

Burning grevilleas, ants, rats and wallabies

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ABSTRACT

Many *Grevillea* spp. in eastern Australia are killed by fire and rely on germination from a soil seedbank to re-establish populations after fire. The magnitude and build-up of this soil seedbank will strongly influence post-fire recovery levels.

Seed predation by native rats and swamp wallabies significantly reduces the size of the soil seedbank in grevilleas. In species where fecundity is low and adults are short-lived, this may severely affect the ability of the species to persist at a site. In such cases, specific management actions are needed to allow fire-free intervals of sufficient length to maximize the magnitude of the soil seedbank. In addition, burns should not be very small in area or seed predation will not be reduced post-fire.

Two ecologically functional seed dispersal syndromes are found in grevilleas in the Sydney region. Species whose seeds lack an elaiosome are not moved by ants. Species that possess an elaiosome are moved by ants. Large ant species that take seeds to nests may be functioning as agents that reduce the impact of seed predators. The importance of such ants depends on a more detailed understanding of the interaction between fire and mammalian seed predator abundance and the fate of seeds moved by ants.

INTRODUCTION

The length of the interval between fires is critical in determining the post-fire abundance of fire-sensitive species. For such species, fires eliminate above-ground plants and the level of recovery depends largely on the magnitude of the soil or canopy seedbank. The length of the fire interval will influence the time seedlings have to mature and replenish the seedbank. The level of post-fire recovery will also be influenced by other factors such as moisture availability, influencing early

seedling survival (Bradstock and Bedward 1992) and soil heating controlling post-fire germination in legumes and some other groups (Auld and O'Connell 1991; Auld, Bradstock and Keith unpubl.). However, an understanding of the rate of build-up and magnitude of the seedbank in fire-sensitive species is essential for predicting their response to fires of varying frequency.

Grevillea is a widespread genus in Australia (McGillvray 1993). In the Sydney region of eastern Australia, many *Grevillea* spp. occur in fire-prone communities and are killed by fire, relying on germination from a soil seedbank for post-fire recovery. For such species, fire management should rely on ensuring fire intervals are long enough for seedlings to reach maturity (primary juvenile period, Benson 1985) and a subsequent period for the seedbank in the soil to build-up (Bradstock and Auld 1987). However, no quantitative data on the nature of the soil seedbank in grevilleas exists and it is difficult to accurately predict appropriate fire frequencies for grevilleas. The magnitude and post-fire build-up of a soil seedbank in *Grevillea* spp. will be governed by a range of demographic factors: the primary juvenile period; fecundity; seedling and adult survivorship; predispersal seed predation; seed viability; post-dispersal seed predation; and the dynamics of the soil seedbank itself.

This paper discusses the role that seed dispersal agents and post-dispersal seed predators play in influencing the post-fire build-up and magnitude of soil seedbanks and how this role may be influenced by fire management.

FUNCTIONAL SEED TYPES IN GREVILLEA

Two distinct seed types exist in *Grevillea* spp. in the Sydney region. Most species, for example, the widespread *G. buxifolia*, *G. linearifolia* and *G. speciosa*, are myrmecochorous, having seeds with an attached lipid body or elaiosome (Fig. 1). Such seeds attract a range of ant species which commonly move seeds from many plant species in the Sydney region (Rice and Westoby 1981). Ants either remove the elaiosome in pieces *in situ* or, if the ants are large enough, they will

try and drag the seeds towards nest entrances and the elaiosome may be removed in the nest (Hughes and Westoby 1992). A few *Grevillea* spp. lack this lipid body (Fig. 2) and seeds are not attractive to ants and have no obvious dispersal mechanisms. These species have toothbrush-type flowers and many are rare or have restricted distributions, e.g. *G. caleyi* and *G. longifolia*.

DISPERSAL AND SEED PREDATION IN GREVILLEA

Seeds Lacking an Elaiosome

Seeds lacking an elaiosome are not moved by ants (Auld *et al.* 1993). However, some 82-94 per cent of seeds are consumed on the soil surface by native mammals (bush rats, *Rattus fuscipes* and swamp wallabies, *Wallabia bicolor*, Figs 3a, 4a)(Auld *et al.* 1993). If these mammals are excluded, some seeds are consumed, presumably by insects, although most seeds escape seed predation.

Seeds with an Elaiosome

Two types of seed interaction with ants occur. Small ants such as *Iridomyrmex* and *Pheidole* may move seeds small distances (up to 20 cm), but such ants usually remove pieces of the elaiosome *in situ*. These ants are small compared with the size of grevillea seeds and seeds can only be moved when several ants work together. This is the most common type of ant/seed interaction. Alternatively, large solitary ants such as *Aphaenogaster* and *Rhytidoponera* may be able to drag seeds towards nests (Fig. 3b). Some seeds are discarded *en route* while some presumably are taken into nests, *c.f.* movement of legume seeds by ants (Auld 1986; Hughes and Westoby 1992). The fate of such seeds is unknown, but it is assumed that the elaiosome is removed in the nest and the seed discarded either in the nest or on the surface near the nest (Auld 1986; Hughes and Westoby 1992). At the same time, native rats and wallabies also eat seeds on the soil surface (Figs 3b, 4b) and a small amount of seeds are lost to insect predators (Auld *et al.* 1993).

The proportion of seeds moved away from mammalian seed predators by large ant species is difficult to estimate since the fates of seeds in nests of these ants is unknown. Seeds may be ejected from nests once the elaiosome is removed (Hughes and Westoby 1992) and they then would be subjected to mammal seed predation. Alternatively, seeds may be discarded in chambers in the soil (Auld 1986). If it is assumed that all seeds encountered by large ants escape mammalian seed predation then, up to 20 per cent of seeds may avoid mammal predation in this manner (Fig. 3b). In reality, seeds moved by large ants may be dropped prior to reaching nests, discarded on the soil surface, buried too deeply for subsequent emergence or buried in 'unsafe sites'. A study of the fates of seeds moved by ants is needed to quantify the proportion of seeds that

may escape seed predation by being moved by ants.

MODELS OF THE REPLENISHMENT OF SOIL SEEDBANKS AFTER FIRE IN GREVILLEA

The impact of ants, rats and wallabies on the soil seedbank can be modelled using demographic data for grevilleas (Auld *et al.* 1993; Auld unpubl.). These models incorporate data on plant survival, fecundity, pre- and post-dispersal seed predation, seed viability and seed longevity in the soil. Three alternative scenarios are presented, with all models representing the number of seeds accumulating in the soil seedbank for each seedling that emerges after a fire at time zero. The residual seedbank that does not germinate after any one fire is not included.

- (1) seed predation by mammals is constant (82-94 per cent) throughout all post-fire fruiting years. This varies slightly between sites and is based on data from populations that were unburnt for 12-18 years (Auld *et al.* 1993).
- (2) no seed predation by mammals. Although escape from mammalian seed predation has not been observed in the field (Auld *et al.* 1993), this scenario allows a consideration of the impact that seed predators (scenario 1) have on the build-up of a soil seedbank after fire.
- (3) seed predation by mammals varies as the density of mammals varies post-fire. Data from Fox and McKay (1981) on changes in post-fire numbers of *Rattus fuscipes* were used to estimate likely levels of mammalian seed predation post-fire. This scenario assumes that there was no seed predation in the first 5 years after a fire and that predation increased linearly to its maximum level (82-94 per cent) 10 years after fire in response to increasing levels of *Rattus fuscipes*. Although other mammals such as *Mus musculus* and *Pseudomys novaehollandiae* may be common in the first few years post-fire in some habitats (Fox and McKay 1991), there is no evidence that these species eat seeds of *Grevillea* species and no seeds will be produced by *Grevillea* seedlings until they mature some 2-4 years after a fire. The impact of fire on population densities of *Wallabia bicolor* is currently unknown.

Under the scenario whereby mammalian seed predators are present in all post-fire years, these seed predators will have a major impact on the build-up and magnitude of the seedbank in all grevilleas. For two species with no elaiosome (*G. caleyi* and *G. longifolia*) mammals consume most of the annual seed output from plants and only a small proportion of each annual seed-crop is expected to reach the soil seedbank (Fig. 5). Differences between *G. caleyi* and *G. longifolia* reflect differences in fecundity and adult

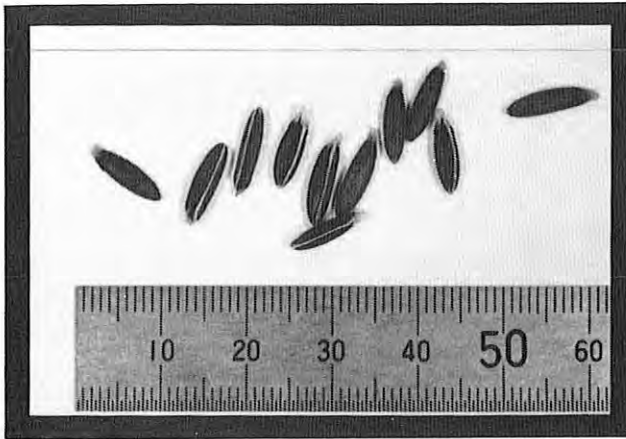
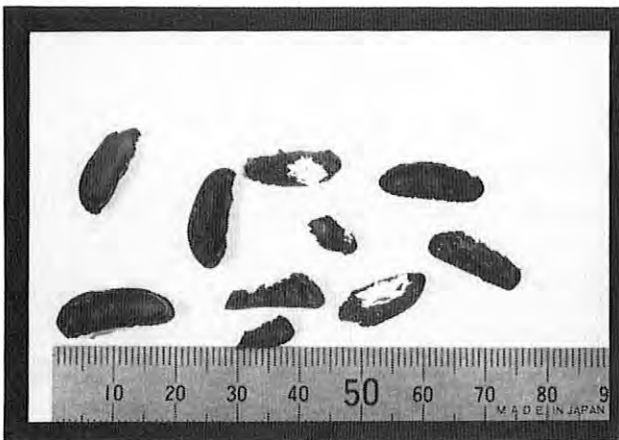


Figure 1. *Grevillea sericea* seeds showing the presence of an elaiosome.



Figure 2. *Grevillea caleyi* seeds lacking an elaiosome.



a) *Grevillea caleyi*

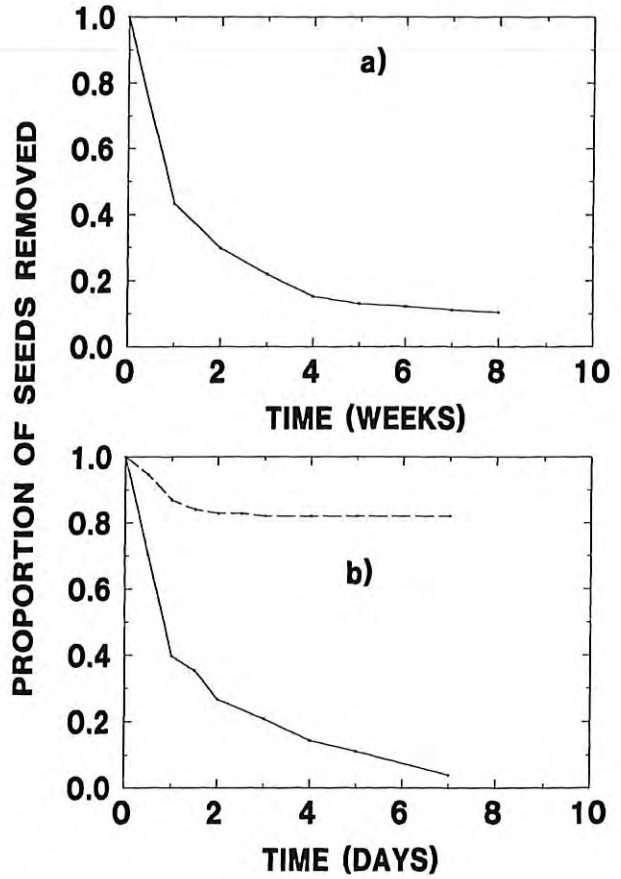


Figure 3. Seed movement and losses during dispersal in *Grevillea*.

- a) *grevilleas* whose seeds lack an elaiosome: seeds lost to native rats and swamp wallabies.
- b) *grevilleas* whose seeds have an elaiosome. — — — — — seeds moved by large ant species. — — — — — seeds moved by all ant species or lost to native rats and swamp wallabies. — — — — —



b) *Grevillea buxifolia*

Figure 4. *Grevillea* seeds eaten by bush rats *Rattus fuscipes*.

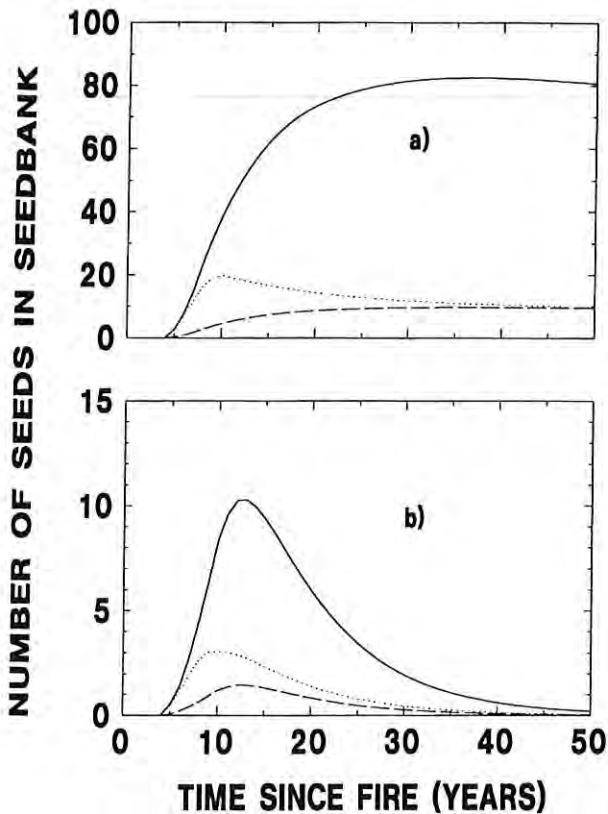


Figure 5. Soil seedbank models for grevilleas whose seeds lack an elaiosome (a) *G. longifolia* and (b) *G. caleyi*. Seedbank size represents the number of seeds added to the soil for each emerging seedling after a fire.

no mammal seed predation. —————
 mammal seed predation reduced in 0-10 years post-fire period in response to reduced mammal abundance (see text)
 constant mammal seed predation in all post-fire years. - - - - -

survivorship. Consequently, *G. longifolia* is the more resilient of the two species to mammalian seed predation. The level of seed loss to mammals in the first few fruiting seasons after fire is critical. The seedbank of *G. caleyi* is relatively small and only a small fraction may be long-lived as adult plants senesce in unburnt populations older than 10-15 years. A suitable fire interval for burning populations of this rare plant may have to include both minimum and maximum fire-free intervals. In comparison, the magnitude of the soil seedbank is increased markedly in these grevilleas if mammal seed predation is assumed to be absent in all post-fire years. A similar, but less substantial increase in the seedbank is achieved if mammal seed predation is reduced in the first few post-fire seed-crops (Fig. 5). If mammal seed predators are not reduced in the immediate post-fire environment then the soil seedbank may not be effectively replenished. In the case of *G. caleyi*, the model where mammalian seed predators are always present would predict a limited window of suitable fire-free interval in order to maintain

population size and much potential for long-term declines in future population size.

Similar patterns in the three seed predation model scenarios are found for a typical species with an elaiosome, *G. speciosa* (Fig. 6). The overall magnitude of the seedbank is greater in this species than in *G. caleyi* or *G. longifolia* as seed viability is higher, predispersal seed predation is less and there can be up to two seeds per fruit in species whose seeds have elaiosomes. If mammalian seed predation follows the predicted abundance of *Rattus fuscipes* post-fire, i.e., it is low in the first few years post-fire, then the build-up of the soil seedbank is greatly enhanced over the constant mammal predation scenario. This impact is more pronounced in *G. speciosa* than in *G. caleyi* or *G. longifolia* as *G. speciosa* seedlings mature earlier (2 years versus 3-4 years). This escape from seed predation in the first few seed-crops produced after a fire may be one method by which all *Grevillea* spp. re-establish their soil seedbanks post-fire. If mammal seed predators are not reduced in the immediate post-fire environment then the soil seedbank may not be effectively replenished.

If it is assumed that up to 20 per cent of released seeds escape seed predation by mammals through movement by large ant species, the impact of ants on the soil seedbank can be inferred. Where mammal seed predation occurs in all post-fire years (Fig. 7a), the magnitude of the seedbank is markedly increased when large ants are present. Where mammal seed predation is removed in the first few fruit crops and then gradually increases to a constant peak at 10 years post-fire (Fig. 7b), movement of seeds by ants has little effect on the magnitude and build-up of the soil seedbank. Thus, the importance of ants as agents for seed escape from mammalian seed predators will depend on the intensity of mammalian seed predation in the first 10 years post-fire. This intensity will reflect the interaction between fire and the abundance of individuals in the mammal populations themselves.

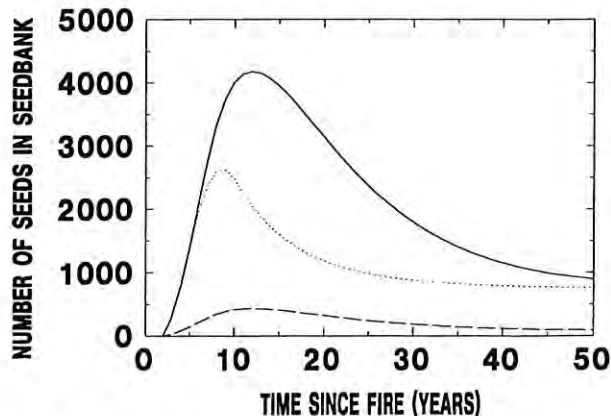


Figure 6. Soil seedbank model for a grevillea (*G. speciosa*) with elaiosomes assuming no ant movement of seeds. Seedbank size represents the number of seeds added to the soil for each emerging seedling after a fire. Lines follow Figure 5.

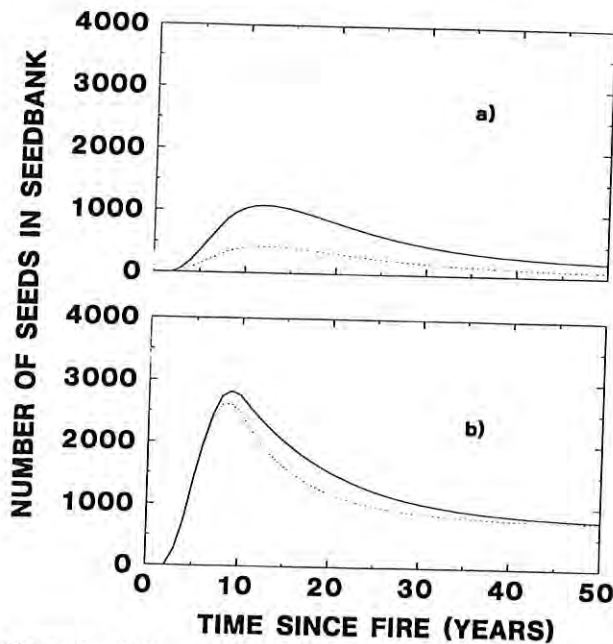


Figure 7. Soil seedbank model for a grevillea (*G. speciosa*) with elaiosomes allowing for some seed escape via movement by large ant species.

- (a) constant mammal seed predation in all post-fire years.
 large ants move some seed to safe sites; _____
 no seed movement by ants.
- (b) mammal seed predation reduced in 0-10 years post-fire period in response to reduced mammal abundance (see text).
 large ants move some seed to safe sites; _____
 no seed movement by ants.

CONCLUSIONS

Native mammals can have a major impact on the post-fire development of soil seedbanks in grevilleas. The interaction between fire and populations of the mammals, in terms of post-fire mammal abundance, has important consequences for grevilleas. This is especially true for rare, relatively short-lived species, with low fecundity. One such species is *G. caleyi* and management of this species needs to address both minimum and maximum fire-free intervals. This grevillea is restricted to several small populations in the Terry Hills areas in the northern suburbs of Sydney. Populations of this species have previously been burnt by small scale burns, 20 x 20 m and 50 x 50 m. Such burning is inappropriate for this grevillea as populations of mammalian seed predators are not reduced in the post-fire environment as they survive in the large surrounding unburnt areas. Consequently, the relationship between the size of an area burnt and post-fire mammal abundance needs further investigation.

For those grevilleas whose seeds possess elaiosomes, ants may function to reduce the impact of mammalian seed predators and hence, to increase the magnitude of

soil seedbanks. However, this remains to be clearly demonstrated. If all large ant species simply eject seeds from nests then seeds can still be consumed by mammals. Models of the soil seedbank of grevilleas with elaiosomes suggest that the movement of seeds by ants will be most important when seed predation by mammals is high in the first few seed-crops produced after a fire. If seed predation by mammals is low in this period, seed movement by ants is relatively unimportant to the build-up of a soil seedbank.

For all grevilleas, the level of recruitment after a fire will be largely influenced by the interaction between fire and mammalian seed predators, while ants may also play a role where seeds possess an elaiosome.

ACKNOWLEDGEMENTS

Thanks to Andrew Denham, Rachael Thomas and Maria Matthes for help in collecting data used in models in this paper.

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