is also important to note that “flower” refers to an individual flower (also called sometimes called a floret) within the compound flower head.

As a limiting factor, we included a variable called “resource” (described above), which is renewed and depleted daily. Any unused resource is carried over to the next day. Although the model does not include any explicit space, the maximum number of flowers which can be created per day (1 000 000 flowers) can be translated into a canopy area of *A. cyclops* between 50 m² and 100 m² (Impson and Kleinjan, personal communication).

2.1.1.3. Process overview and scheduling. The simulation consists of different modules which handle the dynamics over time (see Appendix). The modules govern creation of new individuals (*newFlowers* and *renewResource* in module *beginDay*, *releaseMidge*, *releaseWeevil*), state transitions

(*stateAgeingDeterministic*), stage transitions (*newGrePod* in module *beginDay*, *gallingMidge*, *emergenceMidge*, *ovipositionWeevil*, *emergenceWeevil*, *stateAgeingDeterministic*) (see Fig. 2) and internal book keeping (*beginDay*, *endDay*). Resource is reduced by the processes *stateAgeingDeterministic* as well as *newFlowers* in the module *beginDay*, and renewed by *renewResource*, also in the module *beginDay*.

All transitions are deterministic and no mortality or loss occurs before the maximum age, apart from the galling by the midge (*gallingMidge*) and oviposition by the weevil (*ovipositionWeevil*). Stochasticity is only used to avoid permanent bias when distributing a given number of entities following a given distribution.

Scheduling is done in discrete one-day time steps and the simulation time frame was set to 40 years.

2.1.2. Model details

2.1.2.1. Initialisation. The model is started with no reproductive entities of the IAP nor biological control agents. The BCAs are only released after three years to allow for a stable yearly pattern of *A. cyclops* to develop before. During this initial time, the yearly fluctuations stabilise so that a stable yearly pattern can be observed. This was based on previous test simulations.

2.1.2.2. Input. The input into the model consists of new flowers and the limiting resource, which are both determined daily.

A single one day old midge and weevil respectively is released once at specific dates as defined in the parameter.

2.1.3. Submodels

Here we will describe the submodels in detail.

2.1.3.1. beginDay. This function is re-calculating the *newFlowerDist* on the first day of a new simulation year, defined as the initial date plus one year plus one day.

2.1.3.2. newFlowers. The maximum number of new flowers per day is determined by three parameters: the yearly maximum flower production (*newFlowerNo*) and a normal distribution (*normFlower*), described by *newFlowerDistMean* and *newFlowerDistSd* in days. *newFlowerDistMean* is the day, counted from the beginning of the

simulation year (not a calendar year) with the highest flower production. At the beginning of the simulated year, the maximum number of new flowers per day is determined using these parameters. Each day the maximum number of new flowers determined was then reduced to the maximum number of flowers actually produced as determined by the resource availability, and the actual number of flowers were created. To avoid a bias against the tails of the distribution, we decided to use a stochastic approach to distribute *newFlowerNo* following the defined distribution.

but equals the number of readyPods (last sub-stage in the stage *acaciaFlower*, see Fig. 2 for details of the stages and sub-stages) of the previous year times the probability that a flower will develop into a green pod.

2.1.3.4. *renewResource*. Resource is renewed each day by the same amount (*resourceRenewal*) and added to the resource left over from the last day(s). This renewal is done after the creation of the flowers, as the number of flowers produced is determined by the amount of resource left over from the last day.

2.1.3.5. *releaseWeevil* and *releaseMidge*. At the date for the release of the weevil, as specified in the parameter *releaseWeevil\$date*, one adult female weevil is released. We assume an age of one day of the

released weevil. The same algorithm with a different date is used for the midge.

2.1.3.6. ovipositionWeevil. Weevils oviposit into the green pods. The following assumptions were made in this module:

1. Only one egg per seed is laid.
2. Each female lays a maximum of *eggsPerFemalePerDay*, which is limited by the availability of green pods (*grePod*).
3. Females have a maximum supply of eggs per day, and their maximum life time egg production is only limited by their life span.
4. Eggs are oviposited first in the youngest pods in which there has been no prior oviposition.

The flowchart of this module is shown in the Appendix.

2.1.3.7. gallingMidge. Midges gall the flowers of the *A. cyclops*. The following assumptions were made:

1. A single midge adult does not oviposit twice on the same flower; this leads to a single midge larva in one egg per flower; this is loosely based on [Adair \(2005\)](#).
2. Midges do not know whether a flower has already been parasitised by another midge; this results in a random selection of flowers for oviposition.
3. (1) and (2) result in a certain number of un-oviposited flowers which can be calculated as follows:

$$flowersNonOvi = \left(\frac{flowers - meanEggsPerFemale}{flowers} \right)^{midges}$$

resulting in

$$flowersOvi = flowers - flowersNonOvi$$

flowers to be ovipositioned on.

4. One flower can support the development of a maximum of *maxEggsPerFlower* eggs.
5. Up to these *maxEggsPerFlower*, the developing midges do not influence each other.
6. If more eggs than *flowersOvi* times *maxEggsPerFlower* are available, these are discarded.
7. Flowers are oviposited into according to their age: younger flowers first.

The flowchart of the module is shown in the Appendix.

2.1.3.8. emergenceMidge. In this module, the midges in the last state of the stage “midgeGall” emerge and are moved into the youngest state of the stage “midgeAdult”. We assume that the mortality for all individuals from egg to adult midge is the same, i.e. *midge\$pEmerge*. The length of development into adulthood follows for 99% of all midges a normal distribution with a mean of 35 days and a standard deviation of 5, with a minimum time of development of 10 days. The remaining 1% go into a diapause, which follows a uniform distribution between 60 days and two years (Kleinjan, personal communication).

2.1.3.9. emergenceWeevil. Even if weevils emerge in less than a year, they overwinter and reproduce (and damage the host plant) only the following year. Consequently, we can assume, for practical purposes, that weevils emerge at the beginning of the next year. The number of new adult weevils is *weevil\$pEmerge* multiplied by the number of eggs.

Table 1

Parameter used in the sensitivity analysis to elucidate the effect of these parameters on the seed production on of an invasive alien plant (*Acacia cyclops*) under presence or absence of two biocontrol agents (the midge *Dasineura dielsi* and the weevil *Melanterius servulus*). The “interval” represents the range of the variable used for the construction of the latin hypercube for the sensitivity analysis. Values without decimals are in integer steps, values with decimals are continuous. *pEmerge* values are composite values, representing combinations of *pEmerge* and *sexRatio* (for details see text). Parameter values are based on personal communication with F. Impson and C. Kleinjan, as well as [Impson et al. \(2004, 2011\)](#), [Moseley et al. \(2009\)](#), [Post et al. \(2010\)](#).

Parameter	Interval
midge	
<i>meanEggsPerFemale</i>	[1, 300]
<i>maxEggsPerFlower</i>	[1, 16]
<i>pEmerge</i>	[0.0, 0.5]
weevil	
<i>pEmerge</i>	[0.0, 0.5]
<i>seedsDamagedPerOviposition</i>	[1.0, 10.0]
resource	
<i>resourceRenewal</i>	[1, 10 ⁶]
<i>resourceConsumptionAcaciaFlower</i>	[1, 5]
<i>resourceConsumptionAcaciaPod</i>	
<i>resourceConsumptionAcaciaWeevil</i>	[5, 50]

2.1.3.10. stateAgingDeterministic. The last state of the classes “acaciaWeevil”, “weevilAdult”, “acaciaMidge” and “midgeAdult” are discarded, i.e. are dying (adult weevils live two years, adult midges 5 days) or cannot be identified by sampling any more. The last states of the other two stages (“weevilLarva” and “midgeGall”) will be empty as they emerged (modules *emergenceWeevil* and *emergenceMidge*) or died, giving the probability *pEmerge*. New flowers are set to zero as at the beginning of a new day, no new flowers are present (“sampling in the morning”). Before the actual deterministic ageing of all stages by one day, the oldest *broPod* will be multiplied by the parameter *podsPerFlower* to obtain the number of seeds. Weevils are assumed to be univoltine, i.e. having one generation per year, and the adults live two years, where midges are multivoltine, i.e. having more than one generation per year, and their adults live up to a maximum of five days.

2.1.3.11. reduceResource. Resource is reduced for each individual in each state. In stages related to acacias (“acaciaFlower”, “acaciaPod”, “acaciaWeevil”, “acaciaMidge”) it can be attributed to costs occurring during growth and development, in the case of the BCAs (“weevilLarva”, “weevilAdult”, “midgeGall”, and “midgeAdult”) the resource is adjusted in accordance to the damage inflicted on the plant.

2.1.3.12. endDay. Some final internal book keeping is done before starting the year again.

2.1.4. Parameter

A detailed description of the model parameters is given in the Appendix.

2.1.5. Parameter sets

The parameter sets for the simulations were generated using a Latin hypercube design. The calculations were done in R ([R Development Core Team, 2011](#)) using the function `randomLHS()` from the package `lhs` ([Carnell, 2009](#)).

The selected parameters and their ranges are shown in [Table 1](#). The parameter *pEmerge* is a composite parameter, combining *pEmerge* and *sexRatio*. These two parameters occur twice in the model: *sexRatio* occurs (1) in the calculation of released adult females and (2) *pEmerge* and *sexRatio* occur together in the determination of the number of female offspring. In the first case, the sex ratio is irrelevant (as long as larger than zero), as the number

of females released is rounded up to the next larger integer, which results in exactly one released female in addition to a not calculated number of males. In the second case, the number of emerging females is calculated using the formula

$$\text{emergingFemales} = \text{emergingIndividuals} \cdot \frac{p\text{Emerge} \cdot \text{sexRatio}}{1 + \text{sexRatio}}$$

It is clear that all changes in the parameter *sexRatio* can be represented by a change in the parameter *pEmerge*.

We created 10000 parameter sets with changing values for the selected parameter, which were simulated with agents (released adults = 1) and without agents (released adults = zero). Of these 10000 parameter sets 9989 (without BCA) and 9680 (with BCA) were simulated successfully. The rest did not complete the simulations due to technical problems on the computer cluster used. The results from the simulation without the agents were used as baselines against which the simulations with BCAs were compared.

2.2. Analysis

2.2.1. Fluctuations

To determine the dominant period in the occurring fluctuations, we constructed a periodogram using a fast Fourier transform as implemented in the function `spec.pgram()` in R (R Development Core Team, 2011) (non-default parameter: `spans=c(3,3)`, `na.action=na.exclude`). We analysed the years 11–40 to exclude initial fluctuations caused by initial conditions and the initial releases of the agents.

We identified the maximum of this periodogram and determined the corresponding period. This period was considered being the dominant period. Dominant periods larger than half of the analysed time frame, i.e. 15 years, were considered as being “non-periodic”, while smaller ones as “periodic”.

2.2.2. Sensitivity analysis

To determine the qualitative and quantitative impact of the different parameters on the flowering (sum of number of non oviposited flowers per day over one year) and seed production (sum of seeds produced per year) pattern, a global sensitivity analysis (from now on referred to as sensitivity analysis) was conducted. The function `sens()` (`nn.lhs=600`, `model=btlm`, `R=20`) of the package `tgp` (Gramacy and Taddy, 2010) in R (R Development Core Team (2011)) was used.

The dependant variables were “flower” and “seed”, the independent variables and their analysed ranges can be found in Table 1. As the results for flowering and seed production are daily, the results were grouped by years and the number of flowers and seeds produced per year were calculated for each year (together referred to as “entities”). It is important to note that the sum of flowers does not represent the number of flowers produced per year, but the sum of the numbers of flowers present at each day over one year (i.e. flower days). In contrast, the actual maximum flower production by the *A. cyclops* is, as mentioned above, constant for each year, while the flower days can be reduced by the midge, as only non-oviposited flowers are included in this measure.

To exclude the initial phase after the introduction of the BCAs in which stronger fluctuations can be expected, we started our analysis five years after the introduction of the second agent (midge), and analysed the years 11–40. We calculated the summary values “mean” and “coefficient of variance” of the entities and the “main period” of the fluctuations (referred to as “period”) over this time period. These were then used as the response variable for the sensitivity analysis.

To evaluate the sensitivity of the respective response variable to the input variable, we used the first order sensitivity index (the proportion of the variance explained by the variable) and the total

sensitivity index (the proportion of the total variance explained by the variable, including interaction effects); to determine the nature of the effect, we assessed the main effect.

2.2.3. Biocontrol agent survival

To investigate what is driving the population numbers of the BCAs, we conducted the sensitivity analysis for the mean of the number of adult midges (*midgeAdult*) and adult weevils (*weevilAdult*).

For the purpose of this paper, we defined “co-existence of the BCAs” as both BCAs being present during the last three years of the simulation (the years 38, 39 and 40), i.e. no BCA went extinct after release.

3. Results

Overall, we simulated and analysed $N=9989$ parameter sets without BCAs and $N=9680$ parameter sets with BCAs.

3.1. Flower and seed production

3.1.1. Without biocontrol agents

All simulations without BCAs produced flowers and seeds. Seed production in one year was based on the flower production in the previous year, multiplied with a factor based on the parameter and transitions between the different age classes

$$P_{\text{seed}} = \frac{1}{3} \cdot 0.2 \cdot 7 \cdot P_{\text{flower}} = 0.467 \cdot P_{\text{flower}}$$

where $\frac{1}{3}$ converts from “sum of flowering days” to “sum of actual flowers”, 0.2 is the proportion of flowers developing into pods and 7 is the average number of seeds per pod.

Parameter values of all parameters were evenly distributed for all simulations resulting in flower as well as seed production (see Fig. 5).

The only parameter showing a real impact on the mean of flower production without BCAs is the *resourceRenewal* (see Fig. 6), which explains more than 40% of the variability alone and more than 80% when including interaction effects. The seed production shows the same dependencies as the seed number is effectively determined by the formula above.

3.1.2. With biocontrol agents

In the simulations with BCAs, flowers were produced in 39% of all simulations, while only 3% of all simulations resulted in seed production (see Fig. 5).

In the case of simulations resulting in flower production, the distribution of the values for *resourceRenewal*, *midge pEmerge*, *midge meanEggsPerFemale* and, to a smaller extent, *midge maxEggsPerFlower*, all show a distinct higher likelihood of smaller values. This is in contrast to simulations with seed production, in which only *midge maxEggsPerFlower* and *weevil pEmerge* show a higher likelihood for smaller values, while *weevil seedsDamagedPerOviposition* shows a slightly higher likelihood for larger values (see Fig. 5).

For the simulations with BCAs the sensitivity analysis identified the *meanEggsPerFemale* and *pEmerge* of the midge as the most important parameters for determining the mean of number of flowers produced, which explain together more than 60% of the variability (Table 1).

For the mean seed production per year, *weevil pEmerge* is the most important parameter, but explaining only about 10% of the variation, while the other parameters have a negligible impact when excluding the interaction effects (Table 1).

In contrast to flower production, in which the first order sensitivity indices account for nearly 80% of the variability in the mean flower production and more than 60% in the variability of the period

Fig. 3. Key phenological stages of three species (two biocontrol agents (the midge *Dasineura dielsi* and the weevil *Melanterius servulus*), as well as the invasive alien plant *Acacia cyclops*) based on a simulation. Shown for illustrative purpose. The release dates are marked by the vertical lines. Red curves represent numbers per day. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

flower production, only about 20% of the variability are explained for both measures by the first order sensitivity indices for seed production (see Fig. 6 and Appendix).

3.2. Fluctuations

Apart from the expected yearly (seasonal) fluctuations (see Fig. 3), we see, in most simulations, multi-yearly fluctuations in flowering, resulting in periods of flower production ranging from 2 to 10 years (see Fig. 4).

3.2.1. Without biocontrol agents

Without BCAs introduced, 99.7% of the simulations producing flowers resulted in periodic flowering, with 97.8% of these having a period of two years. For seed production, the same picture emerged, i.e. 99.7% periodic, of which 97.9% had a period of two years (see Figs. 4 and 5). Simulations resulting in flower or seed production periods larger than two, had either very small or very large mean flower or seed productions.

Furthermore, 99.5% of simulations which showed periodicity in flower production also showed periodicity in seed production, with only 0.1% showing periodicity in seed production but not in flower production.

The parameter profiles of the simulations showed no preference for any parameter range (see Fig. 5).

The coefficient of variation, used as a proxy for the strength of the fluctuations, was approximately one for most simulations (see Fig. 4).

Based on the sensitivity analysis, variation in the main period identified can only be attributed to interaction effects. No parameter shows any explanatory value (see Fig. 6). The seed production follows the same pattern as the flower production.

3.2.2. With biocontrol agents

A different picture emerges for the simulations with BCAs. Here, only 29.3% of the simulations were periodic for flower production, with 85.8% of these having a period of two or three years. The picture changes for seed production, where only 1.6% of all simulations

were periodic, but 61.8% of these had a period of two years (see Fig. 5 and Fig. 4). The parameter profiles for simulations being periodic in flowering showed the same patterns as those of flower producing simulations, i.e. small *resourceRenewal*, midge *pEmerge* and *meanEggsPerFemale* as well as slightly smaller *meanEggsPerFemale* (see Fig. 5). Simulations which resulted in periodicity in seed production showed the same pattern as those producing seeds, i.e. small *pEmerge* and slightly higher *seedsDamagedPerOviposition* of the weevil, as well as small *maxEggsPerFlower* of the midge.

1.0% of the simulations showed periodicity in flowers and seeds and 0.6% showed periodicity in seed production, but not in flower production.

The introduction of biocontrol increased the coefficient of variation to values up to more than 5, although the majority remained approximately one (see Fig. 4), meaning that the strength, or amplitude, of the fluctuation in relation to the mean increased dramatically.

The most important parameter in determining the periodicity of the flowering was *meanEggsPerFemale* and *pEmerge* of the midge, which explain together more than 45% of the variability (Table 1), with *resourceRenewal* explaining an additional 10%.

For the period of the seed production, no parameter could be identified as being more important than the others (Table 2).

3.3. Biocontrol agent survival

Co-existence of the BCAs, i.e. presence of both during the years 37–40, only occurred in 21% of all the simulations. The weevil went extinct in 65% of all simulations while the midge only in 14%. The parameter profiles (Fig. 5) show that in the simulations which resulted in the survival of just the midge (i.e. extinction of the weevil only), values for *resourceRenewal* and midge *maxEggsPerFemale* are medium or large, whereas in the case of survival of only the weevil (i.e. extinction of the midge) these values are small. In addition, in the case of midge survival, midge *pEmerge* is medium or large, whereas for weevil survival *resourceConsumption* is larger and midge *meanEggsPerFemale* is small.

meanEggsPerFemale (explaining 20% without interaction effects, but nearly 80% including interaction effects) followed by *pEmerge* (about 10%, nearly 60% including interaction effects).

4.1. General

The model simulates the impact of two BCAs (*M. servulus* and *D. dielsi*) on one IAP (*A. cyclops*). On the plant side, it simulates the development from flower via seed pod to seed release (all of these

Periodicity table showing the periodicity of flowering and seed production in a model simulating the effect of two biological control agents (BCAs; the midge *Dasineura dielsi* and the weevil *Melanterius servulus*) on an invasive alien plant (*Acacia cyclops*) (40 years were simulated, years 11–40 analysed). A simulation is considered as being periodic if the main period is smaller than 15, as non periodic if the main period is larger than or equal to 15; “flower and seed” is defined as periodic if both “flower” and “seed” is periodic.

[illegible]

Fig. 5. Parameter profiles of different outcomes of a model simulating the effect of two biological control agents (the midge *Dasineura dielsi* and the weevil *Melanterius servulus*) on an invasive alien plant (*Acacia cyclops*) regarding flower and seed production. The width of the bars indicates the likelihood of the parameter being in a specific range. Graphs are scaled so that the maximum likelihood is for all results the same. The numbers on the bottom and top of each graph indicate the minimum and maximum value of the parameter. ■ green histograms: without biocontrol (9989 simulations), ■ black histograms: with biocontrol (9680 simulations). Numbers in the left column are the number of simulations ■ without biocontrol and ■ with biocontrol for the respective outcome. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 6. Graph showing the summarised results of the sensitivity analysis, to elucidate the effect of the parameter ■ mpE = *midge_pEmergence*, ■ mFe = *midge_meanEggsPerFemale*, ■ mFI = *midge_maxEggsPerFlower*, ■ wpE = *weevil_pEmergence*, ■ wDO = *weevil_seedsDamagedPerOviposition*, ■ rR = *resourceRenewal*, ■ rCF = *resourceConsumption_acaciaFlower* and ■ rCP = *resourceConsumption_acaciaPod* on flowering and seed production of an invasive alien plant, *Acacia cyclops*, as well as the survival of the two biocontrol agents (the midge *Dasineura dielsi* and the weevil *Melanterius servulus*). The left box-whisker plots show the first order Sensitivity indices, the right ones the total effect Sensitivity indices. The line graphs below show the main effect of the different parameters. The parameter ranges were scaled from -0.5 to $+0.5$, as reflected in the x-axis.

are collectively referred to as a “reproductive entity”) based on a potential maximum number of flowers per year. On the BCA side, different stages of the individual BCA are simulated. Although the two BCAs both impact on the reproductive entities they do so at

different times. As the flower takes about 250 days to develop to the stage suitable for use by the weevil, the impact of the midge in one year influences the availability of the reproductive entity for the weevil in the following season.

In addition, the model includes a limiting resource which is only consumed by the IAP. All stages of the development of the reproductive entity consume a certain amount of the limiting resource per day, although in different quantities. As we assume that the plant allocates resources first to the development of reproductive entities in more advanced developmental stages (to avoid aborting these), the amount of the resource available limits the actual number of flowers which can be produced per day. This limiting resource is the regulating element in the model which reduces the number of flowers actually produced from the potentially possible number which can be produced per year.

Despite the different nutrient requirements for pod/seed and gall development (Moseley et al., 2009), we do assume in our model that the resource requirements of these different entities are the same. As the resource in our simulation does not represent a single entity, but rather an abstract composite of diverse resources, the assumption is here valid. Even Moseley et al. (2009) states that gall abundance has “no effect on vegetative growth rates of trees”, as galls have a higher carbon cost, while pod/seed development has higher nutrient costs.

The number of seeds produced is based on flower production during the previous season. Without BCAs, ageing from flower to released seed is deterministic, except for determining the appearance of the green pods, which follows a given normal distribution. As the emergence date of the green pod is distributed within the following year, the seed production can be predicted using a linear model with a slope equal to the theoretical possible number of seeds per flower. Consequently, the pattern for seed production mirrors the pattern for flower production. As soon as a BCA is introduced, this is not true anymore, as the agents reduce the number of seeds produced per flower.

4.2. The role of seed production in the control of the IAP

The seed production of *A. cyclops* is extremely high (Richardson and Kluge, 2008). Some authors (e.g. Myers and Risley, 2000) argue that seed feeding agents are only effective if a very high percentage of the seeds is destroyed and in some cases the control of the seed production can even lead to increased density of the invader. In contrast, Holmes (1989) and Richardson and Kluge (2008) argue that the control of the seed bank, and consequently their source, i.e. the seed production, can not be underestimated. Richardson and Kluge (2008) discuss the role of seed banks of invasive acacias and their options for management in more detail and identify the seed production as one of the five components of intervention to manage the seed bank over time. They particularly mention the role the two biocontrol agents discussed in this paper play on *A. cyclops* but highlight the fact that data supporting the statement that control of seed production is reducing the spread of the species is missing so far. Even though that in the short term, i.e. within the lifetime of the individual plants, a thinning of the IAP stands cannot be expected, impact in the longer term have been shown by e.g. Louda and Potvin (1995) and Hoffmann and Moran (1998). Impacts on the spread have not been demonstrated in the field, but have been demonstrated by Le Maitre et al. (2008) using a simulation model for *Hakea sericea*, an invasive tree which releases up to 7500 seeds per m² after a fire (Kluge, 1983 in Kluge and Neser, 1991).

4.3. Impact of BCAs

To be able to understand the impact of the BCAs on the IAP, the same parameter sets as simulated including BCAs were simulated but without releasing BCAs. These simulations provide a baseline for assessing the impact of the BCAs on the flowering and seed production of the IAP.

Apart from considering these different scenarios simulated, consisting of randomly chosen parameter sets from the parameter space for the sensitivity analysis, these parameter sets can be seen as different populations of the IAP at different physical locations. Different locations have different amounts of resource renewal rates. Examples of factors influencing the availability of a resource include aspect (exposure to solar radiation), slope (water), altitude (wind), soil (nutrients). The different rates of resource consumption in different parameter sets by the flower and the pod can be interpreted as being influenced by interactions of other non-limiting resources and factors which act differently on the consumption of the limiting resource in different stages of the development of the reproductive entity. Although it would theoretically be possible to map physical locations to locations in the parameter space (i.e. parameter sets) and vice versa, this is virtually impossible due to the abstract nature of the “resource” parameter.

All simulations without BCAs produced flowers and seeds. As can be expected, the *resourceRenewal* is the most important parameter in predicting flower and seed production. This comes as no surprise, as an increase of a limiting resource which impacts on flowering and seed production will lead to increased flowering and seed production (Moseley et al., 2009). It is important to note that an increase of the *resourceRenewal* only leads to an increased flowering and seed production in the lower half of the simulated parameter range, indicating that the resource is not limiting at higher parameter values. This behaviour of the model is not surprising as the model contains a parameter specifying the maximum number of flowers which can be produced. This hard limit can be seen as physiological limits of flowering and seed production in nature or other limiting resources.

Of all the simulations without BCAs introduced, 99.6% were periodic in flower production and also seed production, with 98.7% of these having a period of two years. The periodicity of these simulations can be explained by the impact of reproductive entities on the limiting resource. As the limiting resource is consumed by transitions between all stages of the reproductive entity, and the development from flower to seed takes 18 months, this years flowers (year zero) will still be on the plant and consume the limiting resource when the plant is flowering again in year 1. This will reduce the available resource for flowering and thus reduce the numbers of flowers in year 1 compared to year zero. In year 2, the smaller number of flowers from year 1 will lead to more resource being available for flowering, thus resulting in more flowers in year 3, resulting in cycles of a period of 2.

This is confirmed by field observations, but the period in the field is not as regular as in the simulations (Impson, personal communication). Possible explanations for this are climatic fluctuations between years, causing an overlay of these inherent predictable cycles with irregular and unpredictable fluctuations and thus increasing and possibly amplifying periodicities, which has already been touched upon, but not been discussed further in detail, in Impson et al. (2004).

An additional aspect of the fluctuations observed in situ is the synchronicity within a stand. Given that the fluctuations in our model are inherent to the IAP, the level of stand wide fluctuations observed (Impson and Kleinjan, personal communication) do require an additional synchronisation mechanism (Impson et al., 2004). This synchronisation can be caused by any trigger, which either provides an increased flowering or decreased flowering, resulting in extraordinarily high or low flowering in one year, therefore synchronising the inherent fluctuations in one stand. As this can be any kind of trigger, it is likely that the synchronisation happens only at the stand level and not at the landscape scale, thus explaining a-synchronisities between stands (Impson et al., 2004).

The fact that the pattern of a two-yearly fluctuations without BCAs is inherent in the structural design of the system is reflected

by the sensitivity analysis. In the sensitivity analysis, all factors play quantitatively the same role in regards to their first order effects and their interaction effect. The sensitivity analysis includes parameters related to the BCAs, which are not released in these simulations. These parameters can therefore be regarded as random variables. As all parameters have the same impact as these (in these simulations without BCAs) random variables, no variable plays an actual role in the two-yearly fluctuations.

The introduction of BCAs changes the pattern, strength and parameter predicting the flower and seed production and their fluctuations in some important aspects. The most obvious aspect is the reduction in flower and seed production (only 38% of the simulations are producing flowers and only 3% are producing seeds after introduction of the BCAs), thus demonstrating the effectiveness of the BCAs. Although the proportion of simulations displaying periodic behaviour is dramatically reduced from around 99% to around 1%, the period of the flower and seed production is increased, while the main period is in most simulations still at two years. In addition, the intensity of the fluctuations is also increased. The parameters having the biggest impact on the flowering are as expected midge related parameters, i.e. *pEmerge* and *meanEggsPerFemale*. Interestingly, this is not true for the seeds, for which the most important parameter is *pEmerge* of the weevil. In other words, the weevil is an extremely efficient BCA, and it becomes effective in reducing seed production with relatively small numbers of individuals. If the efficiency was heavily dependant on the number of individuals, the parameter influencing the mean number of weevils most (*meanEggsPerFemale* of the midge) would emerge as influencing the number of seeds, and not only the number of weevils. This effectivity of the weevil can be explained by the continuous reproduction over its life time, whenever ready pods are available. As the weevil lives two years, the number of seeds effectively destroyed by a single individual is much larger than by a midge, whose adult stage only lives five days (also the emergence of new midges depends on reproduction and consequently available flowers). Although the weevil cannot react as quickly to sudden changes in flowering, resulting in pod availability, its long life expectancy provides a kind of baseline-control, i.e. reducing the “normal” seed production. In contrast, the midge, because of its rapid response, forms a kind of peak-control, which can control peak flowering.

Considering that the BCAs have a (proportional) bigger impact if there are a small number of flowers (midge) or seeds (weevil), they can reduce the flower and seed production to zero, therefore increasing the available resources the following year and increasing the number of flowers produced. Due to the small number of flowers and seeds available the previous year, the number of new BCAs will be substantially reduced, therefore limiting their ability to control the flowering and seed production the following year. This leads to increased fluctuations after the introduction of the BCA. Apart from the intensification of these fluctuations, the period of the fluctuations is increased, especially for seed production. As the weevils live for two years, they will be able to survive years with low pod availability, and therefore be able to control seed production more consistently than the adult midges, which live only for 5 days. This short life expectancy is offset by a dormancy of the larvae (Kleinjan, personal communication), enabling the midge population to survive for years with no flowers, but this still reduces considerably the number of midges, making their impact on the flowers more variable over the years. This is reflected in the increase of the period when BCAs are introduced, which is much more pronounced for the seeds than for the flowers.

These fluctuations raise the question about the co-existence of the BCAs (Impson et al., 2004), as midges in particular may reduce the flowers to zero in any given year. The midge therefore has a considerable impact on the reproduction and survival of the weevil, which depends on the pods for reproduction. In contrast, the

weevil cannot reduce the number of available flowers. Even though the weevil oviposits in pods, it has no impact on resource consumption, as the pods and seeds develop as if they had not been oviposited in, but the seeds are finally destroyed by the larvae. Given the same stress caused by resource limitations for both BCAs, the weevil would be more likely to be affected. The simulations show a picture which is consistent with this hypothesis, namely that in 65% of the simulations only the midge survives, i.e. the weevil goes extinct, while in 14% only the weevil survives, i.e. the midge goes extinct. In the remaining 21% of simulations, co-existence between the two biocontrol agents occurs.

The fact that the weevil has no impact on the number of midges is reflected in the sensitivity analysis. On the other side, the parameters of the midge influence not only the mean number of midges but are also the main predictors for the mean number of weevils. Using these results, one can classify the weevil as a “controlled” BCA, while the midge is a “controlling” BCA in regards to the co-existence and numbers of BCAs present. As the number of BCAs present has a direct impact on the reduction of flowers and seeds, these ultimately control the availability of the seeds.

In contrast to our simulations, observations indicate the co-existence of these two BCA (see for example Impson et al., 2011; Moran and Hoffmann, 2012). One factor explaining this apparent discrepancy can be seen in the fact that the parameter ranges in situ are only a subset of the parameter sets analysed in our simulations. This is especially true for parameters for which no clear indications of their ranges could be established from literature. In these cases, a plausible range for that parameter, larger than the expected realistic range, was chosen. However, this meant that parameter combinations which do not occur at the study locations, and probably nowhere, were tested. Another factor which will most definitely contribute to the co-existence of the two BCA in situ can be found in within stand a-synchronicity (Impson et al., 2004). This a-synchronicity can function as a refuge for a BCA and therefore increase the chance of co-existence.

4.4. Implications for management

The reduction of seed production have a demonstrated effect on the population dynamics of some species (e.g. Louda and Potvin, 1995; Hoffmann and Moran, 1998). As an effect on the spread can also be expected (Klinken et al., 2004; Le Maitre et al., 2008), the utilisation of biocontrol agents to control *A. cyclops* must be considered as worthwhile, especially in the context of integrated IAP management, i.e. the combination of biocontrol agents with conventional alien control measures (e.g. clearing) (Impson et al., 2004). Consequently, the results of this modelling exercise have important practical implications for the use of BCAs in integrated IAP management, particularly on the selection of BCAs for the release of the first and second BCA as well as for post-release monitoring.

In the absence of BCAs the most important parameter determining seed production was the resource renewal rate at the site. As expected, this changed dramatically with the release of the BCAs when, irrespective of the flowering and seed production pattern before the release, patterns of flowering and seed production were controlled by the midge. This confirms the common sense approach of releasing BCAs in areas with high seed production.

One aspect that needs to be considered when monitoring flowering and seed production of an IAP is that an introduced BCA is likely to increase the fluctuations between years in seed production as well as introduce or increase periodic fluctuations of flower and seed production. These fluctuations can make it extremely difficult to assess the effectiveness of an introduced BCA, and long term observations are essential.

These fluctuations could motivate the release of a second BCA, but at the same time they make the choice of an appropriate second BCA more important. Not only does the impact of the second BCA on the IAP need to be considered, but also its impact on the previously-established BCA. Possible impacts include intraguild predation (as discussed by [Rosenheim et al. \(1995\)](#)) but also, which is the case in our system here, competition. If the second BCA is (too?) successful, it could drive the other BCA to extinction, as we observed in many parameter sets, where the midge destroyed the resources needed by the weevil which subsequently went extinct. Our simulations indicate that these extinctions becomes less likely if the BCAs are long-lived or exhibit a diapause like the midge, but even in such cases, extinctions are likely if flower and seed production fluctuate. If the two BCAs coexist, the envisaged additive effect on the seed production of the IAP is likely, but this co-existence depends on the “right” conditions at the site as well as characteristics of the BCA. This is in line with [Denoth et al. \(2002\)](#) who show in their review that competition occurs between different BCAs, but that they are more likely when the target species is an insect instead of a weed. One can compare the reproductive entities to insects: they are “killed” by the BCA, i.e. do not develop into reproductive seeds and are not available for other BCAs once they are attacked by one BCA. Consequently, these two seed attacking BCAs are more likely to show interactions comparable to BCAs attacking insect pests than BCAs attacking weeds.

This study indicates that at sites with higher resource renewal, the chance of co-existence of the two BCAs is decreasing. As resource renewal determines the flower and seed production on sites without BCAs, sites with lower flower and seed production are more likely to provide conditions for co-existence. This is rather counterintuitive, as one would expect that large resources would facilitate co-existence. But this can be explained by the fluctuations which are more likely with smaller resource renewal rates as discussed above.

We identified one “controlling” BCA (midge) and one “controlled” BCA (weevil). This classification made it simpler to explain why the midge had the most pronounced impact on the co-existence, as it not only has the strongest impact on the seed production, but also controls the dynamics and survival of the second BCA, the weevil. An agent which is effective in controlling a resource will also control the dynamics of a second agent (the release order of the BCAs is irrelevant) which utilises the same resource at a later stage in the reproductive cycle of the acacia (as in the case with midge and weevil). These two BCA compete with each other about the same resource, but the one which can use the resource earlier, has a competitive advantage. Consequently, the BCA utilising the same resource at a later stage is generally “controlled” and will have a higher risk of being driven to extinction by the other BCA, unless an additional feedback mechanism exists. Such a feedback mechanism would enable the second BCA to impact on the resource of the first BCA. This kind of feedback was not present in our model system as its existence is unlikely in situ.

A system similar to ours in regards to one BCA controlling a second BCA has been described by [Denoth et al. \(2002\)](#), which is the effort to control *Lythrum salicaria*, for which four BCAs were released. Two feed on foliage, and the resulting heavy defoliation leads to increased stress and suppressed flowering, which reduces the food source for one flower feeding BCA.

A safe approach would be to have a two-stage biocontrol. In the first stage, the one BCA attacks the resource earlier in the life cycle, but is not able to utilise the complete resource (e.g. the resource is not to 100% accessible to the one biocontrol agent). The other BCA utilises the remaining resource. In a scenario like this, none is able to control the other to such an extent that one is driven into extinction, while the requirements on the effectiveness of each BCA are not as high as they would be if only one would be released. Nevertheless,

like [Denoth et al. \(2002\)](#) argues, it is preferable to have only one BCA as this will limit the chances of undesired side effects among the BCAs or non-target species.

4.5. Conclusions

Biological control can play an important role in the integrated management of invasive alien plants, as they have a very pronounced impact on seed production (see e.g. [Impson et al., 2004](#); [Moran et al., 2004](#)). Nevertheless, it is essential to choose the right BCA, especially when other BCAs are already present, so as not to cause the extinction of one BCA. In addition to their impact on the actual number of seeds produced, BCAs also increase the fluctuations of seed productions between years, resulting in more pronounced fluctuations after release than before. This emphasises the importance of monitoring of the populations after the release of the BCAs over the long term.

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Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:<http://dx.doi.org/10.1016/j.ecolmodel.2014.01.028>.

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