Modelling the population dynamics of multi-species woody weed infestations

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Summary Multi-species weed infestations are a common feature of the northern Australian rangeland systems, yet little attempt has been made to understand or model their dynamics. We simulated the population dynamics of a multi-species infestation of *Ziziphus mauritiana* (chinee apple), *Acacia nilotica* (prickly acacia), and *Parkinsonia aculeata* (parkinsonia) to determine the most appropriate management strategy for the plant community. Model output suggests multi-species infestations generate higher overall density sooner than single species infestations. However, individual species growth rates are slower. Our model indicates that both prickly acacia and parkinsonia initially dominate chinee apple. Later, prickly acacia out-competes parkinsonia, and eventually, chinee apple out-competes both prickly acacia and parkinsonia. Management activities alter the interactions between species, and management must respond to changes in the structure of the weed community.

Keywords Weed management, multi-species matrix model, stage-based projection matrix.

INTRODUCTION

Some locations in the Australian rangelands have been invaded by multiple plant species. Species such as chinee apple, prickly acacia and parkinsonia can concurrently invade riparian and upland habitats (Lawes *et al.* 2006). In these situations all species must be managed concurrently, as any cleared area will be invaded by a neighbouring weed species.

Long-term forecasting based on the complex interactions among species is required to efficiently manage the entire population and allocate resources appropriately. Therefore a model is required to simulate the dynamics of weed populations, whilst keeping the species and their lifecycles identifiable from one another.

Multi-species matrix population models (Lu and Buongiorno 1993) are a class of multi-state models (Caswell 2001) that take advantage of the matrix formulation to structure the demography of the species and the interactions between them, thus allowing us to predict the ecological processes for economic management decisions. There are similarities between forestry and woody weed management. The primary difference is that the economic returns of foresters increase with the success of the perennial plants, whereas the economic returns of producers decrease with the success of perennial weeds species.

A density-dependent stage-matrix projection model was constructed in MATLAB7.0® to analyse the growth of the weed and the impact of the interaction between species. The model is based on a homogeneous area of riparian terrain in the Australian rangeland landscape with all three species present. This model assists in estimating the population structures and weed growth over time, as well as investigating the efficacy of management strategies.

MATERIALS AND METHODS

Although there are significant ecological differences between chinee apple, prickly acacia and parkinsonia, their life cycles share some common traits (Figure 1).

For all these species the four main stages identified were new seeds (*NS*), seed bank (*SB*), juveniles (*J*), and adults (*A*). Based on the plant size, minimum time to reach maturity and plant longevity, the juvenile and adult stages were decomposed into sub-stages ($J_1, J_2, \ldots, J_{m_k}$) and ($A_1, A_2, \ldots, A_{q_k}$). For example, juveniles of chinee apple require a minimum of four years (four sub-stages) to reach the critical size for maturity, and adults can be divided into four sub-stages based on their size and fecundity. Using this process to decompose their life cycle, and based on evidence from the literature, the number of stages for chinee apple, prickly acacia and parkinsonia were 10, 8 and 7.

The vital rates and the life cycle are then structured in a multi species, stage-based matrix model where the population state transition is given by: $\mathbf{x}_{t+1} = \mathbf{H}_t\mathbf{x}_t$, where $\mathbf{x}_t = [x_{kit}]$ is the population column vector that represents the number of individuals x per weed species k in life cycle stage i, at time t (years).

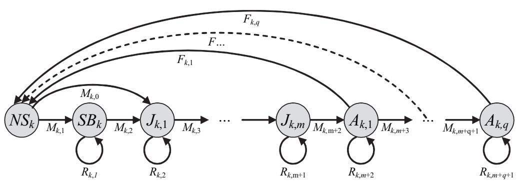

Figure 1. Life cycle graph for a woody weed.

The species are denoted by subscript $k = 1, 2$, and 3, representing chinee apple, prickly acacia and parkinsonia, respectively. $\mathbf{H}_t$ is the annual multi-species stage projection matrix that contains the individual species block-matrices H_{kt} at time t (Figure 2).

H_t is a ($\sum_k n_k \times \sum_k n_k = 25 \times 25$) dimension matrix consisting of $n_1 + n_2 + n_3 = 10 + 8 + 7$ life stages for chinee apple, prickly acacia and parkinsonia, respectively. The non-zero elements of $\mathbf{H}_{kt}$ are scalars and represent the probability of moving (M) from stage i to stage j, or remaining (R) in the current stage. F represents fecundity (new viable seeds produced per plant).

Inter-specific competition for finite resources affects population growth of the three species via density-dependent mechanisms. Density dependence was based on 'gap theory' which uses crown diameter as an indicator of a plants' competition for area and its resources. Gap theory provides a simple yet plausible mechanism of weighting the impact of individual plants on population structures dependent on quantity and size. As a population grows it will approach the maximum carrying capacity (γ) and tend towards a steady state population. Density dependence was implemented by adjusting the entries in $\mathbf{H}_t$ according to the total area occupied by weeds. Following Cacho and Spring (2004), this adjustment (equation 1) consisted of interpolating between two matrices: $\mathbf{H}_0$, the initial stage matrix for a new invasion, and $\mathbf{H}_\infty$, the stage matrix when carrying capacity has been reached:

$$\mathbf{H}_t = \frac{\gamma \mathbf{H}_0}{\gamma + \left(\frac{\mathbf{H}_0}{\mathbf{H}_\infty} - 1 \right) W_t} \qquad (1)$$

Divisions in this equation represent element by element operations on the matrices. $\mathbf{H}_\infty$ is an alteration of $\mathbf{H}_0$ resulting in $\lambda = 1$; γ was set at 10,000 to represent $m^2\ ha^{-1}$, the maximum area that can be occupied by weeds. Parameter values for $\mathbf{H}_0$ are presented in Table 1. W_t is the total area occupied by the population at t, calculated as $W_t = \boldsymbol{\omega}\mathbf{x}_t$. Where ω is a row vector containing the average area occupied by individuals in each stage and for each species (Table 2). When $W_t = W_{t+1}$ the population is at steady-state.

We analysed the emerging population growth rates and the effect of removing plants from the weed populations.

$$\begin{bmatrix} 0 & 0 & 0 & \cdots & 0 & F_{1,1} & F_{1,\cdots} & F_{1,q} \\ M_{1,1} & R_{1,1} & 0 & \cdots & 0 & 0 & \cdots & 0 \\ M_{1,0} & M_{1,2} & R_{1,2} & \cdots & 0 & 0 & \cdots & 0 \\ 0 & 0 & M_{1,3} & \ddots & 0 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \ddots & R_{1,m+2} & 0 & \cdots & 0 \\ 0 & 0 & 0 & \cdots & M_{1,m+3} & R_{1,m+3} & \cdots & 0 \\ 0 & 0 & 0 & \cdots & 0 & M_{1,m+4} & \ddots & 0 \\ 0 & 0 & 0 & \cdots & 0 & 0 & \ddots & R_{1,m+q+1} \end{bmatrix} \begin{bmatrix} NS_1 \\ SB_1 \\ J_{1,1} \\ \cdots \\ J_{1,m} \\ A_{1,1} \\ \cdots \\ A_{1,q} \end{bmatrix}$$

$$\mathrm{H}_t = \begin{bmatrix} \boxed{H_{1t}} & 0 & 0 & 0 \\ 0 & H_{2t} & 0 & 0 \\ 0 & 0 & H_{\cdots t} & 0 \\ 0 & 0 & 0 & H_{zt} \end{bmatrix} \qquad \mathrm{x}_t = \begin{bmatrix} \boxed{x_{1t}} \\ x_{2t} \\ x_{\cdots t} \\ x_{zt} \end{bmatrix}$$

Figure 2. Stage projection matrix and population vector for a multi-species woody weed infestation.

Table 1. $\mathbf{H}_0$ matrix elements for chinee apple prickly acacia, and parkinisonia.

Life stage		Stage transition	Chinee apple $K = 1$ $\mathbf{H}_{1,0}$	Prickly acacia $K = 2$ $\mathbf{H}_{2,0}$	Parkinsonia $K = 3$ $\mathbf{H}_{3,0}$
New Seeds	(NS_k)	$M_{k,0}$	0.004	0.100	0.030
		$M_{k,1}$	0.600	0.370	0.600
Seed Bank	(SB_k)	$R_{k,1}$	0.600	0.370	0.600
		$M_{k,2}$	0.004	0.100	0.030
Juvenile Small	($J_{k,1}$)	$R_{k,2}$	0.100	0.060	0.350
		$M_{k,3}$	0.400	0.150	0.350
Juvenile Medium	($J_{k,2}$)	$R_{k,3}$	0.100	0.150	0.350
		$M_{k,4}$	0.650	0.500	0.450
Juvenile Large	($J_{k,3}$)	$R_{k,4}$	0.100		
		$M_{k,5}$	0.800		
Juvenile Largest	($J_{k,4}$)	$R_{k,5}$	0.100		
		$M_{k,6}$	0.850		
Adults Small	($A_{k,1}$)	$R_{k,6}$	0.700	0.700	0.600
		$M_{k,7}$	0.100	0.150	0.200
		$F_{k,1}$	9	150	1,000
Adults Medium	($A_{k,2}$)	$R_{k,7}$	0.750	0.756	0.700
		$M_{k,8}$	0.100	0.150	0.200
		$F_{k,2}$	880	7,000	5,000
Adults Large	($A_{k,3}$)	$R_{k,8}$	0.800	0.756	0.400
		$M_{k,9}$	0.100	0.120	
		$F_{k,3}$	3,000	27,000	10,000
Adults Largest	($A_{k,4}$)	$R_{k,9}$	0.930	0.832	
		$F_{k,4}$	4,000	35,000	

RESULTS

Our results indicate that both prickly acacia and parkinsonia will initially dominate chinee apple. Later, prickly acacia will out-compete parkinsonia, and eventually, chinee apple will out-compete both prickly acacia and parkinsonia (Figure 3).

Zull *et al.* (2006) found adult woody weeds had the greatest population elasticity and therefore should be targeted for control first. This is represented in Figure 4, where the adults of all the species were removed in years 50, 150 and 300. In all three cases the total area occupied by invasive species returned to the pre-management levels within 25 years. However, management changed the species mix. In fact some

Table 2. Area occupied by different weeds in different life cycle stages.

		Chinee apple	Prickly acacia	Parkin-sonia
		m² = ω_i	m² = ω_i	m² = ω_i
New seeds	(NS_k)	0	0	0
Seed bank	(SB_k)	0	0	0
Juvenile small	($J_{k,1}$)	0.01	0.03	0.05
Juvenile medium	($J_{k,2}$)	0.07	1.131	0.39
Juvenile large	($J_{k,3}$)	0.28		
Juvenile largest	($J_{k,4}$)	0.72		
Adults small	($A_{k,1}$)	2.33	4.714	3.35
Adults	($A_{k,2}$)	6.61	9.348	10.75
Adults	($A_{k,3}$)	17.14	15.55	27.16
Adults	($A_{k,4}$)	52.95	37.94	

species benefited from the management and increased occupancy to the detriment of other species, i.e., management in the 50th year resulted in an increase in parkinsonia whilst prickly acacia decreased. Likewise, in the 150th and 300th year prickly acacia increased and chinee apple decreased.

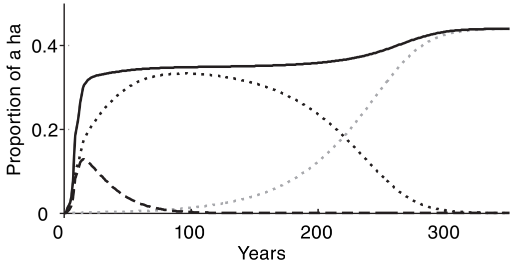

Figure 3. Predicted proportion of a hectare in a riparian zone occupied by chinee apple (▪▪▪▪), prickly acacia (▪▪▪▪), parkinsonia (– –) and total area occupied (——) over time.

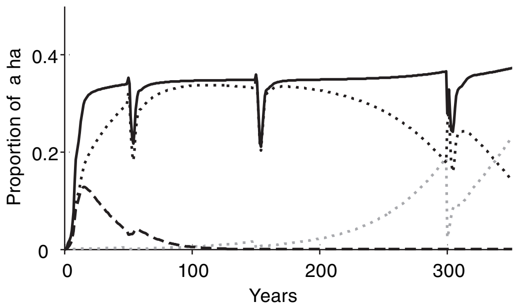

Figure 4. The effect of removing all adults from all species in years 50, 150 and 300.

DISCUSSION

In this simulation, the lifecycles of prickly acacia and parkinsonia are faster than chinee apple, and colonise an area sooner than chinee apple. As a result, prickly acacia and parkinsonia should be targeted early in the invasion. However, with reduced competition chinee apple will establish sooner than it would have in the absence of management and will eventually dominate the area. Therefore secondary management should target chinee apple.

A multi-species infestation will result in a higher overall density faster than a single species infestation (Zull *et al*. 2006). However, the growth rates of individual species within multi-species infestations are slower. Our findings have implications for identifying economically-efficient control strategies which take into account the consequences of reinfestation by other weed species.

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