DESERT KNOWLEDGE CRC

Projecting the effects of grazing and drought on populations of shrubs and trees in the Australian rangelands

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2008

Department of Environment & Climate Change NSW

Department of Agriculture and Food
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The Desert Knowledge Cooperative Research Centre is an unincorporated joint venture with 28 partners whose mission is to develop and disseminate an understanding of sustainable living in remote desert environments, deliver enduring regional economies and livelihoods based on Desert Knowledge, and create the networks to market this knowledge in other desert lands.

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Definitions

DAFWA	Department of Agriculture and Food, Western Australia
DKCRC	Desert Knowledge Cooperative Research Centre
EMS	Environmental Management System – a document describing management objectives and the type of monitoring required to measure whether those objectives are being met
Lambda (λ)	The long-term growth rate of a population. A value of $\lambda > 1$ indicates that the population is increasing; a value of $\lambda=1$ indicates that the population is stable; a value of $\lambda < 1$ indicates that the population is decreasing (Begon et al. 2006).
NSWDPINR	New South Wales Department of Infrastructure, Planning and Natural Resources (now Department of Planning and Department of Natural Resources
NSWDEC	New South Wales Department of Environment and Climate Change
RCD	Rabbit Calicivirus Disease (also known as RHD: Rabbit Haemorrhagic Disease)
SADEH	South Australian Department for Environment and Heritage
WARMS	Western Australian Rangeland Monitoring System

Acknowledgements

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Summary

We present a new stage-structured model, called SHRUBPOP, for projecting potential impacts of grazing and rainfall (drought) over periods of up to 500 years on populations of trees and shrubs in the Australian chenopod rangelands.

Created in Microsoft Excel®, the model is based on functional groups rather than species so that it can be used, with or without modification, for any species of tree or shrub. It includes the effects of grazing pressure of four herbivore species: sheep, rabbits, goats and kangaroos. Rainfall (either modelled or real rainfall records) can be included as another variable. Model runs can be repeated in series, with different herbivore intensities, using the end population numbers of the previous run as the starting numbers for the next run, to model the effects of management interventions such as spelling of paddocks and control of feral herbivores. By using different rainfall data, various climate-change scenarios may also be created. It is simple to adjust the parameter files to model populations of species from other regions and for different climate conditions, or for the effects of grazing by other herbivores, such as cattle.

Introduction

Research shows that, since European settlement, grazing has reduced regeneration levels of a number of species of native trees and shrubs in the arid lands of southern Australia (Crisp & Lange 1976; Crisp 1978; Tiver & Andrew 1997; Tiver & Keiermeyer 2006). The reduced levels of regeneration reported in some species mean that their populations are declining while others are being maintained or are increasing, thereby gradually altering the composition and/or overall cover of vegetation. In the long term, this could result in the loss of some species, and/or the dominance of large areas by undesirable 'woody weed' species, with unknown effects on the overall sustainability of biodiversity and productivity. There could be a corresponding loss of opportunity for marketing Australian rangeland products as being produced by ecologically sustainable industries, so there is a need to predict long-term impacts of grazing on rangeland tree and shrub populations. We can use mathematical modelling to assess the sustainability of shrub populations (equivalent to productivity in rangeland ecosystems) and use the assessment in Environmental Management Systems (Tinning & Carruthers 1999; CSIRO 2000).

Ecological processes commonly operate on timescales of decades or longer (Tyre et al. 2000). Because of the long life spans, compared to humans, of woody trees and shrubs, there has been very little research to follow the progress of plant cohorts as compared to animals (e.g. Volterra 1926; Lotka 1932). So, the field of mathematical modelling of plant populations has also been limited (Czaran 1997). Yet mathematical modelling is a useful tool for predicting a range of population outcomes over hundreds of years.

Age-structured matrix models are widely used in ecology to study population dynamics. These models – also known as population projection models – are based on the Leslie Growth Matrix (Leslie 1945; DeAngelis et al. 1994; Caswell 2001). The models are used to determine the long-term growth rate of populations and to project future population levels under prescribed conditions. The 'conditions' in our study include different grazing regimes and environmental factors such as rainfall events. Our preliminary work indicated that, because of limited longevity of data for some species, we had to use stage rather than age data, and reconstruct ages from these (McArthur et al. 2003). There are some benefits in doing this because many life processes tend to be stage- rather than age-related (Watson et al. 1997a). Stage-structured models have been developed:

- for arid zone shrubs to investigate their basic dynamics (Grice et al. 1994)
- as theoretical models of range dynamics (Watson et al. 1997a)
- to help interpret information from range monitoring systems (Watson 1999)
- to investigate century-scale dynamics in the context of historic degradation episodes (Watson 2002).

The last model used two stocking rates, six grazing strategies and three climatic year types.

Other population models that project plant population trajectories, such as RAMAS (Resit-Akcakaya 2005), are available 'off the shelf', but most of these relate rainfall directly to population growth. However, as long as a plant has sufficient soil-water resources to maintain turgor, it will not respond to soil moisture beyond that level. In an arid ecosystem, a more critical aspect of rainfall is the lack of it – the frequency and duration of drought periods when soil moisture is below critical levels, resulting in plant mortality. This is particularly critical in Australia, a notoriously drought-prone continent (Stafford Smith & Morton 1990). We aimed to develop a model that would use rainfall data in a way that projects the effects of frequency and duration of droughts on plant populations. We have called our model SHRUBPOP.

Methods

We developed a stage-structured population matrix model in Excel to project impacts of grazing (four herbivores) and rainfall (drought) over periods of up to 500 years. The model was based on plant functional groups rather than species so that it can be used, with or without modification, for any species of tree or shrub.

Mathematical structure of the SHRUBPOP model

McArthur et al. (2006) describe in detail the mathematical structure of the model. In brief, it uses a projection matrix of values that represent the vital rates (fecundity and survivorship) of individuals of different stage classes. Most matrix-models use age classes, but there is insufficient knowledge to determine the ages of most Australian trees and shrubs, so we used stage classes. During each iteration of the matrix, representing a time-step (which can be any interval, but we used years), a proportion of the individuals move up one stage class. Thus, for each time-step, each individual either remains at the same stage or proceeds to the next one.

Input data and model parameters

Experimental and existing data in Australia's southern rangelands

The University of South Australia holds data on regeneration levels of 57 species of rangeland trees and shrubs under various levels of grazing by sheep, goats, rabbits and kangaroos (Tiver 1994, 1996, 1998; Tiver & Andrew 1997). These data have been collected over the last 10 years, but reflect the effects of various management strategies over a period of more than 150 years. We also have access to long-term data from a single small site – Koonamore – held by The University of Adelaide. Further data from thousands of monitoring sites over three states, in both pastoral lands and the parks system, are held by the four state government end-users of this research:

- the Department of Agriculture and Food, Western Australia (DAFWA)
- the Department for Environment and Heritage, South Australia (SADEH)

- the Department of Infrastructure, Planning and Natural Resources (now Department of Planning and Department of Natural Resources
- the Department of Environment and Conservation, New South Wales (NSWDEC).

The DAFWA, NSWDPIINR and The University of Adelaide data sets lend themselves to transition matrix modelling because the fate of each individual shrub has been followed through time, which is essential to the individual modelling approach used.

A more detailed list of data sets, for which sites and data sets have been reasonably well-maintained, includes:

- South Australia
    1. North-East Pastoral District of South Australia: Regeneration levels at 342 sites of 57 species of rangeland trees and shrubs under various levels of grazing by sheep, goats, rabbits and kangaroos (Tiver 1994, 1996, 1998; Tiver & Andrew 1997). These sites were re-monitored during 2004 to ascertain whether Rabbit Calicivirus Disease (RCD) had relieved grazing pressure on seedlings and improved regeneration.
    2. Koonamore: Since 1926, The University of Adelaide has maintained data of individual plants, photopoints and plots at the TGB Osborn reserve on Koonamore Station, north of Yunta. This is one of the longest-running continually-monitored plant data sets, and will be invaluable in determining population dynamics of long-lived species.
    3. Middleback: A series of 19 photopoints in Overland Paddock, Middleback Station, provides useful long-term data, particularly for populations of *Maireana sedifolia* and *Atriplex vesicaria*.
    4. SADEH maintains monitoring sites in its desert parks, including the Gawler Ranges and the Gammon Ranges. Data are kept on density and frequency of all woody plants, and an abundance of herbaceous species.

       Because the South Australian data were collected before 1993 – before the release of the RCD (Drollette 1997) and the existence of both pre- and post-RCD data from New South Wales (Denham & Auld 2004a, see below) – we had a unique opportunity to check regeneration levels of a range of trees and shrubs both before and after the arrival of the virus. Therefore, we are able to report on the effectiveness of rabbit control in increasing rangeland sustainability. We monitored a subset of the 1993 sites, and used these data for ‘time zero’ population numbers in the model.
- Western Australia
    1. Boolathana grazing trial data: Chenopod shrubland and *Acacia* sand plain vegetation on two different range conditions, data sets from 1983 to 1993. Both the transects and the data set have been maintained (see Watson 1997 or Watson et al. 1996 for a full species list, approximately 40 species). Methods of data collection are described by Watson et al. (1997a or 1997b).
    2. Western Australian Rangeland Monitoring System (WARMS) data from sites across the Western Australian shrublands: All major vegetation types and all species found on the sites. Sites installed from 1993 and read on a five-year cycle. About 75 per cent of sites have been reassessed. See Watson et al. (2001) for details of sampling methods and Watson and Thomas (2003) for example output. Tens of thousands of individual plants are included in this data set.

3. DAFWA: Old livestock exclosures dating back to the late 1960s. These have been read only periodically, but the data are well managed. For example, see Watson and Holm (1994).
4. Coodardy grazing trial: Would need to be re-monitored. Descriptions are included in Yan et al. (1996).
5. Yeelirrie destocking study: Would need to be assessed to determine if transects are still readable. Descriptions are included in Gardiner (1986a, 1986b).
6. Yerilla goat grazing study: Transects and data have been maintained in good condition. Descriptions are included in Fletcher (1991).

   A sub-set of established sites in the Gascoyne and other districts of Western Australia was re-monitored to obtain decadal-scale data for the reliability of long-term shrub models.

- New South Wales
  1. Kinchega National Park long-term survivorship and fecundity data from a range of arid zone shrubs, including *Casuarina pauper*, *Acacia aneura* and *A. carnei* (Auld 1990; Auld 1995; Denham & Auld 2004a, 2004b; NSWDEC unpub. data)
  2. Monitoring data from a range of reserves managed by NSWDEC for assessing the effects of various grazers including goats, kangaroos and rabbits, particularly post-RCD vegetation impacts.

Experimental data – shrub populations

For the purposes of the model, we initially worked on species that are widespread across the southern chenopod shrublands (see Table 1).

In particular, our analyses were based on mulga (*Acacia aneura*). Mulga is a small tree or large shrub ranging in height from two to eight metres, often multi-stemmed with a spreading crown. Mulga is a very common and significant plant species of Australian arid zone vegetation, and mulga lands occupy a wide geographical range in Australia (Nix & Austin 1973). Flowering occurs after rain, and wet winters are required for viable seed production (Preece 1971a, 1971b). Long-term demographic data for mulga are available from the Koonamore monitoring records (Sinclair & Smith 1983; Sinclair 2005; Sinclair unpub. data).

Some experimental fieldwork on juvenile stages was carried out by Raghunadh Palisetty (as part of a related PhD project) to measure population parameters of species for which we had insufficient data. Very few controlled experiments had been carried out for most species, particularly in early stages of the life cycle. Raghunadh did caged grazing exclosure trials on *Acacia aneura*. Seedlings were planted out in the field and subjected to three treatments (rabbit-fenced, sheep-fenced and unfenced) to determine the relative effects of rabbits. He used further control exclosures in an unstocked paddock to separate the effects of kangaroo grazing from that of the other two herbivores. He also collected baseline data on growth rates and survival at juvenile stages. He carried out this work at Middleback Research Centre – which is a consortium of Middleback Station Proprietors and the South Australian Government – and in the North-East Pastoral District of South Australia. The Middleback Research Centre is located on a working sheep station on the northern Eyre Peninsula.

We also searched the literature for data on our test species (see Table 1), and collated a database of what is known of the population dynamics of these species. The appendices in Watson et al. (1997b) were a useful starting point for this process.

We were not able to get population parameters (Appendices 1 and 2) for all species from the literature, and neither was it possible within the timeframe of our project to obtain them experimentally. We had to estimate some parameters, particularly those involving long time spans. Since our main aim for the model was to identify 'critical parameters' and indicate possible trajectories, this should not impair the usefulness of the model as a management tool. As more data becomes available on the modelled species, you will be able to modify the spreadsheet-based parameter sets in the model accordingly. Likewise, if you wish to use the model on another species for which you have more data, you can easily do so.

Modelling rainfall in SHRUBPOP

It is crucial that we can effectively characterise the rainfall for locations to be modelled – both return rates and intensities. We did this using statistical and time series techniques (Boland 1995, 1997; Boland & Dik 2001; Boland & Ridley 2002; Rosenberg et al. 2002a, 2002b). From our analysis, we created simulated rainfall data that was statistically identical to observed data. We decoupled the rainfall into deterministic and stochastic (probabilistic) components, and then looked for any serial correlation within the stochastic component. We needed to determine the appropriate probability distribution for the stochastic component. Rosenberg et al. (2002a, 2002b) found that, for rainfall in Adelaide, a Gamma distribution is most suitable. We tested this assumption for our study locations, and determined whether the parameters of the distribution change from location to location and also throughout the year.

Table 1: Functional groups of species included in the model

Functional group	Representative species	Height	Palatability	Longevity	Defoliation recovery
1	*Callitris glaucophylla* ***Myoporum platycarpum***	> 2 m	High (decreaser)	Long (> 200 years)	Low
2	***Acacia aneura*** *A. oswaldii*	> 2 m	High (decreaser)	Long (> 200 years)	Low
3	***Acacia ligulata*** *A. victoriae* *Cassia chatelaniana* *Dodonaea viscosa* *Eremophila sturtii* *Senna artemisioides*	2 m	Low (increaser)	Short/Medium (20–50 years)	High
4	*Maireana polypteryga* ***M. sedifolia*** *M. pyramidata* *Rhagodia parabolica* *R. eremaea* *R. spinescens*	< 2 m	Low (increaser)	Long (> 600 years)	High
5	***Atriplex vesicaria*** *Maireana georgei* *M. platycarpa* *M. trichoptera*	< 1 m	High (decreaser)	Short (c. 20 years)	Low
6	***Eremophila forrestii*** *E duttonii* *E. alternifolia* *E. maitlandii*	2 m	Low (increaser)	Long (> 200 years)	Unknown
7	***Acacia carnei*** *A. loderi* *Alectryon oleifolius* *Casuarina pauper* *Exocarpos aphyllus* *Pittosporum phylliraeoides*	> 2 m	Variable	Long (> 200 years)	High

Note: Type species are shown in bold type

Sensitivity analysis and testing the model

Lambda (λ) is the long-term growth rate of the population (Begon et al. 2006), calculated from the final projection matrix. A λ value greater than one indicates that the population is increasing. A value of less than one indicates a declining population. The magnitude of the change in λ due to a change in one of the vital rates is known as the sensitivity of λ to that particular rate. Perhaps more useful quantities are the elasticities of λ which are interpreted as the relative contributions of each of the vital rates to λ. For example, we might say that the survival of stage class II contributes about 20 per cent to λ. Sensitivity analysis of an earlier version of our model (McArthur et al. 2006) indicated that the duration of stage class V individuals imposed the most influence on long-term survival of the population, probably because stage class V is the longest and the most fertile.

As part of a related PhD project, Raghunadh Palisetty tested the model against population data collected in the North-East Pastoral District of South Australia, using analytical tools to assess the sensitivities and elasticities of λ to all the vital rates (McArthur et al. 2003, Appendix 2). This indicated which of the vital rates are most important in determining long-term sustainability of the species, and, therefore, where future field research needs to be concentrated if these vital rates are not known for a particular species. When the vital rates are functions of 'lower-level parameters', these parameters can also be tested for their relative importance to the variation in λ.

Results

Capabilities of the model

The model's capabilities are described by Tiver et al. (2006), and some examples of output are included in Palisetty et al. (2006). Detailed instructions for using the model are included as Appendix 3. Firstly, you select from among seven functional groups the one that best matches your study species (see Table 1). Each functional group has a data file containing parameters (probabilities) of fertility and survivorship, and how these are affected by grazing and rainfall. The parameters are derived from both literature sources and our experimental data. You can edit these parameter files for each functional group to more closely represent your study species. Alternatively, you can select a generic group and enter your own parameters.

As a starting point (representing time-step zero), you enter the frequency of individuals in each of seven life-stage classes. The stage classes we use are those of Tiver and Andrew (1997), but you could use a subsidiary model (Rosenberg et al. 2005) to assign plants of known height and diameter from previously existing data sets to artificial stage classes. Not everyone will want to use all seven stage classes, and Functional Groups 5 and 7 use only five stages. The model can easily be adjusted to use fewer stages, by setting all survivorship probabilities in the earlier stages to 100 per cent so that these stages do not affect the output.

In the traditional Leslie (1945) models, the stable state is defined as λ=1, i.e. the resulting population is neither increasing nor decreasing, and fecundity levels are adjusted to achieve stability of the population. However, through reproduction, all real plant populations have an intrinsic exponential growth rate (Begon et al. 2006) which is usually suppressed by variables, such as grazing or drought, which we include in the model. To allow for the intrinsic growth rate, you may alter the baseline λ by adjusting 'Doubling Time' – the longer the doubling time, the higher the fertility and intrinsic growth rate of the population (Palisetty et al. 2006).

As set out in McArthur et al. (2006), you may add the effects of up to four herbivore species (sheep, rabbits, goats and kangaroos) at the five levels of grazing intensity of Tiver and Andrew (1997). The grazing variables reduce survivorship probabilities. You can set the model to run the same grazing parameters for every year (non-varying management regime), or, alternatively, you can change the grazing regime at intervals to model management strategies, such as the control of rabbits and spelling or grazing rotations.

The default values for rainfall are 116 years of Koonamore (South Australia) historical records. You can enter your own regional historical rainfall data, and you can also edit rainfall data sets to create climate-change scenarios, such as increased or decreased summer rainfall or drought frequency. Alternatively, you can create rainfall data using the rainfall sub-model, which uses the historical data set to create 1–199 years of 'synthetic' rainfall. In the Australian arid zone, variation in rainfall (drought and flooding rain) has significant impacts on ecosystems (Stafford Smith & Morton 1990). So, rather than using rainfall totals for each time-step, plant response parameters are set to be sensitive to droughts, defined as months without effective rainfall. Effective rainfall varies with stage class; juvenile individuals need less rainfall but are only able to survive short periods of drought, whereas older individuals need larger rainfall for maintenance, but are able to tolerate much longer periods of drought.

Model output

Examples of model output are given in Palisetty et al. (2006). The output is a plot of numbers of individuals in each stage class, as well as the total population number (sum of all the stage classes) at each annual time-step (see Figure 1). Once you have set the parameters, you can run the model with grazing and rainfall, either separately or together. The aim of the model is not necessarily to produce accurate predictions, but to indicate the magnitude of variation of various management and climate scenarios as a risk management tool. Identifying the variables to which plant populations are highly sensitive also provides focus for future research which, by providing greater accuracy on plant responses to variables, would in turn increase the predictive power of the model.

Figure 1 shows the model output when λ is set to produce an intrinsic growth-rate (Begon et al. 2006), and grazing by all herbivores is set to zero. You can use this state as a baseline (Palisetty et al. 2006) against which you gauge the effects of grazing and artificially manipulated climate change (such as increased intensity and frequency of droughts). Alternatively, you can set the baseline to an intrinsic growth rate that produces a stable population against existing rainfall, with light grazing by rabbits and kangaroos (see Figure 2), and then compare it with grazing and climate change. A doubling time of 15.92 years gives an intrinsic growth rate (λ=1.043) to achieve a stable population against a background of grazing by rabbits and kangaroos for road reserve populations of *Acacia aneura* (see Figure 2). Stability was confirmed by a non-significant regression slope (p = 0.41). This stability was maintained in spite of fluctuations in population number caused by rainfall variation.

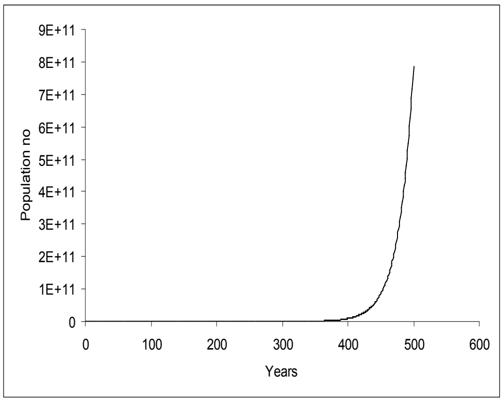

Figure 1: Model projection for a totally ungrazed population of Acacia aneura

Note: Grazing combination: sheep=0, rabbits=0, kangaroos=0. Doubling time = 15.92 years, an intrinsic growth rate. λ=1.046, indicating that the population is increasing at t=500 years. A regression of population numbers over time has a significant slope ($p < 0.001$).

Testing the model

Populations of mulga (*Acacia aneura*) were surveyed during 2003 in the North-East Pastoral District of South Australia. These sites had been previously surveyed by Tiver and Andrew (1997).

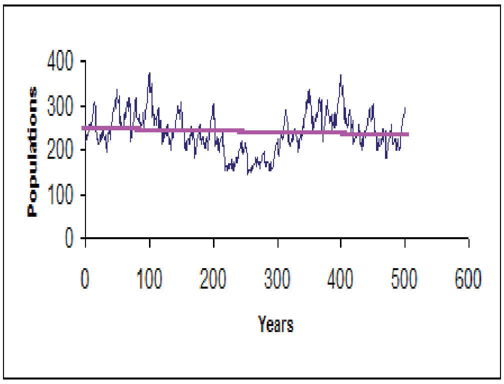

Figure 2: Model projection showing a relatively stable population of Functional Group 2 (representative species Acacia aneura*) in roadside reserves*

Note: Grazing combination: sheep=0, rabbits=1, kangaroos=1. Doubling time = 15.92 years, an intrinsic growth rate. λ=1.043, indicating that the population is increasing at t=500 years, but a regression line fitted to the output, p = 0.41, indicates that that there is no significant upward or downward trend overall.

We recorded the mulga individuals of each species at each site as being in one of seven possible stage classes, based on the nine stage classes of Tiver and Andrew (1997). We excluded ‘dead standing’ and ‘dead fall’ (lying dead) individuals because they cannot be assigned vital rates. We used a modified ‘random walk’ method (Kent & Coker 1992) to measure the populations, following the technique previously used by Tiver and Andrew (1997). At each site, the recorder left a fixed point and followed a roughly circular path covering 300–400 metres, returning to the starting point. All mulga individuals that could be observed about 20 metres either side of the transect line were recorded, including seedlings of more than five centimetres high.

We used the model to project demographic structures of populations of *Acacia aneura* using as input the data collected in 2003, and parameters derived from Preece (1971a, 1971b). We used different grazing combinations to project the possible demography of plant populations over 500 years. The rainfall data we used were 116 years of rainfall records from Koonamore Station (South Australia), the file was copied and pasted to provide data for the required 500 years. It is well known that watering points in sheep paddocks, by concentrating grazing, have resulted in drastic effects on plant populations (Lange 1969). Taking this into account, we modelled three grazing scenarios:

- heavy sheep grazing and moderate rabbit and kangaroo grazing near the watering points
- moderate sheep grazing and low grazing levels of kangaroos and rabbits far from the watering points

- a grazing rotation (10 years sheep in and 10 years sheep out) to predict the usefulness of spelling for restoring plant species in paddocks.

We compared these three grazing scenarios (see Figures 3, 4 and 5) with the previous projection showing intrinsic growth rate of populations ($\lambda > 1$), following Begon et.al. (2006), by setting the model to $\lambda=1.046$ and including no grazing variables (Figure 1).

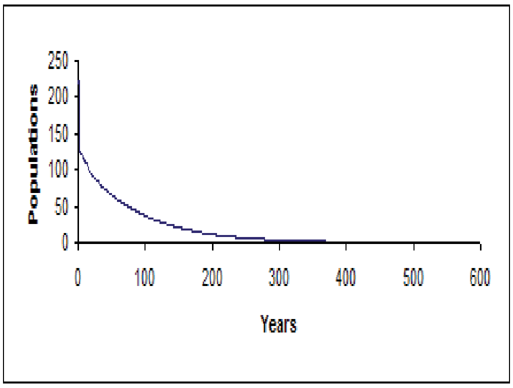

Figure 3: Model projection showing extinction of a population of Functional Group 2 (representative species Acacia aneura*) at sites nearest the watering point*

Note: Grazing combination: sheep=4, rabbits=1, kangaroos=1. Doubling time = 15.92, an intrinsic growth-rate. $\lambda=0.998$, indicating that the population is decreasing at t=500 years. A regression of population extinction over time gives a significant negative slope ($p < 0.001$).

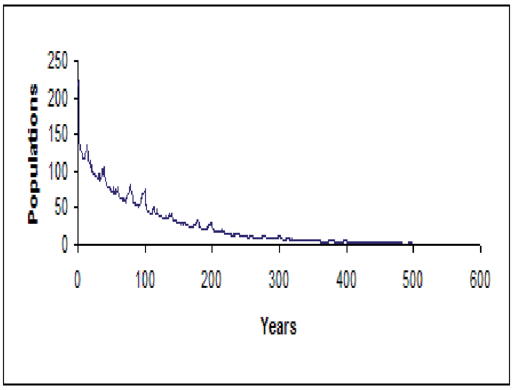

Figure 4: Model projection showing extinction of a population of Functional Group 2 (representative species Acacia aneura*) at sites furthest from the watering point*

Note: Grazing combination: sheep=2, rabbits=1, kangaroos=1). Doubling time = 15.92 years, an intrinsic growth-rate. $\lambda=0.998$, indicating that the population is decreasing at t=500 years. A regression of population numbers over time gives a significant negative slope ($p < 0.001$).

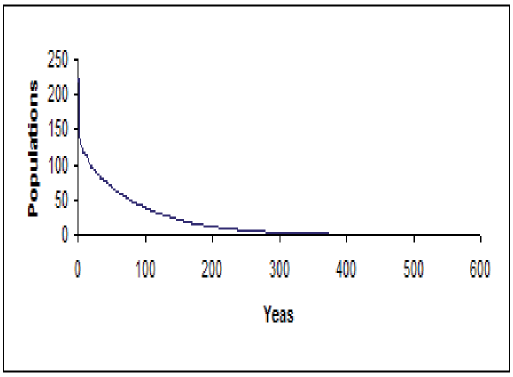

Figure 5: Model projection showing extinction of a population of Functional Group 2 (representative species Acacia aneura*) under a rotational grazing regime*

Note: Rotational grazing regime: 10 years of sheep=2, alternating with 10 years of sheep=0, rabbits=1, kangaroos=1). Doubling time = 15.92 years, an intrinsic growth-rate. $\lambda=0.998$, indicating that the population is decreasing at t=500 years. A regression of population numbers over time gives a significant negative slope ($p < 0.001$).

Discussion and conclusions

In the two set-stocked sheep-grazing scenarios (Figures 3 and 4), λ is < 1.0, indicating extinction of *A. aneura* populations within 500 years. The downward slope was confirmed by regression analysis, giving a significant negative slope ($p < 0.001$). In the site nearest to the watering point (Figure 3) there is a drastic fall in the plant numbers and they reach half-extinction in 66 years. Extinction was very slightly slower in the sites far from the watering points, with the population still above zero at 300 years. But extinction was still inevitable, with half-extinction reached in 86 years (Figure 4). Rotational grazing did not prevent extinction, with the population reaching half-extinction at 70 years (Figure 5), an almost identical outcome to the scenario shown in Figure 3.

The model indicates that sheep have the potential to cause extinction of *A. aneura* plant populations in all parts of paddocks. A large proportion of the Australian arid lands is not preserved as parks or reserves, and is subject to extensive grazing by domestic herbivores. It is, therefore, essential that the effect of livestock is taken into account when planning for conservation and management of biodiversity in the arid lands.

The model's projected population growth rates indicated that the sheep-grazed *A. aneura* populations will all decline over 500 years in the southern chenopod rangelands, with the most rapid decline in the first 100 years. This prediction is supported by an observed decline in real populations of *A. aneura* grazed for 120 years at Koonamore (Crisp & Lange 1976; Crisp 1978). Plant populations in the roadside reserves, in the absence of domestic animals, were assumed to be stable over 500 years. Assuming that the parameters input to the model (which we based on literature and experimental data) are correct, the projections show that sheep grazing is the most critical factor affecting population dynamics of *A. aneura* populations, with populations able to survive drought and grazing by rabbits and kangaroos at low numbers. There is spatial variation of plant populations: those nearer to the watering point decline at a greater rate than those far from the watering point where there is less grazing pressure, resulting in the elimination of palatable perennial plant populations around the watering points. These results are consistent with those of Hunt (2002), who found greater extinction of *Atriplex vesicaria* populations nearer to the watering point. However, our results indicate that palatable species will also be eliminated at points further from the watering points, confirming the predictions of Lange and Willcocks (1978).

Our model has proved to be a useful tool in that it can predict a range of possible outcomes for a shrub or tree population against real, artificially generated, or manipulated rainfall (climate change) regimes. Its main value is that it can graphically present the range of outcomes over 500 years, which it is not possible to do in human life spans through field monitoring studies. The model is not necessarily precise, because we know that our knowledge of Australian arid zone trees and shrubs is not yet sufficient to develop complete and accurate parameters. However, the parameters we used for our test case, *Acacia aneura* in the chenopod shrublands of eastern South Australia, are based on best possible current knowledge (literature and our own experimental grazing exclosure results), representing a best current attempt at prediction. Neither can the model be fully validated because, to do so, it would be necessary to have access to 500 years of demographic and climate data for the target species and region, which is not available.

Therefore, we advise that users of the model, whether researchers, or rural advisers working with pastoral managers, should take the following approach. Firstly, collect the best information possible on the target species. Invariably, there will be gaps in the scientific literature available, and many parameters will need to be estimated. This could be done by using data from a similar species. Alternatively, you could use the knowledge of local pastoral managers to develop parameters that are best estimates for a particular locality. Where you have estimated parameters, it is advisable to express them as a range of values, and to carry out repeat runs of the model for different values within the range. You should also carry out multiple runs for a range of rainfall scenarios, whether randomly derived by the model, or deliberately manipulated.

The output from the model runs will comprise a set of projected population outcomes, from which you can identify worst- and best-case scenarios and potential risks. Through comparing multiple runs, you will be able to identify variables to which the target species is most sensitive. In the examples given, populations were highly sensitive to sheep grazing, whether set-stocked or rotational, while populations had a high ability to recover from drought in an ungrazed situation.

Therefore, we advise that the model be used to identify and clarify questions and risks rather than to provide definitive answers. Once sensitive variables are identified, research can be targeted more efficiently to provide more accurate values for these variables. In a more practical sense, pastoral managers could be advised of potential high-risk management variables, and their local knowledge will be valuable in providing 'best guess' parameters until accurate research data can be obtained. This interactive process will allow the model to better predict in specific situations. The model can therefore assist with identifying current 'best practice' for management, and identify where more knowledge is required for a continuing process of adaptive management.

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Appendix 1: SHRUBPOP parameters

Grazing initial parameters

Grazing parameters specify the different grazing levels for sheep, rabbits, kangaroos and goats (see Table 2). For each grazing level, stage class of plant species (Appendix 2) and species of grazing animal, the following estimates are included in the parameter datasets for each functional group of plants:

- the percentage by which the current survivability ratio of each stage is reduced (0–100)
- the percentage by which the probability of progressing to the next stage is reduced (0–100).

Table 2: Grazing levels available in the model

Sheep	**Rabbit**
0 = Nil (ungrazed)	0 = Nil (dung and soil scratchings absent)
1 = Light or intermittent (> 5 km from water, or rarely stocked, old spoor only)	1 = Light or intermittent (old dung, soil scratchings infrequent)
2 = Moderate (1–5 km from water, fresh spoor)	2 = Moderate (fresh dung and scratchings present, more frequent)
3 = Heavy (500 m – 1 km from water, frequent fresh spoor)	3 = Heavy (100–500 m from warren)
4 = Severe (< 500 m from water/heavy fresh spoor)	4 = Severe (within 100 m of warren)
Goat	**Kangaroo**
0 = Nil (dung and tracks absent)	0 = Nil (dung and tracks absent)
1 = Light or intermittent (old dung, tracks infrequent)	1 = Light or intermittent (old dung, tracks infrequent)
2 = Moderate (fresh dung and tracks present)	2 = Moderate (fresh dung and tracks present)
3 = Heavy (frequent fresh dung and tracks, animals may be seen)	3 = Heavy (frequent fresh dung and tracks, animals may be seen)
4 = Severe (heavy fresh dung tracks, animals usually seen)	4 = Severe (heavy fresh dung tracks, animals usually seen)

Rainfall initial parameters

The maximum number of consecutive drought months is set to 30, which exceeds the maximum drought-length found in the Koonamore data. For each stage-class for each species, two critical rain levels (mm) need to be set – one for the summer months (October to March) and one for the winter months (April to September). These rain levels represent the minimum amount of rainfall required for survival and growth of that particular stage class of that particular species. If the critical rain level in a month is not reached, then that month is designated by the model as a 'drought month'. The effects on each stage class (survival and progression) of the range of drought lengths (consecutive drought months), from one to 30 months, is also included in the parameter sets.

Other initial parameters

For each stage class (I to VII), you must supply the following estimates:

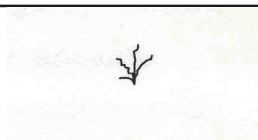
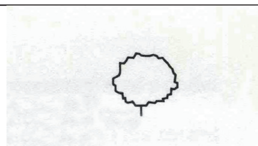
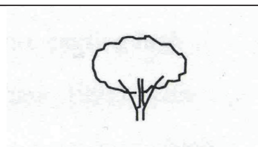
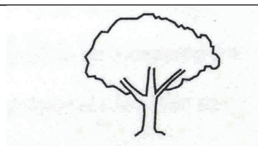
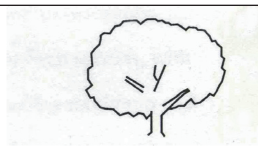
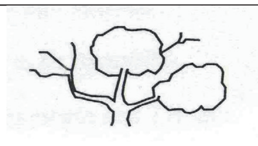
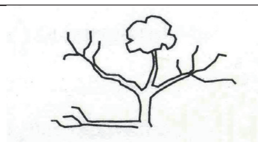
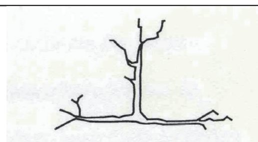
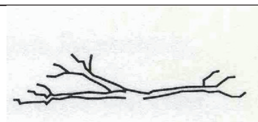
- Initial numbers: The initial number of plants in each stage class
- Duration: The time spent by an individual in each stage class (figures are already included for each functional type)
- Survivorship: The probability of surviving each stage class (or probability of not dying)
- Relative fertility: The most fertile stage class, usually stage class V, is set to 100%. The other stages are the maximum percentage, of this most fertile stage, that the given stage is likely to produce. For example, if stage class V is the most fertile stage, and is set to 100%, stage class IV is not likely to produce more that 75% of the amount of seeds that stage class V produces, and so should be set to 75%. Stage classes I–III, being non-productive juveniles, are set to a fertility of 0%.

Note: All probabilities are between zero and 100.

Appendix 2: The stage classes of woody perennial plant species used in SHRUBPOP

Table 3 lists the nine stage classes of woody perennial plant species, the rules for assigning individuals to classes, and a theoretical diagram of each stage class. We have adapted these stage classes from the phenological condition classes of Tiver and Andrew (1997, after Mueller-Dombois & Ellenberg 1974, Gatsuk et al. 1980). Stage classes VIII and IX are not included in the model.

Table 3: Stage classes used in the model (I–VII)

Stage class number	Stage class	Description	Diagram
I	Seedling/sucker	< 20 cm high single-stemmed may have juvenile foliage	
II	Bushy juvenile	branching apparent often multi-stemmed rounded crown	
III	Older juvenile	one stem dominant	
IV	Young mature	crown not fully formed reproductive full size not reached	
V	Mature	full size crown fully developed fully reproductive growth vigorous	
VI	Old mature	canopy spreading dead branches present vigour decreased	
VII	Senescent	> 50% dead branches some fallen branches pronounced canopy spread	
VIII	Standing dead	completely dead still standing many branches fallen	
IX	Lying dead	whole plant fallen over many branches rotting	

Appendix 3: SHRUBPOP user manual

Getting started

1. Open the Excel files data_file.xls, matrix_store.xls, and DKCRC 2-702_Shrub popn model.xls
2. Read the online help to find out how to set up your computer to run the model.
3. On the Tools menu, you should see menu items 'Solver' and 'Macros'. If not, go to 'Add-ins' and tick the appropriate boxes.

Running the model

Each of these steps corresponds to the links in the file 'Shrub popn model.xls'.

Step 1: Initialise the model

Select the Initialise menu item. The initial parameters for each functional group (group of plant species) are copied into a working area from data_file.xls. They include set initial population numbers, stage duration, survivorship, relative fertility and probability of progression for each grazing and drought combination. You can modify these parameters if you wish to tailor the model for another species or for the same species in another region and climate regime. You may also choose the 'default' functional group, and enter all your own values.

Next, select the 'Doubling Time' button. A decrease in population doubling-time causes an increase in population growth-rate (λ). Because a plant population can literally double overnight when a cohort of seeds germinates, we found that it is best to ignore the non-reproductive stages when estimating doubling time – otherwise unrealistic population growth rates are set. The model will not run unless a value for doubling time is set.

Step 2: Select a functional group

Click on the 'Functional group' drop-down menu. A description of each group as selected is given to the left of the menu. Select a functional group. The model then finds a steady state for the population. This entails finding the fertility factor to ensure equilibrium under no grazing.

Step 3: Edit fertility and survival parameters

The parameters selected in Step 1 are displayed in text entry boxes where they can be modified. The changes you make are kept on the 'Selecting Functional Type' worksheet for future reference. You can restore the original parameters by starting again at Step 1. Save your version of the model (we suggest you open a new folder and copy the file into it with a different name) with your parameters to suit your own species, region and climate, so that you can use it again later.

Step 4: Edit grazing parameters

When you select 'Edit grazing parameters', you are presented with a screen where you can select initial grazing levels for all types of herbivores. You can also edit how the level of grazing reduces the survivability. Any changes you make replace the initial values in the matrix_setup.xls worksheet. Before the grazing parameters take effect, the model will re-calculate the steady state it reached during Step 3.

Step 5: Run with set parameters

The options are:

1. Grazing
2. Rainfall (drought)
3. Grazing and rainfall
4. None (neither grazing nor drought affects the population).

1. **Grazing**

- The model checks to see if you want to change the grazing levels of each of the four herbivores every few years (to model grazing rotations, rabbit control etc), and if so, after how many years.
- Old history is cleared from the matrix_store.xls file.
- The initial population and initial matrix is copied over to the output area, under the steady state conditions, upon which the grazing regime is introduced.
- There is a series of matrix multiplications reflecting the progression of the population under the grazing regime, but with no alterations to the parameters because of adverse environmental conditions.
- The population distribution at each year is copied to a sheet on the matrix_store.xls worksheet and the whole assemblage of years is graphed.

2. **Rainfall**

- Select the 'Rainfall' button.
- Select whether you wish to use your own rainfall data (historical or generated) or to synthetically generate the data. If you wish to generate a series of typical monthly totals for a number of years, you must make sure that that the historical rainfall records are placed in the monthly_rain sheet. Note that the rainfall generation process takes some time.
- For each stage for the selected functional group, the model reads in the critical rainfall levels from the data_file.xls.
- If the amount of rainfall data is less than the number of years selected for study, then the process stops. The model can be run for 500 years, but you need to make sure that there are enough years of rainfall in the 'Rainfall' file. The default rainfall file is 116 years of rainfall records from Koonamore, South Australia. You may replicate (copy and paste) this file (or a modelled rainfall data set) to repeat the same set of data over and over until you have 500, or you may enter a set of rainfall figures from your own region. You may also edit any rainfall file to create climate-change scenarios (by increasing drought frequency, increasing summer rain, decreasing winter rain etc).
- The matrix_store.xls is initialised before the process begins.
- Stage classes I and II are changed to reflect the last 12 months' rainfall deficiencies (cannot survive droughts of more than 12 months).
- Stage classes III and IV are changed to reflect the past three years' rainfall deficiencies (able to survive droughts of less than 12 months).
- The changes are reduction in survivability and progression.

3. **Rainfall and grazing**

- Any changes are due to the combined effects of deficiencies in rainfall and changes to grazing.

Output

- In 'data_file.xls' there is a column for the generated yearly rainfall, as well as the monthly amounts.
- In the output file 'Matrix_store.xls', the lambda value is shown at the end of each year.
- Total population size at the end of each year is also shown, as well as the transition matrix for that time-interval.
- On the sheet 'generated rainfall' in rangelands_model.xls, there are options to examine the monthly totals, yearly totals, and also the monthly means compared to the means from the historical data.
- There are graphs of the time trends for total numbers in all stage classes, as well as total population number.

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