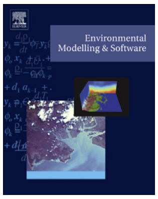
Environmental Modelling & Software xxx (2015) 1–9

Contents lists available at ScienceDirect

Environmental Modelling & Software

journal homepage: www.elsevier.com/locate/envsoft



A crowding-dependent population model for woody weeds — Where size does matter

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ARTICLE INFO

Article history:
Received 28 September 2015
Received in revised form
23 October 2015
Accepted 29 October 2015
Available online xxx

Keywords:
Ziziphus mauritiana
Density dependence
Population modelling
Matrix model
Rangeland
Weed

ABSTRACT

Integrated weed management for woody weeds is difficult to implement, partly due to the unknown effects of plant size on intraspecific plant competition. Moreover, weed literature often uses density (quantity) as a measure of control efficacy; this is insufficient for woody weeds due to varying plant sizes within populations.

Using *Ziziphus mauritiana* as a case study, we describe a method of simultaneously measuring plant sizes and density: crowdedness. A new deterministic crowding-dependent matrix population model was developed by grouping the population into ten life stages. Elasticity analyses and simulations showed that removing the largest plant had the greatest control efficacy on new and old infestations in riparian and upland zones; despite subsequent mass recruitments. The model also accommodated for shocks without overcompensating. The alternative measure of plant abundance developed in this paper, provides a useful tool to assist in woody-weed control decisions and provide a better measure of weed-control efficacy.

1. Introduction

Rangelands are important systems that represent 20% of the World's land mass and more than 70% of mainland Australia (Grice, 2006; Sankaran et al., 2005). They provide essential environmental services and, in some areas, economic benefits through grazing. The environmental and economic values of these areas are affected by woody weeds (Harrington et al., 1984; Scanlan et al., 1991) through decreasing land carrying capacity and land condition. In grazing areas, woody-weed encroachment also increases effort required to herd cattle, hinders cattle from accessing waterways that lay within woody-weed infestations, and causes livestock losses (Grice, 2000; Mackey, 1997; Parsons and Cuthbertson, 2001). The spread of woody weeds has been attributed to many causes: changing climate; high stocking rates; changes in livestock types; fire suppression; soil disturbance; the transportation of livestock, feed, and equipment; and deliberate plant relocation (Grice, 2004; Kriticos et al., 2003b; Noble et al., 1997).

There are many native and introduced shrubs and trees within the Australian rangelands colloquially labelled woody weeds (Grice, 2000). These include *Acacia catechu* (cutch tree), *Acacia nilotica* (prickly acacia), *Azadirachta indica* (neem tree), *Calotropis procera* (calotrope), *Cascabela thevetia* (Captain Cook tree, yellow oleander), *Cryptostegia grandiflora* (rubber vine), *Jatropha gossypifolia* (bellyache bush), *Lantana camara* (lantana), *Leucaena leucocephala* (leucaena), *Mimosa farnesiana* (mimosa bush, prickly Moses), *Mimosa pigra* (giant sensitive tree), *Parkinsonia aculeata* (parkinsonia), *Prosopis* spp. (mesquite, algarroba), *Ricinus communis* (castor-oil plant), *Tamarix aphylla* (Athel pine), and *Ziziphus mauritiana* (chinee apple, Indian jujube) (Grice, 2003; Parsons and Cuthbertson, 2001; Thorpe and Lynch, 2000). We will use the latter species as a case study to demonstrate the method.

Despite the significance of woody weeds in rangeland systems there has been limited focus on the economics of managing these weeds. To evaluate the economic merits of weed management decisions requires an understanding of key ecological processes, the benefits of control, and the costs and effectiveness of control methods (Odom et al., 2003; Scanlan et al., 1991). Much of the bioeconomic literature on optimising weed control is based on annual cropping systems, with weed management throughout the

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http://dx.doi.org/10.1016/j.envsoft.2015.10.026
1364-8152/

Please cite this article in press as: Zull, A.F., et al., A crowding-dependent population model for woody weeds — Where size does matter, Environmental Modelling & Software (2015), http://dx.doi.org/10.1016/j.envsoft.2015.10.026

year using combinations of control methods (Jones, 2003; Lawes and Renton, 2010). Woody-weed management decisions differ in two important aspects: the frequency of control and the description of the state of an infestation. Control events of woody weeds are infrequent, often with long time lags between controls and typically only using one type of control in any one year. The four main woody-weed control methods (mechanical, chemical, burning, and biocontrol) differ in terms of costs and effectiveness, in part due to variations in the size of individual weeds and life stage.[1] Little is known about the long-term population dynamics of woody weeds and even less is known about the temporal benefits of their control (Downey and Brown, 2000; Martin et al., 2006). The lack of such studies may be due to the difficulty in evaluating the net benefits of managing long-lived weeds, where the benefits accrue over many years in the future, and where it is difficult to predict and quantify changes in populations. This paper describes a dynamic woody-weed population framework that captures the effect of management on both the number and size of individual plants within populations. The model provides a solid foundation for bioeconomic analysis of woody-weed management.

The state of a weed infestation within a crop can be adequately described by the quantity of plants per unit area. This variable allows us to calculate damages, density dependence effects and cost of control. In the case of woody weeds, this measure of abundance is not enough to fully describe the invasion. Other measures of plant abundance per unit area (crowding) exist; including: total crown cover (Parker, 2000), leaf area (Lotz et al., 1996), breast height diameter (Liedloff and Cook, 2007), basal area (Liedloff and Cook, 2007), and above-ground dry weight (Grice, 2002). Total crown cover can be measured with aerial photography (Fensham et al., 2005) but may not provide all the information required to estimate the efficacy and costs of weed control, which depend on plant size. Total leaf area of woody weeds is laborious to estimate and is a poor indicator of their impact on grazing yields (Lotz et al., 1996; Pearcy et al., 1989). Breast height diameter and basal area are difficult to estimate where access is restricted by thickets. Estimating dry weight requires plants to be harvested, dried and weighed (Neubert and Parker, 2004; Parker, 2000) and therefore is not a practical measure for management purposes.

The reason size matters in the case of long-lived woody weed populations is that small plants have little effect on large plants, but large plants can greatly reduce the survival rates of smaller plants growing in close proximity (Higgins et al., 2000). The term crowding-dependency is used to indicate the existence of both density and size effects. To capture both effects it is necessary to follow several cohorts of differing sizes. Long-term studies that produce data for this type of evaluation are rare, and there is a long time lag between designing an experiment and obtaining the required information on long-lived species. Some of the gaps can be filled through transversal studies of populations in different stages of development, but models will normally be needed to produce useful economic evaluations for current decisions that account for future consequences (Jones, 2003).

Matrix population models are a well-established tool for research in conservation biology and invasive species management (Caswell, 2001; Davis, 2006). Standard matrix models result in exponential growth, unless modified to account for crowding effects, the method we use to introduce the crowding effect on the matrix model is a novel aspect of this study. Once the model is calibrated, analysis of elasticities allows the life-cycle stages that have the greatest marginal effect on population growth to be identified (Caswell, 2009; Parker, 2000). This information makes it possible to design management strategies that are better targeted to the mix of life stages present in an infestation.

In this study we develop a crowding-dependent stage projection matrix (SPM) model that considers population cohorts represented by seeds, juveniles, and adult life stages. The model is used to investigate the impacts of managing different life-cycle stages as a basis of future bioeconomic analysis. The model is applied to a *Z. mauritiana* invasion in the Charters Towers region of Northern Queensland, Australia. The calibration process is presented in some detail and the model is used to explore the population dynamics of this long-lived plant. The model is implemented in MATLAB 7.0® (2007).

2. Methods

2.1. The model

The growth of weed invasions can be modelled using a stage matrix. This is a standard technique for population dynamics modelling and is explained in detail in Caswell (2001). The plant population at year t is represented by a column vector, $\mathbf{x}_t$, whose elements x_i ($i \in 1, \ldots n$) represent the number of individuals ha^{-1} for life stage i (Table 1). The population state transition is given by:

$$\mathbf{x}_{t+1} = \mathbf{H}\mathbf{x}_t \tag{1}$$

where $\mathbf{H}$ is the annual stage projection matrix (SPM) (Brault and Caswell, 1993; Caswell, 2001), of dimensions $n \times n$; where n represents the number of life-cycle stages. The main assumptions of

Table 1
Model variables and parameters.

Variables:	Description
$\mathbf{X}_t$	Annual population vector of size n x 1 at time t
$x_{i,t}$	Element of **X,** the number of individuals in life stage i
$\mathbf{H}_t$	Annual stage projection matrix (SPM) of size $n \times n$
$h_{ij,t}$	Element of $\mathbf{H}_{\boldsymbol{t}}$
$\mathbf{H}_0$, $\mathbf{H}_\infty$	New and steady-state SPM
NS	New seeds
SB	Seedbank
$J_{1 \ldots m}$	Juveniles at stages 1 to m
$A_{1 \ldots q}$	Adults at stages 1 to q
$F_{i \ldots q}$	Fecundity of adult life stage 1 to q
M_i	Probability of individuals moving to next life stage
R_i	Probability of individuals remaining in their current life stage
W_t	Population abundance (m^2)
O_t	Level of weed occupancy within a unit area ($0 \le \mathrm{O}_t \le 1$)
λ_t	Dominant eigenvalue of matrix $\mathbf{H}_t$
r_t	Annual population growth rate
$e_{ij,t}$	Elasticity of elements in $\mathbf{H}_t$
$C_{i,t}$	Elasticity of life stage i at time t
$\mathbf{T}_{\boldsymbol{t}}$	Identical to $\mathbf{H}_t$ matrix with F_i elements set to zero
$\mathbf{N}_t$	Markov chain fundamental matrix of life expectancy
$\upsilon_{ij,t}$	Expected time spent in each transition; element of $\mathbf{N}_t$
$\mathbf{I}_t$	Identiy matrix
Parameters:	
n	Number of life stages
γ	Maximum weed occupancy (1ha = 10,000 m^2)
$\boldsymbol{\omega}_i$	Area required (m^2) by individuals in life stage (i) to exist
v_i	Maximum number of individuals in life stage (i) ha^{-1}
Subscripts:	
t	Time (year)
n	Number of life cycle stages for a weed species
m	Number of juvenile stages
q	Number of adult stages
Superscripts:	
T	Transpose matrix/vector

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[1] Although life stage and plant size are not synonyms, we have used plant size as a surrogate for life stage, as this is an easy and effective method of estimating the state of a woody-weed population from a weed management perspective.

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