MODELING INVASION BY Allocasuarina huegeliana IN KWONGAN HEATHLAND AND ITS MANAGEMENT IMPLICATIONS

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ABSTRACT

In most natural systems worldwide, land managers are combating the spread of invasive weeds and attempting to minimize their damaging impacts. Often invasion is linked to disturbance regime shifts, and particularly in case of native invasives disturbance is often critical in the incursion behavior. Manipulation of disturbance regimes can provide effective control methods for managers. Modeling as an informative tool in invasive species control is common, though underutilized when applying disturbance as management strategy. We constructed and analyzed a population model to inform management of native invasive tree Allocasuarina huegeliana. Local managers believe that its spread is due to an altered fire frequency. We built a population model of A. huegeliana and simulated fire and fire coupled with managed removal over a range of strategies. We found that current fire frequencies likely cause high densities leading to biodiversity loss unacceptable in local adaptive management plan. Losses could be mitigated by managed removal, a strategy most effective at high levels of effort.

Keywords: Native invasive, individual-based model, fire, sandplain heathland, rock sheoak, adaptive management, disturbance-based management

INTRODUCTION

Invasive species have been shown to negatively impact ecosystem biodiversity levels and function through direct and indirect effects (Vitousek *et al.*, 1996; D'Antonio *et al.*, 1996; Mack and D'Antonio, 1998; Parker *et al.*, 1999; Simberloff *et al.*, 1999; Valery, Fritz *et al.*, 2009). Though the term invasion most often applies to non-natives, similar effects can be seen in human-induced spread of some species within their own native range (Reise *et al.*, 2006; Olenin *et al.*, 2006; Valery, 2008 & 2009; Fritz *et al.*, 2008; Davis, 2009). The causes of native invasion are not fully understood. However, a strong link between disturbance in a system and biological invasion has been shown in many studies (Hobbs and Huenneke, 1992; Dudley

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et al., 1999; Hierro *et al.*, 2006; Villarreal *et al.*, 2006). The theoretical link between disturbance and invasion is intuitively strong in native invasion. To control a native invasion, the underlying cause must often be treated in addition to managing the species itself (Hobbs, 2000). Thus, returning a system to historical disturbance regimes – or implementing well-planned novel regimes – must be used in conjunction with more direct treatments such as chemical, manual, and biological control to manage the spread of disturbance-linked invasion in a system.

In many systems worldwide, fire is a major mechanism of disturbance and alteration of historic fire regimes is thought to have led to major shifts in vegetation, including invasion by non-native as well as native species (Vitousek, D'Antonio *et al.*, 1996; Van Auken, 2000). In this study, we investigated population modeling techniques to assess fire as a disturbance-based management tool for the control of a native invasive in a fire-prone Australian system. We focus on land manager concerns about invasion in kwongan heathland, found predominantly in wheatbelt region of Western Australia.

In the past several decades, the native tree species *Allocasuarina huegeliana*, a fire sensitive tree species, has been invading in kwongan habitat where previously it was recorded as rare or absent (Main, 1993; Bamford, 1995). There is increasing concern that a shift to high *A. huegeliana* densities will cause a large decrease in kwongan biodiversity. We developed an individual-based model of *A. huegeliana* populations to examine the efficacy of a number of single and combined management techniques with a focus on fire as the predominant method of control. Our goal was to determine how fire frequency and regularity, and its pairing with managed removal affect *A. huegeliana* spread in Kwongan. We analyzed rates of increase, spatial distribution, and the point at which acceptable thresholds of alpha diversity impacts are crossed under each treatment.

Species

Allocasuarina huegeliana is a species native to Western Australia. As a reseeder species, *A. huegeliana* is at a potential disadvantage to resprouting kwongan species more fire tolerant when subjected to high frequencies. It has been shown to have dramatically increased seedling occurrence immediately post-fire (Yates, Hopper *et al.*, 2003). However, there is a corresponding occurrence of heightened seedling mortality post-fire (Maher, Hobbs *et al.*, 2010). **Site**

Kwongan is a highly diverse shrub-dominated ecosystem found in wheatbelt of Western Australia. It is composed mainly of woody and herbaceous cover less than two meters tall. Vegetation in kwongan has adapted to frequent fires, with many life history characteristics dependent on fire for optimal growth (Keith, Holman *et al.*, 2007). Fire can also preserve the high diversity between canopy layers (Keith and Bradstock, 1994; Keith, McCaw *et al.*, 2002).

MATERIALS AND METHODS Model

The A. huegeliana population model was coded in R and is an individual-based matrix model. A single cell has three possible states: absence of A. huegeliana, presence of A. huegeliana seedling, or presence of A. huegeliana adult individual. Timesteps are annual and include production, establishment, seed aging, and death. Allocasuarina huegeliana is dioecious, and we estimated 40% of total population as female, as per field data. Once reproductive age is achieved, each female tree produces a uniform number of seeds each year. Newly produced seeds are distributed throughout the model landscape with a dispersal distance drawn randomly from a Cauchy distribution with location $x_0 = 4$ and scale $\gamma = 1$, and the direction of dispersal randomly determined. All seeds are assumed to germinate immediately, and become seedlings of age one. Seedlings are more vulnerable to environmental mortality than fully established adults. Therefore, a high rate of seedling mortality is assumed for first two years, at which point any surviving seedling becomes an adult. In this adult stage, a set mortality probability of 5% per year is assumed.

All environments experience 'good' and 'bad' years. To simulate this stochasticity, our model randomly assigns an annual seasonal suitability based on a truncated normal distribution with mean $\mu = 0.5$ and standard deviation $\sigma = 0.1$. Three parameters vary dependent upon seasonal suitability: seedling mortality, seed production, and reproductive age (Fig. 1).

We examined two methods of control: fire and managed removal of adult trees. Fire is simulated as homogeneous across the site. Following fire, 100% mortality of *A. huegeliana* within the burned site is assumed. Additionally, simulated seed production in years of fire occurrence increases by a magnitude of ten to imitate the increased germination of reseeder species post-fire. Once the simulated site is burned, it is considered bare of vegetation. In accordance with higher seedling mortality rates observed in the field, increased seedling mortality of *A. huegeliana* is assumed for three years post-fire. Finally, we simulated managed removal of *A. huegeliana* adults in conjunction with fire. Adult trees are 'cut down' and experience mortality without the increased seed rain or harsher seedling environment. We assume some human error, so adult trees have a 90% chance of removal. Because of inevitable presence of fire in the system – both wildfires

and management fires for fuel load and heath regeneration purposes, we did not look at managed removal alone.

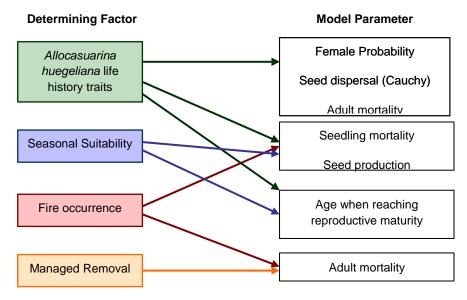


Figure 1. Model parameters and the factors influencing their values.

Virtual Experiments

A series of virtual experiments was conducted. In kwongan patches, there is generally an adjacent A. huegeliana seed source such as an *A. huegeliana* stand at the base of a granite outcrop. To simulate this situation in our model, 10% of the landscape was designated as a fire refuge that did not burn during the model runs. The remaining area represented the fire-prone heath patch and was subjected to a range of management strategies. We considered several different management regimes: regular fire occurrence, random fire occurrence, and regular fire occurrence in conjunction with managed removal. In regular fire occurrence, we considered burn frequencies of between 10 and 80 years, in increments of 5 years. For random pattern, fire occurred each year with a certain probability. We considered a range of probabilities corresponding to same 10-80 year range of frequencies considered for regular pattern. Managed removal was simulated by testing managed removal of adults every 9 years, every 18 years, and every 27 years and a range of removal areas, starting with entire site or rather center 75%, 50%, and 25% of the site.

Measure of Impact

We used species richness as our measure of impact. The estimated richness impact was based on field data collected at field

sites and the species-area curve. We calculated the mean species richness for each area within a nested design and fitted this data to a species-area curve using the power function species-area relationship: $S = cA^z$ where S is species richness, A is area, c is a constant, and z is the rate at which species accumulate with increasing area. We assumed that each *A. huegeliana* individual reduced available area by area of one cell (2.25 m * 2.25 m \approx 5 m²). We calculated impact as reduction of species based on the reduction of area inhabited by *A. huegeliana*. At a level of only one species, the invasion had a measurable, negative impact on the system. At five species, some of the sites dropped below 90% of original site diversity. Therefore, we defined the thresholds of major interest as one, three, and five species loss, corresponding with densities of 134, 380, and 595 trees per ha, respectively.

RESULTS AND DISCUSSION

The model was able to predict population dynamics of native invasive of concern (Fig. 2) and its response to different management tactics. The simulated populations showed many of the behaviors commonly found in invasions, such as satellite population development and density edge effects from the seed source.

Changes in fire frequency made a gradual but significant difference in increase and spread of species post-fire. DEC states in their management plan that purpose of *A. huegeliana* control is to maintain biodiversity levels in kwongan heath (Beecham, Lacey *et al.*, 2009). It is important to understand the management strategies that will effectively attain that goal. Biodiversity loss thresholds were crossed under many of the management scenarios. However, the model was able to predict levels of each strategy necessary to delay or prevent that loss, thus maintaining current biodiversity levels.

Disturbance-based management has the potential ability to not only control invasion itself but also to address the underlying cause. Our model focuses on fire, only one of the many disturbance regimes contributing to global invasive species establishment and spread (Tylianakis *et al.*, 2007). Similar modeling applications would be effective in looking at other disturbance-based management techniques, such as hydrologic disturbance in ephemeral or tidal wetlands or grazing by native or introduced herbivores. Additionally, there are many potential further impacts of invasive species beyond our measure in the current model, including competition, nutrient shifts, allelopathy, microclimate changes or shifts in pollinator/plant interactions. We used a very conservative measure, looking only at the physical space occupied by the invader. Further research needs to be

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undertaken to establish ecologically sound thresholds for use in management-focused modeling.

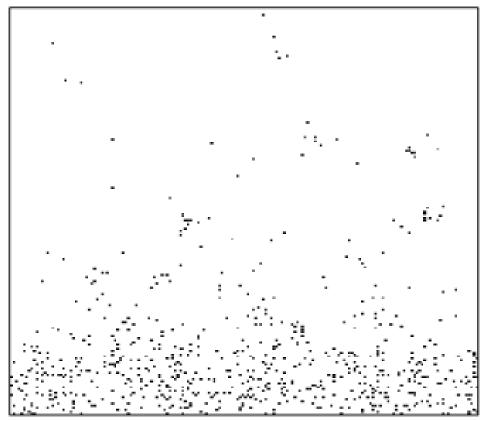


Figure 2. Typical output of simulation. The area depicted, totaling 20.25 ha, is both the simulated fire refuge (lower 10% of area) and heath patch (upper 90% of area), with white space being those cells unoccupied by *A. huegeliana*. Each black cell represents an *A. huegeliana* individual.

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