

Getting trees on farms the easy way? Lessons from a model of eucalypt regeneration on pastures

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Abstract. Substantial revegetation is required across much of Australian agricultural landscapes. Managers need to minimise the risks of failure and costs associated with revegetation. Whereas ‘natural regeneration’ of eucalypts is relatively cheap compared with direct seeding or planting tubes, natural regeneration in grazed lands occurs infrequently and under limited circumstances. Management needs to understand the situations in which natural regeneration is most likely to occur and what actions can improve the chances of regeneration. We used a rule- and stage-based model of eucalypt regeneration focusing on events between seed supply and sapling escape to synthesise current knowledge and learn how to improve the success rate of natural regeneration of eucalypts. The model used deterministic rules but with stochastic rainfall, and fire was applied stochastically as well as deterministically. Results from simulations suggested that low-productivity pastures have greater likelihood of supporting saplings than do high-productivity pastures. Fire and grazing can increase the chances of subsequent germination and early seedling survival, particularly in high-productivity pastures. As a result, management actions, such as fire and strategic grazing, can improve the probability of sapling establishment in a high-productivity pasture; however, frequency and timing of management actions are important. The following three sources of uncertainty appear crucial: first, variability in rainfall; second, uncertainty about rainfall effects on stage transitions; and third, variability in seed supply. These uncertainties can overwhelm improvements to the chances of regeneration owing to management interventions. Because rainfall and seed supply have overwhelming effects on the process of regeneration, they limit the ability of managers to influence the outcomes and this makes investment in natural regeneration inherently risky. Thus, better data are needed on the effect of rainfall on stage transitions and on spatial and temporal variation in seed supply. This would aid managers to estimate the likelihood of success of regeneration, and make decisions about if, when and where to invest in natural regeneration and what actions to implement.

Introduction

Land use is changing rapidly in agricultural zones in the world. In southern Australia and other regions of the world, there are efforts to re-establish native woody perennial vegetation on lands previously cleared for agriculture. Revegetation is needed to address declining biodiversity and for restoring ecosystem processes such as control of ground-water recharge and discharge and soil retention (Saunders and Hobbs 1995; Yates and Hobbs 1997). Active regeneration through direct seeding or tubestock-planting methods is expensive (>AU\$1500 ha⁻¹ for 10 ha), with tubestock the more expensive approach (Schirmer and Field 2000). ‘Natural regeneration’, the colonisation of woody plants from remnant trees, potentially offers an inexpensive

alternative. Natural regeneration is essentially analogous to old-field succession (Inouye *et al.* 1987). In both cases, colonisation by woody plants is less likely to occur at sites that are distant from potential seed trees, that are regularly grazed by livestock, that support high loads of annual exotic grass cover and that have been recently cultivated (Pettit and Froend 2000; Spooner *et al.* 2002; Dorrrough and Moxham 2005). It has been suggested that there is considerable potential for natural regeneration in agricultural lands of south-eastern Australia (Cluff and Semple 1994), even in landscapes with 2–5% remnant tree cover (Dorrrough and Moxham 2005). However, widespread adoption of policy and management actions designed to encourage natural regeneration at broad scales are limited, partially because

natural regeneration of trees is infrequent and not easy to predict.

There are three main forms of information about eucalypt-seedling regeneration important to management and decision-making. These include the following:

- (1) Fine-scale experimental studies that aim to identify the relative importance of germination, seedling emergence and survival in the process of regeneration. These commonly use a mix of laboratory-based germination trials, pot trials and small field experiments on sown seed or planted seedlings (Yates *et al.* 1996; Clarke and Davison 2001; Semple and Koen 2001; Clarke 2002; Allcock and Hik 2004). For an example of a larger experiment, see Yates *et al.* (2000). Although specifically targeting process, such studies are of uncertain generality because they are of short duration (typically 1–2 years) and limited extent (covering ~1–100 m²).
- (2) Broad-scale surveys of regeneration in the field (Yates *et al.* 1994b; Pettit and Froend 2000; Spooner *et al.* 2002; Dorrrough and Moxham 2005). These provide general information on patterns of regeneration, but yield little insight into processes.
- (3) Expert opinion, agency reports, and extension material. This information is often rich in process detail over long times and, although invaluable, is problematic because it is highly contingent on the particular individual's experience, and the mental models used by practitioners are not explicit. Hence, the logic of these mental models cannot readily be examined; the domain over which they operate is unknown, as is their sensitivity to the various drivers (e.g. grazing, rainfall, pasture competition, fire), and they cannot be simply modified or improved (Starfield and Bleloch 1986).

We developed a qualitative, rule-based model of eucalypt regeneration in pastures to draw together and summarise the fragmented information on natural regeneration in an explicit model. A qualitative approach is appropriate for a generalised process model where quantitative data are unavailable or of uncertain generality (Starfield and Bleloch 1986). We investigated the behaviour of the model in relation to specific management actions or analogues of them. There are several actions that managers use to try to facilitate natural seedling recruitment, including the following: (1) excluding stock, (2) reducing biomass by using (a) herbicides, (b) intense 'crash' grazing or (c) scalping or other mechanical removal of biomass and topsoil, and (3) burning. Note that some of these actions can be taken at different times in the regeneration process. We also examined natural regeneration from an allocation perspective. That is, if a manager is deciding where to attempt regeneration, how might past management and current site conditions affect the likelihood of regeneration?

Our purpose in this paper was to (1) present explicitly our current understanding of the process of regeneration,

which is based on literature and observations; (2) identify conditions in which natural regeneration can be expected and those where it is unpredictable; (3) identify management actions that influence natural regeneration; and (4) ask whether management actions can increase the chance of regeneration.

Materials and methods

We used a qualitative, rule-based approach to modelling the regeneration (seed to sapling) process (Starfield and Bleloch 1986). This was appropriate because external events, such as rainfall, grazing and fires, strongly influence the dynamics. The species intended for this model were *Eucalyptus microcarpa* (grey box), *E. albens* (white box) and *E. melliodora* (yellow box), although we expect that application to a wide range of temperate woodland eucalypts is reasonable. Our model was non-spatial and seed supply was controlled by the user, because we lacked a means to predict its variation other than a quasi-exponential decline with distance from the canopy drip line (Cremer 1977; Dorrrough and Moxham 2005). The other clear spatial effect, which we do not explore, is increased competition close to adult trees (Stoneman *et al.* 1994).

The model was stage-based with a yearly time step. Qualitative states (e.g. low/medium/high) described stage abundances and driving variables. Broadly, abundance should be thought as of a logarithmic scale, so that differences between abundance classes are multiplicative not additive. Different stages will have different abundance scales; e.g. abundances for germinants will be orders of magnitude greater than that for saplings. Rainfall was split between winter (for germination and driving pasture growth) and summer (for seedling survival) and was stochastic. Fire was modelled as a stochastic event or could be applied directly. Grazing was treated as light or heavy. The model was implemented as a Microsoft Excel 2003 spreadsheet driven by a Microsoft Visual Basic 6.3 program. The following two types of model runs were considered: long runs of 500 years to give information on frequencies of occurrence, and short runs of 3–6 years to evaluate specified management scenarios.

The program is available on request from the corresponding author.

Sequencing of events and priority of effects

The model is based on the various stages of plant growth, including seeds, germinants, seedlings and saplings (Fig. 1). The year runs from April to March, reflecting seasonal change in rainfall, evaporation and fire risk. Germination occurs between April and the end of September. Germination responds to cool-season rainfall (Apr.–Sept.). At ~2 weeks, when cotyledonary reserves are exhausted, germinants become seedlings, i.e. any time after April. Seedling establishment refers to survival of new seedlings through their first year, i.e. until March.

The order of events for each yearly time-step was as follows. First, environmental conditions for the year were set—summer and winter rainfall; grazing pressure; pasture growth, which determined pasture biomass; fuel load (from pasture) and summer rainfall determined probability of ignition (also controllable by user); fires (optional) were applied. Fires occur before germination; for management fires that occur after March, we assumed that they happened in the previous year. Second, eucalypt-stage transitions were handled in the following order of size. Seedling 2 (0.5–1.0 m) transitions were affected, in order, by fire, grazing and summer rain. Seedling 1 (<0.5 m) transitions were affected by fire, grazing, summer rainfall and pasture suppression, in that order. Seed germination was equally affected by pasture suppression and winter rain. Finally, germinants were affected by summer rain, grazing and pasture suppression, in turn. Stages and drivers are described further below.

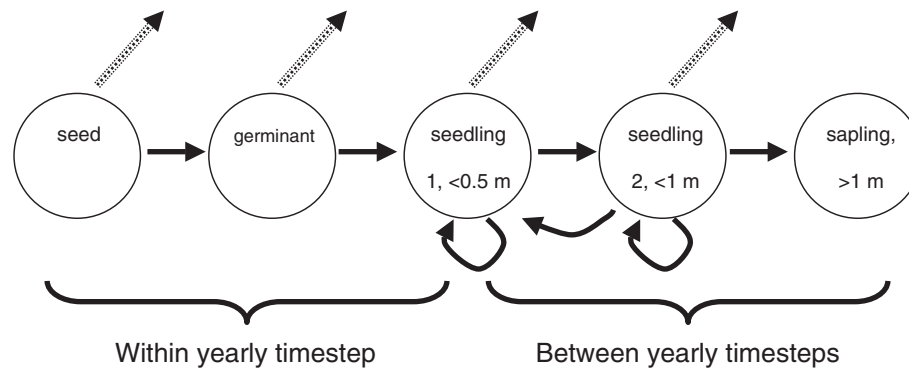


Fig. 1. Stage structure of the tree regeneration model. Germinants are reliant on cotyledonary reserves, less than ~2 weeks old. Seedlings establish after 1 year. Saplings have escaped grazing and competition. Transitions indicated by arrows include mortality, progress, reversion and stasis.

Seed supply

Interannual variability in flowering intensity and seed production of eucalypts is thought to be high (Yates *et al.* 1994a; Pook *et al.* 1997; Law *et al.* 2000). However, it should be noted that few long-term data exist (but see Pook *et al.* 1997). Attempts to relate rainfall to flowering and seed production have provided equivocal results (Law *et al.* 2000; Keatley *et al.* 2002). Yates *et al.* (1994a) found that at four sites over 2 years flowers were produced at all sites, but 23% of trees did not flower at all, and no tree flowered in both years. Variation in flowering intensity among years may be relatively unimportant if several years' crop of fruit and seed can be retained in the canopy and released continuously or *en masse* after disturbance (Yates *et al.* 1994b). Indeed, most temperate eucalypts are serotinous, retaining seeds in the canopy for several years, but probably releasing some seeds year-round (Wellington and Noble 1985b; Yates *et al.* 1994a; House 1997).

Eucalypt seeds are often harvested by ants and, to a far lesser extent, by small vertebrates; dramatic reductions in seed abundances often result (Andersen and Ashton 1985; Wellington and Noble 1985b; Yates *et al.* 1995). However, it is not clear whether ant predation actually affects the eventual numbers of surviving seedlings in intact woodlands. Rather, opportunities for surviving summer drought may control seedling survival (Andersen 1989). Furthermore, post-dispersal predation of eucalypt seed is highly variable, both spatially and temporally, and is likely to be modified by grazing and fire management (Jansen and Robertson 2001). Here, we do not directly model seed predation; however, one can think of low seed supply as the result of pervasive seed predation.

In view of the variability, rather than model seed supply as stochastic or being affected by rainfall, landscape-scale disturbance or predation, we investigated the effect of varying seed supply (low, medium or high) controlled by the user. Thus, interpretation must be in the light of a proportion of years in which seed supply is sufficient and within dispersal distance of parent trees. High seed supply may correspond to a landscape-scale disturbance.

Germination and establishment

High soil moisture and access to suitable microsites are essential for seedling germination. In temperate Australia, eucalypt emergence may be restricted to cool months following above-average rainfall (Andersen 1989; Stoneman and Dell 1994; Yates *et al.* 1996). When soil moisture is non-limiting, microsites lacking litter or plant cover may not be necessary for germination (Clarke and Davison 2001), although light soil disturbance and an ash bed apparently result in optimal microsites (Stoneman and Dell 1994; Yates *et al.* 1996; Clarke and Davison 2001). Cultivation may have multiple effects, initially reducing competition

through removing plants and enhancing soil moisture retention through breaking up soil, although subsequent establishment of weeds and pasture could limit germination and establishment (Spooner *et al.* 2002; Dorrough and Moxham 2005). Grazing and fire events, although detrimental to early seedling growth and survival (see below), may enhance germination, particularly in pastures with high biomass and growth rates (Yates *et al.* 1994b; Clarke and Davison 2001). We included no direct detrimental effect of grazing on germination, rather leaving it to affect small seedlings in the same year. Similarly, fire had no direct effect on germinants because they were not exposed to fire; fires either occurred at the end of the previous year, and thus before germination, or at the end of the year and thus after germinants had become seedlings. We considered germinants to be utilising cotyledonary reserves and to be about <2 weeks old. In the model, the number of germinants increased with seed supply and winter rain, and was suppressed by high pasture biomass.

Seedling growth, survival and sapling escape

We distinguished the following two size classes of seedlings on the basis of height: 0–50 and 50–100 cm. We considered a seedling to have established when it had survived its first year. Seedlings of both size classes could each be absent or present at one of three levels (low, medium or high). We considered saplings to have escaped when they had reached 1 m in height. At this stage, they would be little troubled by grazing (Semple and Koen 2001; Allcock and Hik 2004). Seedlings progressed to the next stage if summer rainfall was medium or high (and they were not burnt or eaten; see below) and were unaffected by winter rainfall.

The major general causes of seedling mortality are drought, herbivory and pathogen attack (Wellington and Noble 1985a; Stoneman 1994; Moles and Westoby 2004). Summer rains are crucial to survival of seedlings through their first year, and also to their survival in each subsequent summer until they become saplings (Lawrence *et al.* 1998; Semple and Koen 2003). Indeed, mortality of young trees can still occur and this is primarily driven by the high evaporation rates in summer, and subsequent soil-moisture deficits (Davidson and Reid 1989). Fires and grazing are also likely to have greatest impact during a seedling's first year (Leigh and Holgate 1979). Frequent defoliation in subsequent years (via fire or grazing), once seedlings have established a lignotuber, may be less likely to result in mortality, although it will suppress growth (Leigh and Holgate 1979; Allcock and Hik 2004). For seedlings, establishing in dense understoreys such as pasture, competition can be an important source of mortality as well as suppressing growth (Semple and Koen 1997; Yates *et al.* 2000; Clarke and Davison 2001; Allcock and Hik 2004). Pathogen attack may also contribute to seedling mortality in dense pasture.

Fires, grazing, rainfall and pasture all influence the probability of seedlings to survive, and their progression to the next stage. Fires do not allow any seedlings to progress; large seedlings become small seedlings by resprouting and some small seedlings die, although most persist by resprouting. No seedlings progress under heavy grazing; some large seedlings are killed, most are returned to small-seedling class and most small seedlings die. In wet years, all seedlings can progress; in average years, most progress and some remain, whereas in dry years, none progresses and some die. Pasture can suppress the transition from small seedlings to large seedlings; however, most progress.

If a fire in an ungrazed paddock burns pasture in summer or early autumn and is then followed by sufficient seed fall, the survival is unaffected by pasture competition or grazing. In this case, the success is determined solely by sufficient rainfall for germination (winter rains) and for seedling survival (summer rains).

Rainfall

Rainfall was modelled in two 6-month seasons. Rainfall for winter (W_r , April–September) and summer (S_r , October–March) were modelled independently and randomly, and could each take levels of dry, medium and wet (1, 2, 3). Dry and wet seasons each occurred in one-quarter of years, on average, and one-half of years were medium. We were uncertain how to define ‘dry’ and ‘wet’, so we conducted a sensitivity analysis in which the frequencies of wet and dry years were varied from 15 to 35% of years. For comparison, records for Bendigo (latitude: 36.753°S, longitude: 144.283°E, recording >100 years, data from How Often v2.0.0, Agricultural Production Systems Research Unit) report an annual median rainfall of ~540 mm, with seasonal medians of 325 and 210 mm for winter and summer, respectively. A dry winter (with 15th and 35th percentiles) is one with <245 mm (215, 270), a wet winter with >395 mm (370, 450). A dry summer has <145 mm (125, 170), a wet summer has >275 mm (240, 305).

Pasture growth

Competition from pasture species can be intense where introduced pastures have been sown and productivity is high (Semple and Koen 2003). We wanted to distinguish between high-productivity, cultivated introduced annual pastures and low-productivity, native perennial pastures. We modelled high-productivity pasture as producing more biomass and at a greater rate than did low-productivity pasture in response to good growth conditions (Garden *et al.* 2003). High-productivity pastures achieved high biomass in more years than did low-productivity pastures, ~65% cf. ~35% of years.

Pasture was tracked as a continuous variable (Past) on (0,1), but each year was converted to a binary (low, high) at a threshold of 0.5. We explored varying this threshold—reducing it made the two pasture types more similar and raising the threshold made them less similar (not shown). Current pasture was estimated in late spring (November–December) and was modelled as a weighted mean of the previous year’s pasture and the previous year’s winter rainfall, divided by the grazing offtake (1, 2 for light or heavy). Thus, pasture biomass ‘lags’, owing to the influence of prior conditions. This lag is most marked in low-productivity native perennial pasture and reflects the slower growth rates and greater drought tolerance of these pastures, i.e.

$$\text{Past}_t = (0.3 \times \text{Past}_{t-1} + 0.15 \times W_{r,t-1})/G.$$

In high-productivity pasture, current biomass is thought to reflect recent rainfall events much more, i.e.

$$\text{Past}_t = (0.08 \times \text{Past}_{t-1} + 0.23 \times W_{r,t-1})/G.$$

Grazing

Observational studies indicate that sapling regeneration is restricted to pastures with none or light intermittent grazing (Pettit and Froend 2000;

Semple and Koen 2001; Dorrrough and Moxham 2005). We assumed that under sustained heavy grazing, sapling regeneration never occurs. We are unaware of any data that can be used to attribute seedling regeneration to the length or season of rests from grazing or to the grazing animal. Thus, we took a simple view of grazing. However, grazing also reduces pasture biomass and this will modify germination opportunities and fire frequency and intensity. Grazing (G) took a binary value of 1 for none-to-light, or 2 for heavy. The effect of grazing on seedlings was modified (G_m) for interactions with fire. This reflects reduced growth and increased mortality owing to heavy grazing after weakening by fire, and increased mortality should fire occur after heavy grazing, either through chance or management; thus,

$$G_m = G + (F_{t-1} + F_t) \times (G - 1),$$

where F_{t-1} is fire in the previous year and F_t is fire in the current year.

Fire

We included fires in the current model, because although rare in today’s agricultural landscapes of southern Australia, historically they would have played an important role in the dynamics of temperate woodlands and they can potentially modify the likelihoods of sapling establishment through a variety of processes. The probability of wildfire was modelled as a function of fuel load and summer rainfall. Fuel was lagged from pasture growth by summing the present- and past-year biomass. We assumed that fires occur in warmer months, December–March, and that germination always occurs in following months in the next model year. Wildfires may occur earlier in the season and management fires occur later. We note that spring fires are proposed for controlling nitrophilous weeds (Prober *et al.* 2004), but we did not examine that case here. Wildfires were modelled in long simulation runs; however, for short runs, wildfire was precluded because fire suppression is pervasive in the region.

Interactive effects of drought and fire were modelled to account for seedlings being more drought-sensitive in the year following burning, by subtracting 1 from the summer rain level if there was a fire in the previous year, i.e.

$$\text{if } S_r < 2, \text{ then } S_{r,m} = S_r - F_{t-1}, \text{ else } S_{r,m} = S_r,$$

where $S_{r,m}$ is the modified summer rain and F_{t-1} is fire in previous year (0,1).

Simulations—effect of fire frequency over long model runs

Various annual fire probabilities were examined in long-run simulations. For each fire probability, 10 replications of nine combinations of summer- and winter-rainfall probabilities for 500-year simulations were run. Results were presented as the number of years with particular stages (germinants, small seedlings, large seedlings, saplings) present across a range of fire probabilities.

Planned fire in short model runs

First, we considered the case of a planned fire. The motivation was that it removes biomass and increases bare space, thereby improving chances of germination and reducing competitive effects. To investigate the effect of single fires, we ran the model for short periods, starting with a fire and then reducing the probability of fire so that there would be no subsequent fires, and tallied whether saplings escaped. We ran the model for 3 years, the shortest period in which saplings could escape or, in 5-year runs to account for slower progress from germinant to sapling. We only present the 5-year runs, as they were generally similar to the 3-year runs, except that they had more saplings escaping. We used 100 replicate runs and tracked the number of runs that resulted in saplings. We considered low- and high-productivity pastures, and average, as well as reduced and increased effect of rainfall for each

winter and summer, resulting in 18 rainfall–pasture combinations. We also varied seed supply, but kept grazing light.

Short model runs starting with seedlings

Next, we considered the case where seedlings were known to be present at some sites, but not at others. Some of the sites without seedlings might appear otherwise to be good prospects for natural regeneration. How should a manager decide which sites to invest in? We ran the model for 100×4 -year runs (and with increased and reduced effect of seasonal rainfall as above), starting with 1-year-old seedlings or without seedlings. A run of 4 years with seedlings was considered equivalent to a 5-year run without seedlings.

Pasture biomass manipulation

Many management activities are aimed at removing or reducing herbaceous competition, e.g. scalping, burning, herbicide application and crash grazing. We examined the effects of reducing herbaceous competition, in the absence of disturbance to soil structure, on the likelihood of germination, growth and survival of seedlings. We considered the effects of one-off or multiple pasture reductions on the likelihood of sapling escape in 100×3 -year runs in the absence of grazing. Both seed supply and rainfall were varied, as above.

A role for heavy grazing?

The standard model does not allow saplings under sustained heavy grazing. However, short periods of heavy grazing may have a role for reducing biomass before or after seedlings have established, either to increase the number of seedlings from subsequent germination events or to reduce the competitive effects of pasture biomass. Here, we ran the model for 6-year periods, with different sequences of heavy and light grazing years in high-productivity pasture. For each sequence, we ran the model 100 times, with varying rain and varying seed supply, as above.

Data presentation

Results were displayed as boxplots of the frequency of germination events, and presence of seedlings or saplings in simulations. Boxes and whiskers present the median and quartiles. Outlying (circles) and extreme values (asterisks) correspond to cases 1.5–3 and >3 times the interquartile range from the upper or lower edge of the interquartile range, respectively.

Results

General behaviour in long simulation runs

Increasing probability of fire (represented by the parameter $Pr(\text{fire})$ scaled from -5 to $+5$) increased the frequency of years with fires (Fig. 2). The effects of fire on germination, seedling survival and transition from a seedling to a sapling varied depending on grazing intensity and pasture productivity (Fig. 3).

Germination

With substantial (medium) seed supply, germination was consistently high under heavy grazing and fire had no effect because low pasture did not limit germination, and reducing biomass was the primary effect of fire on germination (Fig. 3a). Under light grazing at high probability of fire, fire events cleared biomass, thus increasing germination opportunities, although this effect was weak.

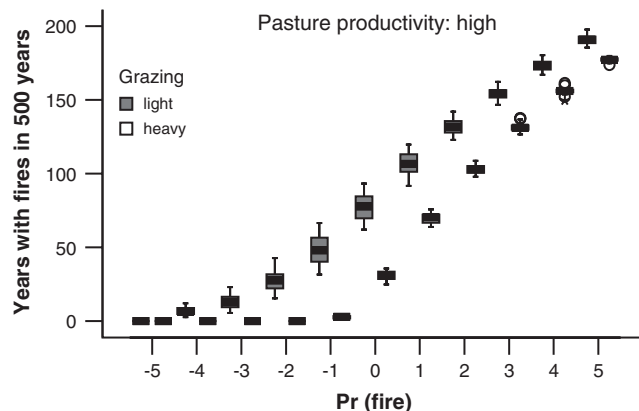


Fig. 2. Relationship between fire frequency, in runs of 500 years, and the model parameter $Pr(\text{fire})$, which represents the probability of fire, but scaled from -5 to $+5$. Fire frequency is greater under light grazing because of greater fuel build up. Boxes and whiskers present the median and quartiles. Heavy-grazing boxes are to the right of each pair. Circles are 1.5–3 times the interquartile range and asterisks correspond to extreme values >3 times the interquartile range.

Seedling establishment

Under light grazing, effects of improved germination from higher fire frequency persisted. Further, early seedling survival was improved after fires because the competitive effect of pasture was reduced. This resulted in more years with seedling establishment (Fig. 3b).

In general, seedling establishment (surviving their first year) occurred in fewer years under heavy grazing than under light grazing (Fig. 3b). Heavy grazing negated the competitive effect of pasture but reduced seedling establishment through direct mortality. Further, the interaction of fire and grazing reduced establishment when burnt seedlings were heavily grazed (and when grazing-stressed seedlings were burnt) and as a result, increased fire frequency under heavy grazing marginally reduced the frequency of seedling establishment (Fig. 3b).

Seedling survival

Small seedlings could persist over multiple years (compare scales for new seedlings and years with seedlings) but could not withstand sustained heavy grazing pressure. Under light grazing, the increased frequency of establishment with increased fire frequency was negated by increased mortality from fires, resulting in little systematic variation in the number of years with seedlings (Fig. 3c).

Sapling escape

Across a wide range of fire frequencies, fire that was more frequent led to fewer sapling years in both low- and high-productivity pastures (Fig. 3d). At low fire frequency, saplings escaped more often in a low-productivity pasture, largely because of poor germination conditions and competitive suppression in a high-productivity pasture.

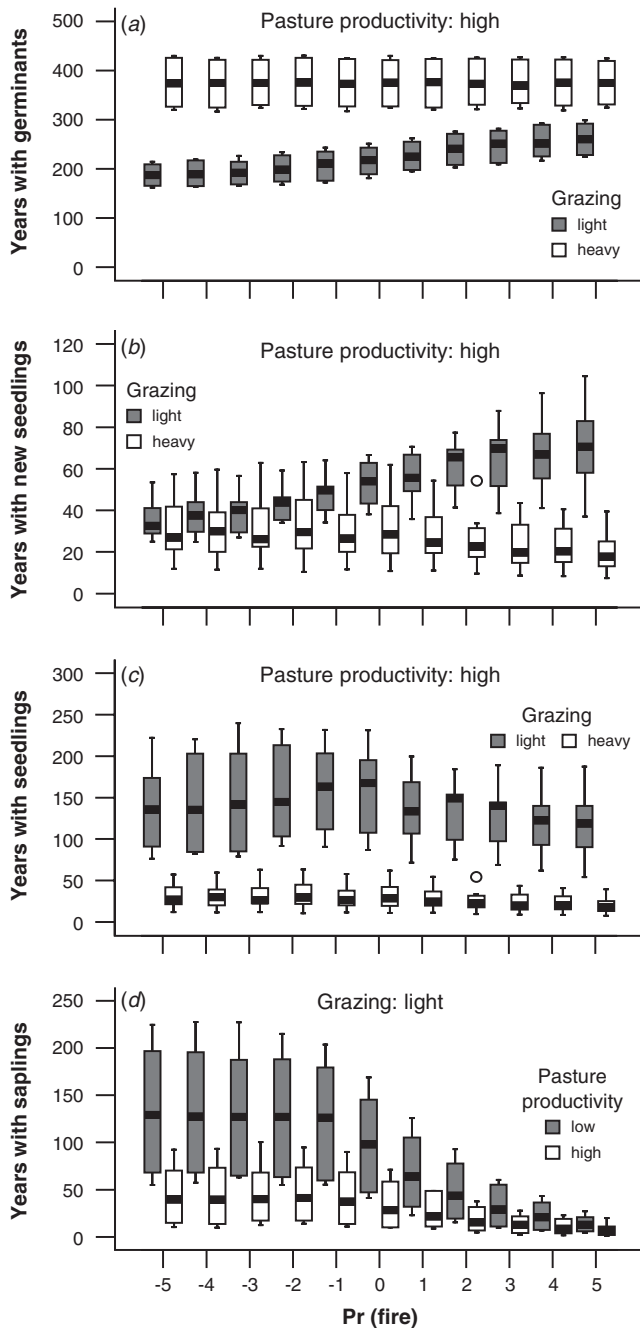


Fig. 3. The effect of fire risk on years with (a) germinants, (b) new and (c) persisting seedlings, and (d) saplings. The model parameter $Pr(\text{fire})$ represents the probability of fire, but scaled from -5 to $+5$. Simulation runs were 500 years. Grazing is light in (d) as saplings never escape under sustained heavy grazing. At low fire risk, productive pasture can achieve high biomass and so reduce germination and suppress seedling growth compared with low-productivity pasture, in turn reducing the number of sapling-escape events. Boxes and whiskers present the median and quartiles. Circles are 1.5–3 times the interquartile range and asterisks correspond to extreme values >3 times the interquartile range.

As fires became more frequent, the differences owing to pasture productivity declined (Fig. 3d).

Management scenarios in short model runs—planned fire

With or without planned fire, the frequency of sapling escape was higher in low-productivity pastures (Fig. 4). Planned fires led to very slight increases in the frequency of sapling escape, but only in high-productivity pasture, in which case the proportion of runs producing saplings was still quite low (Fig. 4). In both low- and high-productivity pasture, seed supply had the greatest influence on the number of runs producing saplings, regardless of fire. The variation around these estimates is high and rainfall events could negate the effect of seed fall and also negate any improvements to germination resulting from fire.

Starting with seedlings

There was a substantially greater chance of getting saplings if one started with abundant seedlings (Fig. 5). However, if there was consistent, heavy seed supply then this improvement was reduced, particularly in a low-productivity pasture. This was because both germination from seed and seedling survival are higher in low-biomass pastures (see no-seedlings case, Fig. 5). If seed supply was high, variation in rainfall could negate the gains owing to starting with seedlings in a low-biomass pasture. In a high-biomass pasture, variation in rainfall had less effect, particularly when seedlings were abundant.

As the time horizon was extended, so that we were not just counting the occasions where saplings escaped at 5 years, but in 6, 7, 8, ... years, then the probability that seedlings would arise at some time increased and the benefit of starting with seedlings was reduced. Longer periods also reduced the differences between low- and high-productivity pastures as the suppression of seedling growth by high-productivity pasture was reduced over the longer term.

Pasture biomass manipulation

Clearing pasture in the initial year increased the chances of subsequent sapling escape (Fig. 6). In subsequent years, low biomass aided growth; however, the first year was critical. Low biomass was more influential earlier in the run and in seedlings' life (HNN cf. NHH, Fig. 6). Complete clearance of vegetation was no better than keeping biomass low for producing saplings, but both were substantially more likely to yield saplings than was high-biomass pasture (Fig. 6). Runs NLH and NHH, which differed only in reduced biomass in the second year, might reflect a residual effect of treatment in Year 1 (Fig. 6). Suppression by pasture diminished as seedlings became larger and more established. Seed supply had a large effect, indicating the high rate of attrition of seedlings through time. All else being equal, a bumper seed crop improved the chances of getting saplings. However, rainfall variability could overwhelm the seed-supply effect; a moderate seed supply in moderate rainfall conditions could have greater

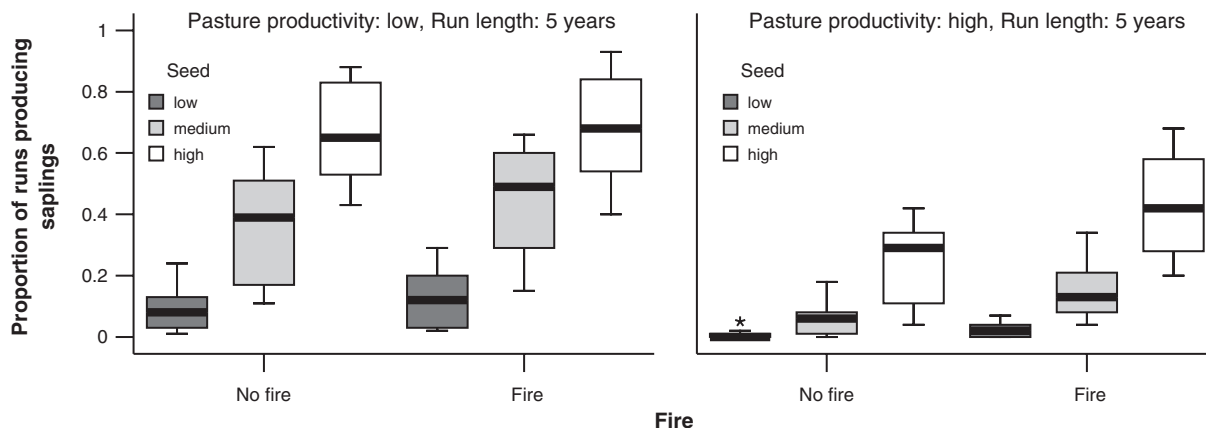


Fig. 4. The influence of a single fire on the chance of saplings escaping in the subsequent 5 years in low- (left panel) and high-productivity (right panel) pasture. Boxes and whiskers present the median and quartiles. Circles are 1.5–3 times the interquartile range and asterisks correspond to extreme values >3 times the interquartile range.

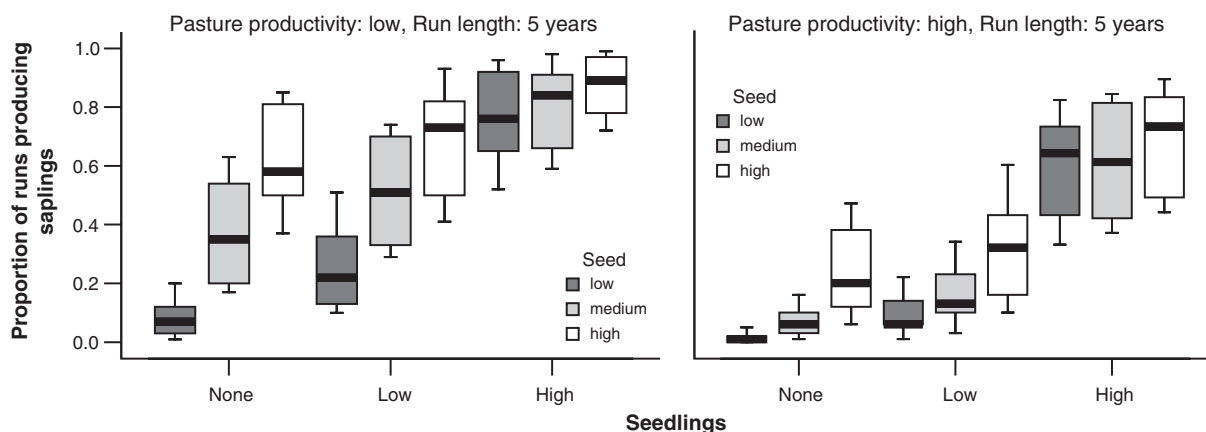


Fig. 5. The influence of starting a run with seedlings on the chance of saplings escaping in subsequent 5 years in low- (left panel) and high-productivity (right panel) pasture.

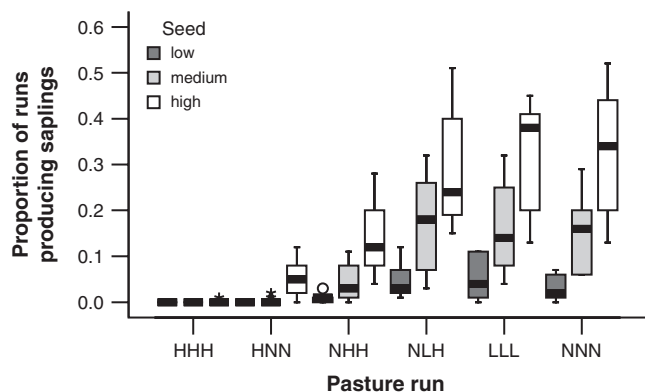


Fig. 6. Influence of pasture on the chance of saplings escaping at the end of 3 years under light grazing. Letters on pasture-run axis represent biomass levels in each of three subsequent years: N, none; L, low; H, high. Boxes and whiskers present the median and quartiles. Circles are 1.5–3 times the interquartile range and asterisks correspond to extreme values >3 times the interquartile range.

probability of producing saplings than a heavy seed supply in dry conditions.

A role for heavy grazing?

Grazing management was more important and effective in a high-productivity than in a low-productivity pasture because high-productivity pasture was a more hostile environment for the seedlings. As a result, simply resting from grazing for 6 years was not the best strategy in a high-productivity pasture; grazing for 1 year then resting for 5 years was better (compare HLLLLL and LLLLLL, Fig. 7), whether or not seedlings were already present. Blocking years of rest from grazing was important, whereas alternating years of heavy grazing and rest did not help because seedlings never had enough time to escape, even if they persisted in a suppressed condition. At least 2 years without grazing were needed and the benefits increased with time rested (Fig. 7).

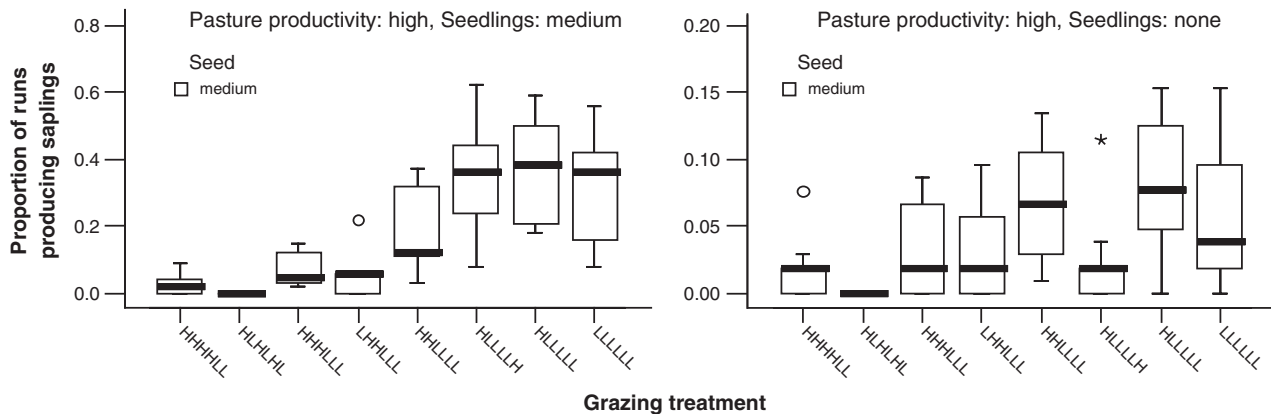


Fig. 7. Influence of grazing management on chances of getting saplings in 6-year runs in high-productivity pasture with either medium or no seedlings in the first year. Boxes and whiskers present the median and quartiles. Circles are 1.5–3 times the interquartile range and asterisks correspond to extreme values >3 times the interquartile range.

In general, if no seedlings were present, saplings were more likely to arise when grazing occurred early in the sequence of years followed by rest from grazing for the subsequent ≥ 3 years (see treatments HLLLLL, HHLLLL and HHHLLL, Fig. 7). This reflects the importance of competition early in the regeneration process. If seedlings were present, the importance of grazing early was diminished (but not extinguished), because the benefit of controlling competition was negated by the cost of grazing mortality.

Discussion

Our simulations suggest that site conditions and management can influence the success of sapling regeneration in pastures. However, three sources of uncertainty can overwhelm their effects, including variability in rainfall, uncertainty about the influence of rainfall amount and timing on stage transitions, and variability in seed supply. Regeneration will occur, given adequate seed supply, a suitable germination site, suitable soil moisture for germination and survival through summers, and freedom from pathogen attack, herbivory, competition, fire and other setbacks. Our model indicates that these conditions are rarely coordinated. Regeneration can fail in many ways and only some of these are controllable by management (e.g. grazing, pasture biomass, fire). Our results demonstrate that variation in seed supply and rainfall, particularly the likelihood of adequate summer rains, as well as uncertainty in its effects, make it difficult to decide whether, where, when and how to invest in natural regeneration. Without better understanding of these uncertainties, there is little chance that policies aimed at encouraging regeneration will be widely adopted, and if they are, failure rates may be unacceptably high.

The long-run simulations clearly demonstrated that frequent fire or heavy grazing, despite increasing the number of germinants, particularly in a high-productivity pasture, reduced the frequency of sapling escape. This is

because, although seedlings can resprout after fire (and heavy grazing), there is a limit to resprouting after multiple disturbances (Leigh and Holgate 1979; Noble 1984), and this overwhelms any advantage of fire or grazing through increased germination. This result accords with demographic bottleneck models of tree-grass coexistence in savannas (Sankaran *et al.* 2004) and the dearth of regeneration observed in grazed temperate grassy woodlands (Pettit *et al.* 1998; Gibbons and Boak 2002; Dorrrough and Moxham 2005).

Management options

Despite the long-run disadvantage, the shorter simulation runs suggest that appropriately timed grazing and fire can improve the chances of sapling establishment. Although climate is apparently the over-riding factor in determining the likelihood of germination and seedling escape, management can be used to manipulate these likelihoods. In any particular situation—that is, given the rainfall and the seed fall for a year—fire or other pasture manipulation does improve the chances of sapling establishment. In addition, the improvement because of burning or grazing is better under some conditions than in others, e.g. high seed fall on a high-productivity pasture with high winter and summer rainfall.

One indication from these simulation experiments is that, in general, low-productivity pastures offer potentially better outcomes for natural regeneration. However obvious this seems in hindsight, it is not a direct consequence of our assumptions. We assumed that pasture productivity determined the maximum achievable biomass and the biomass growth rate. The biomass can be controlled by management, but this presumably comes at a cost. Furthermore, complete clearance of vegetation is no better than keeping biomass low, at increasing the frequency of saplings, whereas both are better than a high-productivity pasture. This means that native pastures may not need to

be treated to reduce biomass, and short periods of grazing seem sufficient. However, in an exotic pasture supporting high biomass, activities to reduce the biomass would be beneficial.

Once seedlings have established (i.e. survived their first year), high biomass principally reduces the growth rate, hence delaying sapling escape—pasture has less effect on mortality. Thus, managing biomass before seedling establishment appears most critical. This was also borne out by our short simulation runs applying annual grazing management. These suggested that heavy grazing followed by rest would have better outcomes than complete rest from grazing. This result supports field studies where seedlings do not necessarily recruit after grazing exclusion, particularly where soil nutrients are high and understorey vegetation is dominated by exotic vegetation (Yates *et al.* 1994b; Pettit and Froend 2000; Spooner *et al.* 2002).

If there is no native pasture component, then there seems little reason not to use intense methods, such as scalping or herbicide, if these have greater residual effect to reduce pasture cover. That is, if they keep down the pasture for more years then there is a greater chance of seedlings establishing in one of those years. If there is a native perennial pasture component, then grazing management may be preferable. For instance, animals could be grazed for a short time, closely monitored and removed at the first sign of seedling damage. The assumption here, seemingly borne out by actual practice, is that pasture species are preferred to the tree seedlings and it is not until the supply of desirable leaf material declines that grazers turn their attention to the seedlings, although this may vary seasonally (Semple and Koen 2001).

Results of the model also can be interpreted as applying to direct seeding, when we assume pasture clearance and heavy seed supply. Most direct seeding efforts are accompanied by some form of pre-seeding herbicide application, often with soil cultivation and often followed by post-emergence weed control through herbicides or short-term grazing (Schirmer and Field 2000). In the modelled cases most like direct seeding, saplings establish relatively frequently, with variation still owing to rainfall.

Limits to management

Although management can improve chances of regeneration, the variation around the expectations is high, thus rendering management prioritisation and allocation difficult and risky. This is because, first, rainfall is patchy in space and time and managers rarely have the opportunity to choose between years for investment even if they had some idea of the likelihoods of wet years. Second, understanding of how rainfall affects germination and seedling survival is still crude. Third, seed supply is variable in space and through time and we have little ability to predict it.

Rainfall variability can overwhelm the seed-supply effect; a moderate seed supply in moderate rainfall conditions can have greater probability of producing saplings than a heavy

seed supply in dry conditions. This fits with the idea that seedling survival through drought is a bottleneck that is unrelated to seed supply *as long as* the number of germinants exceeds the number of safe sites through drought (Andersen 1989).

Improvements in seasonal-rainfall forecasting (6–12-month periods) should serve to reduce some, but not all, of the uncertainty around predictions of regeneration outcomes. Rainfall forecasting will not help with our uncertainty about the *effect* of rainfall. For this, more data on seedling germination, establishment and survival in response to different rainfall conditions are required.

In this study, we did not model variation in seed supply; instead we controlled it manually. We know that it varies substantially, and it has large effect on regeneration; however, we were not confident that our understanding was sufficient to model it appropriately. Thus, we need better data on seed supply as affected by seed rain and seed predation. Seed predation has been argued to be effectively unimportant to recruitment in stable populations of long-lived perennials in natural conditions (Wellington and Noble 1985b; Andersen 1989). This is because most seedlings die and recruitment needs to occur only a few times in the average lifespan. However, in sparsely treed woodlands, where there is room for increase in the tree population, safe sites would be more frequent. Filling those safe sites with potential recruits is important and seed predation may possibly reduce this potential.

Management and investment implications

The uncertainty, primarily owing to climate, means that investment in natural regeneration is risky. However, some general recommendations can be made. First, investment in locations with low-productivity pasture and already supporting seedlings are most likely to result in saplings in the long term. Second, because of the uncertainty, contracts for longer periods will be more likely to be successful. Presumably, there would be an optimal period because longer periods devoted to ‘natural regeneration service’ carry an opportunity cost of forgone livestock production.

This study has utilised simple rule-based modelling and has proved useful for conceptualising the system and identifying some key drivers and sources of uncertainty. However, for the purpose of supporting risk-based investment decisions, approaches are required that better account for uncertainty, incorporate quantitative data collected from a range of sources and at a range of scales, and provide probabilistic estimates of sapling escape. Another extension to this work is to consider state-dependent management, i.e. how should a manager act, given the current state of the system (McCarthy *et al.* 2001). This would enable identification of optimal and robust management strategies.

For natural regeneration to achieve its potential for revegetating agricultural landscapes, substantial

improvements are needed in understanding how to manage, the limits to management and the associated risks. This study has made some steps towards this goal by articulating the process of regeneration and examining the relative effects of different drivers and transitions on the process. Further work would benefit from the application of risk management analytical frameworks and better data on the role of variability in rainfall and seed supply.

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