A matrix model for the management of perennial weeds in the North Queensland rangelands system: application to *Ziziphus mauritiana* (Lam.)

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Summary Woody weeds impose significant economic costs to graziers in the Australian rangelands. Weed management in these heterogeneous areas is distinct from that in agricultural systems reliant on weed threshold management strategies. In this paper we construct a stage matrix model that considers density dependence, and apply it to the woody weed *Ziziphus mauritiana* (Lam.) based on published data. Results indicate that expected population growth for newly established infestations is in the order of 57% for the first couple of seasons. This growth rate declines over time towards an established steady state population. Analysis of elasticities derived from the population matrix indicates that targeting medium to large adults would have the greatest effect in reducing population growth. We conclude with a discussion of the application of this approach.

Keywords Invasive species, weeds, eradication, dynamic population modelling, stage matrix.

INTRODUCTION

Invasive species in rangelands may reduce stocking rates, increase mustering effort, limit water access for cattle or poison cattle. Additional labour, chemicals and capital costs will be incurred to manage the weeds. Land managers are, therefore, faced with the dilemma of having to decide when the benefit of managing weeds outweighs the cost of the weeds. Weed cohorts will progress through a series of stages, from a seed to a fully mature adult plant. As the weed population matures, the density of the weed increases and graziers' production costs may also increase.

To date, population models of weed invasions in the rangelands have not been allied with detailed economic analysis. However, ecophysiology models of weed invasion have been successfully combined with economic analysis in cropping systems throughout Australia. The underlying principle of combining economic and ecological analyses has been widely employed. However, critical ecological and economic components of the system must be captured and incorporated into a modelling framework before the system can be legitimately analysed.

The Australian rangelands are complex. They contain large and variable properties that are subjected to irregular climatic conditions that may trigger episodes of weed recruitment (Watson *et al.* 1997). In this paper we develop a dynamic stage matrix population model for *Ziziphus mauritiana* Lam. (Chinee apple) with annual time intervals for a perennial weed in MATLAB7.0® (Caswell 2001, Buhle *et al.* 2005) using parameters derived from Grice (1996, 1997, 1998, 2002). Our model accounts for density dependence based on a rectangular hyperbola to provide a reasonable relationship for a sigmoid population biomass growth curve (Cacho and Spring 2004). This paper presents population elasticities for Chinee apple to provide insight into the proportional effect that lifecycle stages have on the weed's population growth. This will assist in determining which stages of the lifecycle should be targeted for weed management and is the first stage in the development of a framework to evaluate the management of invasive species in the rangelands of Australia.

Chinee apple was first introduced to Australia over 100 years ago and can grow to 8 m, produce over 5000 fruit per season with the seeds predominately dispersed by cattle. Chinee apple occurs on a wide range of soil types in the drier tropics (Grice 1996, 1998, 2002). The weed can create impenetrable thickets hampering graziers (James 1995) and is declared as a Class 2 weed under the *Land Protection Act 2002* (NRM 2006b). Currently Chinee apple is found in isolated pockets throughout North Queensland with populations from Townsville to Charters Towers. Vast areas along the entire eastern coast of Queensland have been reported as highly suitable for the spread of Chinee apple (NRM 2006a).

MATERIALS AND METHODS

The growth of the weed invasion was modelled using a stage matrix. This is a standard technique for population dynamics modelling and is explained in detail in Caswell (2001). The stage matrix **H** has dimensions $n \times n$; where n is the number of stages in the lifecycle of the plant. The time to maturity and the longevity of the plant determine the minimum value of n. The life stages represent new seeds (NS), the seed bank (SB), juvenile stages ($J_1,\dots J_m$), and adult stages ($A_1,\dots Aq$). The number of juvenile and adult stages are denoted by m and q respectively; therefore $n = NS + SB + m + q$. Chinee apple reaches maturity in a minimum of five years, so $m = 4$. The value of q was set to 4 to allow the large differences in fecundity between small and large adults to be reflected in the model. Therefore, $n = 2 + 4 + 4 = 10$ in our model. The elements h_{ij} of $\mathbf{H}$ represent the probability of survival from stage i to stage j, except for the first row, where h_{1j} represents the fecundity of stage j (new viable seeds produced per plant). The stage matrix for a new invasion (before density-dependence has an effect on population growth) is denoted by $\mathbf{H_0}$; the non-zero values of this matrix are presented in Table 1. The column vector $\mathbf{x}_t$ contains the number of individuals in each stage ($1,\dots,n$) at time t. The population state transition for a new invasion is given by $\mathbf{x}_{t+1} = \mathbf{H}_0\,\mathbf{x}_t$. Repeated application of this operation results in exponential growth. To implement density dependence as the population grows and approaches carrying capacity (k), a steady-state matrix $\mathbf{H}_\infty$ was defined. The non-zero elements of $\mathbf{H}_\infty$ are presented in Table 1. Density dependence was modelled based on biomass; with carrying capacity (k) set at 10,000 kg ha^{-1}. The vector $\mathbf{w}$ contains the average dry weight of individuals in each stage (Table 1).

The total biomass at any time is given by $b_t = \mathbf{w}^{\mathrm{T}}\,\mathbf{x}_t$. When $b_t = k$ the population reaches a steady state, so that $\mathbf{x}_{t+1} = \mathbf{H}_\infty\,\mathbf{x}_t = \mathbf{x}_t$. This implies that the dominant eigenvalue (λ) of $\mathbf{H}_\infty$ equals 1.0 (see Caswell 2001). In other words, a population growth rate $\lambda = 1.0$ means that, in the absence of external disturbances, the population biomass will remain constant. The transition between exponential growth in the early stages of invasion and the steady state of a mature invasion is simulated by interpolation between $\mathbf{H}_0$ and $\mathbf{H}_\infty$, based on total biomass, using the formula for a rectangular hyperbola:

$$\mathbf{H}_t = \frac{k\mathbf{H}_0}{k + \left(\dfrac{\mathbf{H}_0}{\mathbf{H}_\infty} - 1\right) b_t}$$

where matrix divisions represent element-by-element operations. Biomass-dependent growth is then calculated as $\mathbf{x}_{t+1} = \mathbf{H}_t\,\mathbf{x}_t$. Figure 1 presents the lifecycle diagram associated with this matrix model.

The stage matrix contains information that can be useful in the design of efficient weed control strategies. Eigenvalue analysis is used to estimate population elasticities. The elasticity e_{ij} measures the contribution of the parameter h_{ij} to population growth and, therefore, indicates the potential effectiveness of selecting a

Table 1. Parameters for Chinee apple matrix model.

Life stage		Weight (kg)	Transition to stage	New invasion (H_0)	Steady state (H_∞)
				Stage matrix elements	
New seeds	NS	0	SB	0.50	0.50
			J_1	0.07	0.02
Seed bank	SB	0	SB	0.50	0.50
			J_1	0.07	0.02
Juvenile	J_1	.005	J_1	0.10	0.05
Small <0.2 m			J_2	0.49	0.25
Juvenile	J_2	0.01	J_2	0.10	0.06
Medium 0.2–0.4 m			J_3	0.58	0.33
Juvenile	J_3	0.02	J_3	0.10	0.06
Large 0.4–0.7 m			J_4	0.66	0.41
Juvenile	J_4	0.04	J_4	0.10	0.07
Largest 0.7–1.0 m			A_1	0.72	0.52
Adults	A_1	2	A_1	0.60	0.51
Small 1–2 m			A_2	0.20	0.06
			NS	9	9
Adults	A_2	12	A_2	0.70	0.65
Medium 2–3 m			A_3	0.20	0.06
			NS	880	880
Adults	A_3	110	A_3	0.79	0.74
Large 3–5 m			A_4	0.120	0.06
			NS	4000	4000
Adults	A_4	210	A_4	0.93	0.93
Largest >5 m			NS	5000	5000

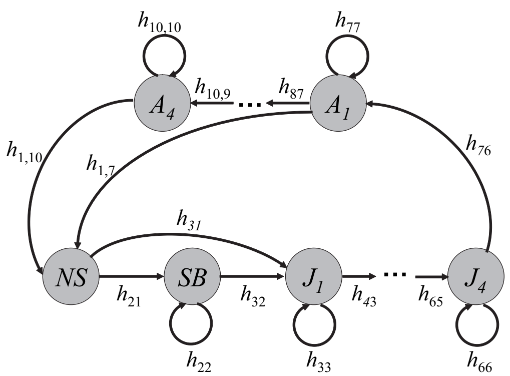

Figure 1. Lifecycle diagram corresponding to the stage matrix model.

control method that targets life stage *i*. This method is used below to draw some preliminary conclusions regarding the best strategies to control Chinee apple.

RESULTS

The results of the modelling indicate that the estimated annual population growth for a new Chinee apple infestation is in the order of 57% ($\lambda = 1.565$). Over time the population growth rate decreases to a steady state ($\lambda = 1.0$) where the population's biomass remains relatively constant. Interestingly, the modelled long-run maximum biomass of approximately 2500 kg ha^{-1} (Figure 2d) is substantially lower than the maximum theoretical biomass (k) of 10,000 kg ha^{-1}. This is due to the density dependent function of the model restricting the population's growth as its biomass approaches (k). Additionally, the highest number of juveniles exists (Figure 2b) when there are fewer adults (Figure 2c). This is due to the competitive advantage of larger plants. At the very early stages of the simulation, the seed bank decreases and then increases (Figure 2a). This is caused by the initial depletion of the seed bank due to germination and then replenishment as a result of adults appearing in the population (Figure 2c). If early detection of the weed was possible and seedlings were managed before they matured, the seed bank could be depleted and potentially eradicated. This scenario is highly unlikely because the size of the Australian rangelands makes early detection improbable; hence management at later stages is more likely to occur. In this case, assuming an established Chinee apple population has been detected, a grazier needs to determine the most effective and efficient method of weed management.

An Eigenvalue analysis was used to estimate population elasticities for Chinee apple for both a new invasion ($\mathbf{H_0}$) and a mature invasion ($\mathbf{H_\infty}$) (Table 2). This will help determine the most effective method of weed management. The analysis shows that removing medium and small adults, (stages *A2* and *A1*) for new invasions ($\mathbf{H_0}$) will have the greatest impact on the population growth of Chinee apple. However, for an established population ($\mathbf{H_\infty}$) the largest and medium size adults (stages *A4* and *A2*) should be targeted first. It should be noted that if a mature infestation is treated in this way, it will in effect have a similar population structure to that of a new invasion ($\mathbf{H_0}$) but with a larger seed bank. The grazier can then wait for the seed bank to deplete itself through germination and natural mortality while managing new recruitment as either seedlings (stages *J1* to *J4*) or young adults (stages *A1* to *A3*). Although the new seed stage (*NS*) only ranked the fifth and ninth (Table 2) respectively for new ($\mathbf{H_0}$) and established ($\mathbf{H_\infty}$) weed populations, this stage is the only vector through which a new weed infestation can occur in another area and therefore should not be ignored. As the old saying goes 'prevention is better than cure'.

DISCUSSION

Weed management methodology and cost is dependant on life cycle stage and density. Vitelli (2000) outlines five weed management strategies of which only three are effective on Chinee apple: seed containment, and

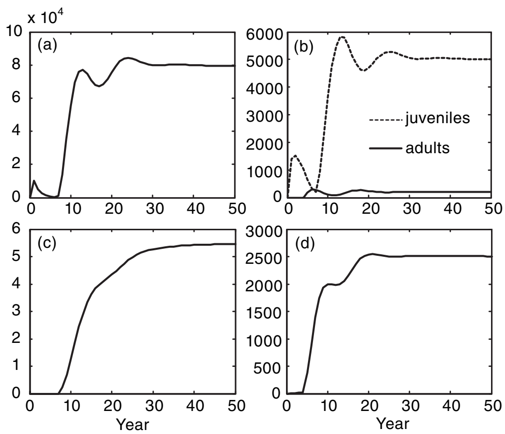

Figure 2. Predicted population size of Chinee apples over time for a hectare; (a) seedbank, (b) juveniles, (c) large adults, (a) biomass kg ha^{-1}.

Table 2. Elasticities of new invasions (stage matrix H_0) and mature invasions (stage matrix H_∞), expressed as the % contribution of each life stage.

	New invasion H_0		Mature invasion H_∞	
Stage	Elasticity (%)	Rank	Elasticity (%)	Rank
NS	9.44	5	5.40	9
SB	4.43	6	5.41	10
J1	10.09	4	5.69	8
J2	10.09	4	5.74	7
J3	10.09	4	5.77	6
J4	10.09	4	5.83	5
A1	15.32	2	11.13	4
A2	**16.78**	**1**	15.24	2
A3	11.09	3	14.07	3
A4	2.59	7	**25.70**	**1**
Total	100.0		100.0	

chemical and mechanical removal. Biological control of Chinee apple to date has not been attempted (Grice 2002) and fire control has only resulted in a small number of younger plants being killed (Grice 1997)

A new infestation begins at the new seed stage (*NS*). New infestations from (*NS*) can be contained by quarantining cattle for 10 days in a small weed free paddock during fruiting season before transferring them to weed free areas (Grice 2002). However, this method of weed management does result in additional labour, fencing, and feed costs to graziers and is only truly effective at scales greater than an individual paddock (Grice 1998). Herbicides are also available for controlling Chinee apple and may be applied to the weed stump, bark, foliage or soil. Each type of herbicide has varying efficacies and side-effects (Grice 2002). Although herbicides are low in capital cost they require a substantial amount of labour and the practice is restricted by limited access to invaded areas. This practice is therefore generally reserved for small, young populations, represented by stages *J1* to *J4* in the lifecycle diagram (Figure 1). Dense infestations can be controlled by mechanical means; however, Chinee apple can resprout after it has been cut or broken above ground level if left untreated (Grice 2002). A blade-plough that cuts the plant 150–200 mm below ground level is only effective on plants large enough to have a substantial root system but small enough for the machine's capacity; represented by stages *A1* to *A3*. The largest weeds (*A4*) are too large for blade-ploughing, and therefore require manual cutting (by chainsaw) and poisoning.

This analysis has not considered the monetary cost associated with the various weed management approaches or the opportunity cost of the weed infestation itself. In addition, the model has not considered weed migration, which is only possible at the new seed stage and where cattle containment is the recommended practice. Another important issue for future consideration is the effect episodic climatic events have on rates of survival. The model developed and the analysis undertaken in this paper provide the groundwork for the next step in this research, where economic measures will be incorporated to determine the best options for dealing with invasions in different stages of their life cycle.

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