

Future spread of lippia in the Murray-Darling Basin under climate change

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Summary Lippia (*Phyla canescens*) is a severe environmental and agronomic weed in the Murray-Darling Basin that exploits extreme flood events to colonise new habitat.

We present a spatially-explicit, process-based simulation model (PLANTSIM), incorporating empirical data on the performance of lippia under different soil moisture and temperature regimes. Model simulations were run to explore the response of lippia to differing combinations of flood depth and duration. Results indicate the spatial location of recruits in floodplains represents a trade-off between hydrological conditions which enhance recruitment versus those that induce mortality, resulting in a narrow spatial and temporal regeneration window critical to successful establishment of lippia.

In a future scenario of lower flows with a higher incidence of extreme flow events lippia is likely to recruit sporadically from the seedbank, despite widespread declines in soil moisture resulting from decreased annual precipitation and increased annual temperature.

Keywords Flood disturbance, spatial-spread model, floodplain weed, invasion rate.

INTRODUCTION

Lippia (*Phyla canescens* (Knuth) Greene (Verbenaceae)) is an invasive perennial herb native to South America. It occurs predominately on clay soil floodplains within the 500–800 mm annual precipitation zone of Queensland and New South Wales, although it has been recorded in all catchments of the Murray-Darling Basin (Earl 2003). In 2003 lippia was estimated to cover approximately 5.3 million hectares of floodplain throughout the Murray-Darling Basin (MDB), costing approximately \$38 million in lost annual production to the grazing industry (Earl 2003).

Lippia is a prostrate plant that grows rapidly to produce dense mats covering large areas. Vegetative fragments which detach and spread downstream during flood events can regenerate to produce new individuals. Lippia also produces seed, leading to the formation of dense seedbanks in Australia (Macdonald 2007). Ultimately the achievement of specific management

objectives for lippia is dependent on understanding the link between hydrological regimes and population dynamics.

Spatially-explicit population spread models are particularly useful in the early stages of invasions, when population size is frequently constrained by propagule availability to a greater extent than by habitat availability. This study aimed to achieve the following: (1) determine which demographic processes have the greatest effect on growth rate and spread speed of lippia, (2) obtain quantitative information on how key hydrological parameters influence these demographic processes and (3) provide a modelling platform to simulate future alterations in key hydrological parameters resulting from climate change, enabling predictions of the future extent of lippia growth and spatial spread under specific environmental scenarios.

MATERIALS AND METHODS

The PLANTSIM model was parameterised with data collected from field and laboratory experiments reported in the literature (Macdonald 2007).

Response of lippia to hydrological parameters In order to effectively model the response of lippia as a function of water depth we combined data from two glasshouse experiments (Hobson 1999, Taylor and Ganff 2003). The response variable in both studies was the difference between initial and final lippia biomass over the duration of the experiment, which was converted into a relative growth rate (RGR),

$$\text{RGR} = (\ln W_2 - \ln W_1) / \Delta t$$

where W_1 = initial weight, W_2 = final weight and Δt = days elapsed between sampling W_1 and W_2 . A quadratic regression can be fitted to this data (Figure 1), indicating that lippia has a narrow tolerance range to water depth for optimal performance.

The PLANTSIM model The model describes species growth (N) at location (x, y) at time (t) for each life-history stage ($N_{i,s}$), where N_1 = adult plants, N_2 = seeds attached to plants, N_3 = dispersed seeds,

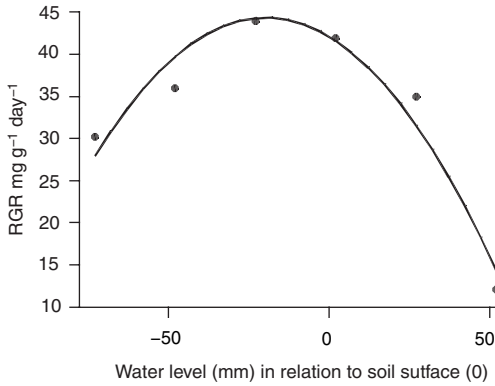


Figure 1. The relationship between above and below ground water level (WL) and RGR of lippia. The fitted quadratic equation is $RGR = 41.543 - 0.255 \times WL - 0.006WL^2$, $R^2 = 0.91$.

N_4 = seeds in the seedbank and N_5 = seedlings. A key feature of the PLANTSIM model is that simulations can be run in either virtual terrains or real systems, incorporating aerial photographs or Googlemap images. Additionally, the spatial scale for simulations is adaptable and can be defined by the user. This allows compartmentalisation of regions within the overall spatial domain, allowing the user to set carrying capacity to zero in regions where growth cannot occur (e.g. permanent lakes). To evaluate the impacts of altering specific plant parameters on model outputs we have chosen a standard habitat template for cross-comparison, thereby reducing potential variability resulting from spatial complexity. The standard template contains a river running vertically through the spatial domain, with terrain height rising symmetrically on either side of the river.

The density of lippia, $N_1(x,y,t)$, is measured as the number of branches m^{-2} . The equation for growth of mature plants is given below,

$$\frac{\partial N_1^*}{\partial t}(x,y,t) = [c_9 - c_{10}N_1^*(x,y,t) + N_5(x,y,t - dt_2)] \left(1 - \frac{N_1^*(x,y,t)}{N_m} \right)$$

where N_m is the maximum carrying capacity, c_9 is the growth rate, which varies with water depth according to Figure 1, c_{10} is the death rate and dt_2 is the time delay for seeds to mature into seedlings.

Seed production is continuous in adult plants (Macdonald 2007) but constrained by density-dependence as the density of plants approaches carrying capacity. Seeds are dispersed in three ways represented in K_1 : (1) seed is transported long distances described by a decaying exponential kernel (r_1), (2) seed is

spread locally following a Gaussian dispersal kernel (r_2) and (3) seed falls directly below the parent plant, represented by the delta function.

$$K_1(r) = \frac{1}{r_1} c_2 \exp(-r/r_1) + c_3 \frac{1}{\pi r_2^2} \exp(-r^2/r_2^2) + c_4 \delta(r)$$

The proportion of seed in each type of dispersal is represented by c_2 , c_3 and c_4 . Dispersed seeds are added to the seed bank, $N_4(x,y,t)$ (seeds m^{-2}),

$$\frac{\partial N_4}{\partial t} = -c_5 N_4 + N_3 - c_6 N_4$$

where c_5 represents the death rate of seeds in the seed-bank, the N_3 term represents new seeds being deposited and c_6 represents seed germination rate, dependent on the presence or absence of flooding. The number of seedlings, N_5 (seedlings m^{-2}) is given by,

$$N_5(x,y,t) = c_6 N_4(x,y,t - dt_1)$$

where dt_1 is the time taken for seeds to germinate into seedlings. The death rate and maturation rate of seedlings is for simplicity factored into the constant c_6 .

Lippia plant fragments which are produced during flooding are re-dispersed along the river described by an exponential dispersal kernel,

$$N_1^*(x,y,t) = \int_s K_2(s-s') N_1(x',y',t-dt) ds'$$

where s' and s are distances along the river, dt is the time discretisation and x, y are the spatial positions, with $s \equiv (x,y)$, $s' \equiv (x',y')$. The dispersal kernel is,

$$K_2(r) = \frac{1}{r_0} e^{-r/r_0}$$

with r the distance along the river and r_0 assumed a linear function of flood strength, so that dispersal speed ranges from a low value for no flood up to greater values for floods of greater height. Flood duration is controlled in the model by altering the start and finish time of floods, influencing the following plant parameters: (1) lippia growth rate as a function of water depth, (2) seed to seedling maturation rate, (3) plant death rate and (4) seedling death rate. A range of model simulations were run to examine the influence of flood duration and flood height in influencing spread speed and the area of land occupied by the weed.

RESULTS

All flood events increase the germination rate (c_6) and the dispersal of lippia fragments to new habitat, leading to the establishment of new invasion foci downstream. However, longer duration floods (>3 months) decrease the density of lippia in currently established invasion patches, due to the death of seedling cohorts resulting from excessive inundation.

Flood height is a key parameter controlling final plant density and the spatial extent of lippia (Figure 2). Shallow floods increase both lippia growth rate and the germination rate, whereas deep floods increase germination rate but decrease plant growth rate, as higher flood depths represent the suboptimal range of the performance curve (Figure 1).

To summarise, floods of differing height will have idiosyncratic effects on weed spread, due to a trade-off between increases in suitable habitat, created by increased availability of flooded land and hence increased germination, and subsequent decreases in optimal habitat resulting from increased flood depth. This indicates that small scale changes in local terrain are important in structuring the spread of lippia and effective management is likely to require consideration of local topography and hydrology.

The PLANTSIM model indicates that the spatial position of the invasion front is most sensitive to the distance travelled by lippia propagules. Seed dispersal to new territory is crucial in controlling the rate of occupancy and spread because seed production within a region is subject to density-dependence and decreases per unit area as plant density approaches the maximum carrying capacity the environment can support. In addition, because seeds 'stockpile' within the seed bank at distant locations, thereby contributing to future generations, the proportion of seeds travelling long distances also influences the rate and area of occupancy. Finally, model results are sensitive to the seed to seedling maturation rate and any factor either increasing (i.e. flooding) or decreasing (i.e. drought conditions) germination will subsequently influence weed abundance and spatial spread. Whilst temperature does influence the success of germination, large areas of Australia are within the climatic range of temperatures which lippia can tolerate (Macdonald *et al.* 2006).

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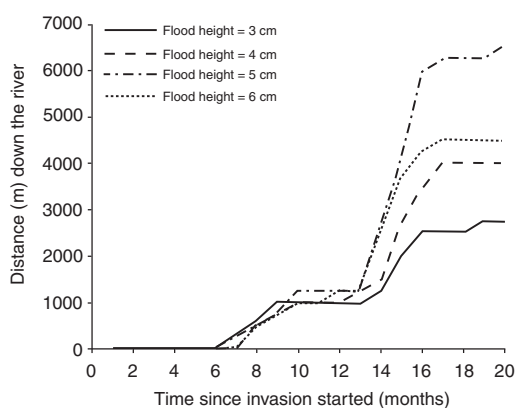


Figure 2. Comparison of lippia spread speed for floods of differing height (3–6 cm), showing the position of the leading edge of the invasion front.

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