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Original article

Temperature thresholds for germination and survival of *Pittosporum undulatum*: implications for management by fire[☆]

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ABSTRACT

One consequence of human-induced changes in fire regimes has been the invasion of fire-prone Mediterranean ecosystems by weeds from more mesic habitats. In southern Australia, the tree *Pittosporum undulatum* Vent. has established in new areas, causing a serious reduction in floristic and structural diversity. *Pittosporum undulatum* has a high competitive ability and creates an environment that favours its own progeny at the expense of other species, making control difficult. We tested the hypothesis that fire effectively disrupts this invasion cycle by (1) eliminating the soil and canopy seed bank, (2) reducing the competitive ability of adults, and (3) minimising the number of sites favourable to invasion. To test this, the ability of *P. undulatum* to re-establish after a prescribed burn was estimated in a field study. The field data were then compared with the experimentally determined sensitivity of seeds and seedlings to elevated temperatures. The experimentally determined combination of temperatures and exposure time required for seed mortality (90–120 °C, depending on duration) was such that most seed stored in the canopy would be killed by prescribed burning. In addition, 90% of seedlings (ca. 0.4 m tall) were killed when heated to 180 °C for 5–10 min in the laboratory, consistent with the observed 100% seedling mortality in the burnt plots. Of the adult trees, 20% resprouted within 6 months of the fire. We conclude that the temperatures associated with wildfires are sufficient to act as a circuit breaker on the invasion cycle allowing other control measures, such as poisoning and weeding to be employed to greater effect.

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1. Introduction

Episodic fire is a key factor in maintaining diversity in most ecosystems which have a pronounced summer drought

(Grubb and Hopkins, 1986). The impact of fire has been particularly well studied in Mediterranean ecosystems on various continents (e.g. Tyler, 1995; Hanley and Fenner, 1998; Mills and Fey, 2005). Over the past 50,000 years there have been

[☆] This paper is dedicated to the late Dr David Ashton who inspired a generation of ecologists in Australia and initiated the research on *Pittosporum undulatum* in the 1970s.

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large changes in fire regimes in most of these ecosystems (Singh et al., 1981; Mooney and Hobbs, 1986). As areas have become more densely settled by humans, the frequency and intensity of fires have both increased and decreased at different times (Webb, 1998), leading to changes in structure and species composition (e.g. Bradstock et al., 1997; de las Heras et al., 2002).

Many environmental weeds of Mediterranean communities originate in mesic habitats and are often more fire sensitive, and anthropogenic suppression of fires is likely to have played a part in their invasion (Mooney and Hobbs, 1986). The rationale in managing such weeds has been to attempt to restore pre-settlement fire regimes using prescribed burning (Grubb and Hopkins, 1986). Fire is not always effective as the resulting disturbance can facilitate subsequent invasions (e.g. Singer and Burgman, 1999). Before recommending fire as a management tool it is essential, therefore, that the life-cycle processes are understood and critical limits are established.

Pittosporum undulatum is an aggressive invader of indigenous communities on three continents (Australia, North America and southern Africa) and many oceanic islands (Gleadow and Ashton, 1981; Healey et al., 1993; Ramos, 1996). The seed is not readily distributed over long distances but it has been introduced to regions beyond its traditional range even within Australia, bringing it into proximity to previously uncolonised areas (Gleadow and Ashton, 1981; Mullet and Simmons, 1995). Interestingly, it is also increasing in density in areas where it is undoubtedly indigenous, such as forest remnants in suburban Sydney (Rose and Fairweather, 1997) and where it should not necessarily be regarded as a problem (Howell, 2003).

The invasive capacity of *P. undulatum* is determined by its high competitive ability, its seed dispersal into favourable sites by avian vectors and the higher survival of *P. undulatum*

seedlings under its own canopy relative to seedlings of other trees species (Fig. 1; Gleadow and Ashton, 1981; Gleadow, 1982; Gleadow and Rowan, 1982; Gleadow et al., 1983; Kentish et al., 1995; Goodland and Healey, 1997). Moreover, the presence of existing trees increases the likelihood of more *P. undulatum* becoming established in the area, reinforcing the cycle of invasion (Fig. 1). Once a population has become established, the various canopies begin to coalesce, and ultimately almost all the original species are suppressed (Gleadow and Ashton, 1981; Mullet and Simmons, 1995). *P. undulatum* is unusual in that it does not store seed in the soil from year to year (Gleadow and Ashton, 1981; Gleadow, 1982).

Fire has frequently been advocated as a method of control (e.g. Gleadow and Ashton, 1981). The ability of seeds to survive fire depends on the heat sensitivity of seeds, the depth of burial and the degree of penetration of heat through the substratum (Auld et al., 2000). It is not clear, however, what temperatures are required to prevent re-establishment from existing seed stocks nor has it been established how fire could be effective in halting the invasion, given the proximity of seed producing adults in neighbouring areas. Moreover, the total heat required to kill seedlings (i.e. temperature coupled with the duration of exposure) has never been determined experimentally.

In this paper we hypothesise that fire effectively disrupts the invasion cycle by (1) eliminating the canopy seed bank, (2) reducing the competitive ability of adults, and (3) minimising the number of sites favourable to invasion. To test this hypothesis, a field study was conducted to estimate the ability of *P. undulatum* to resprout or germinate after a prescribed burn. In addition, we determined the sensitivity of seeds and seedlings to heat by exposing them to elevated temperatures in the laboratory for different lengths of time.

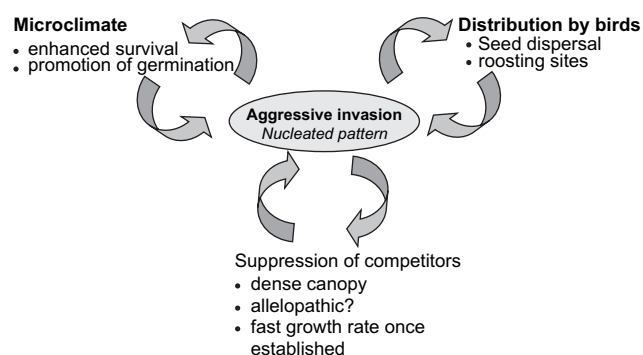


Fig. 1 – Invasion cycle of *Pittosporum undulatum*. Seeds are initially delivered by birds (predominantly) to sites favourable for germination and establishment, such as at the base of existing trees. The invading plants quickly establish a dense canopy suitable for roosting by avian vectors, and creating a microclimate that further enhances *P. undulatum* seedling recruitment and survival. Also growth by other, potential competitor, plants is inhibited reinforcing the initial invasion pattern. The result is a nucleated pattern of invasion such that, over time, the canopies coalesce and dominate the vegetation (Gleadow, 1980).

2. Materials and methods

2.1. Field studies

Woods Reserve is situated on the Mornington Peninsula, approximately 70 km SSE of Melbourne, Victoria, Australia. The reserve contains extensive stands of mixed eucalypt woodland (*Eucalyptus obliqua* L'Herit., *E. radiata* Sieber ex DC., and *E. viminalis* var. *racemosa* F.Muell. ex Blakely) and is considered to be of high regional significance for conservation (Bedggood et al., 1989). Average precipitation for the area is 743 mm, with most rain falling between May and October (Australian Bureau of Meteorology Station 86079). Mean maximum temperatures are approximately 24 °C and 13 °C for summer and winter, respectively. The area was previously burnt more than 30 years before the present study (Bedggood et al., 1989). All *P. undulatum* plants at the site have arrived since the last fire.

A proposal to burn an area of woodland was initiated by the local municipal authority with the express aim of controlling *Pittosporum undulatum*. Approximately 3.5 ha of the 48 ha reserve was burnt on 15 March 1993. Air temperature was approximately 20 °C, 5.2 mm of rain had fallen in the previous 2 weeks and wind strength was light to moderate (approx. 10–15 km h⁻¹, Bureau of Meteorology Station 86079,

Mornington). As a safety requirement, the fire was contained within defined fire breaks. Soil surface temperature was measured in ten random locations in the area designated for burning (see below), using ceramic tiles marked with temperature sensitive crayons (Thermochrom, Faber-Castell; Hobbs et al., 1984) with temperature ranges from 60 to 400 °C.

In order to randomly select *P. undulatum* of various ages and sizes, ten quadrats (10 × 1 m) were established *a priori* across the area to be burnt. The locations of these quadrats were chosen by generating random co-ordinates and were 70–150 m apart. In addition, a 50 m transect (1 m wide) was taken *a priori* across the area, oriented in order to intersect trees and seedlings of different heights. Age, height and diameter are highly correlated in *P. undulatum* (Gleadow, 1982). Existing *P. undulatum* were monitored for 6 months in both the quadrats and along the transect. In addition, the number of seedlings that emerged following the fire in the ten quadrats was recorded and compared with a set of 10 reference quadrats, randomly located in an adjacent, large unburnt area (ca. 4 ha) on the other side of the fire break.

In order to establish that burnt and unburnt areas were comparable, quadrats were surveyed before the fire. All species were identified in each quadrat (presence/absence) and compared using ANOSIM, a non-parametric analysis of similarity based on rank order of Bray-Curtis values. This is a robust method for comparing taxonomic composition, with values over 0.4 indicating highly concordant, or similar, taxonomic similarity (Faith et al., 1987; Clarke, 1993). In addition, the number of individual *P. undulatum* was determined and the degree of cover afforded by the canopy estimated. Burnt and unburnt quadrats were found to support similar number and diversity of plants with a high taxonomic similarity (ANOSIM = 0.42; Clarke, 1993). Importantly, the two areas had a similar density and canopy cover of *P. undulatum*, with a canopy cover for the whole 48 ha site of about 20%.

2.2. Laboratory studies

Pittosporum undulatum seeds were placed in foil cups and heated in ovens at six temperatures between 30 and 120 °C for 1, 3, 5 or 10 min (Auld and O'Connell, 1991). Each treatment contained four replicates, each of 30 seeds (120 seeds, $n = 4$). Germination capacity was tested by incubating seeds on moist filter paper in the dark at 24.4 ± 1.2 °C for 2 months (Gleadow, 1982). Exact oven temperatures, measured every 10 min using a copper-constantin thermocouple, were (mean \pm SD) 32.1 ± 1.9 , 41.9 ± 0.3 , 49.6 ± 1.7 , 64.4 ± 0.9 , 94.1 ± 2.6 and 118.8 ± 1.1 °C (see Table 3). To determine control rates of germination in unheated seeds, 16 replicates of 30 seeds were left at room temperature, and then incubated as for the treated seeds (480 seeds, $n = 16$). Germination rates of heated seeds were compared with the controls.

Seedlings of *P. undulatum* were placed individually ($n = 10$) in ovens at six temperatures between 80 and 180 °C for 5 or 10 min (Moore et al., 1977). Seedlings (2.5 years old), approximately 0.4 m tall and 0.2 m in diameter, were grown in 5 l pots containing a mixture of pine bark, peat moss and sand (1:1:1, v/v/v). After exposure, seedlings were transferred to a temperature controlled greenhouse where they were watered daily and flushed weekly with a complete liquid

inorganic fertiliser (Aquasol®, 1 g l⁻¹). Oven temperatures, measured as above, were (mean \pm SD): 83.2 ± 0.2 ; 111.1 ± 1.2 ; 134.6 ± 1.3 ; 152.2 ± 1.6 ; 167.1 ± 3.5 .

2.3. Statistics

ANOVAs were performed on arc-sine transformed laboratory germination data (temperature \times time \times block, with each block consisting of 30 seeds) using Minitab 10Xtra, and Scheffé's confidence intervals were calculated (Sokal and Rohlf, 1995). The proportion of seedlings that recovered from the different heat treatments (alive/dead: binary data) was compared using chi-squared tests for each temperature. Seedling emergence in the burnt and reference quadrats was compared using *t*-tests. Regression lines and equations were calculated using SigmaPlot 2000.

3. Results

3.1. Field studies

Standing foliage (including *P. undulatum* canopies) and surface litter in much of the 3.5 ha site were burnt, with flame height reaching approximately 20 m. Soil surface temperatures ranged from 100 to 350 °C, with an average of approximately 230 °C (Table 1). Temperatures were also measured at depth (5–10 cm), but only one site recorded a temperature over 65 °C (data not shown).

In total, the fate of 114 *P. undulatum* plants was followed in ten quadrats (10 × 1 m) and along a 50 m transect through the site. Nearly 20% of trees (i.e. plants >2 m tall) had resprouted from the base 6 months after the fire (Fig. 2). Most individuals (ca. 85%) showing signs of recovery were from areas exposed to less than 200–250 °C during the fire, as recorded with the thermal crayons (Table 1). All seedlings (<0.5 m tall) were killed by the fire but no positive correlation was detected between adult tree height and their ability to survive (Fig. 2).

Very few seedlings germinated in the burnt area in the months after the fire ($P < 0.01$; Table 2). In May, 2 months after the fire, 38 new seedlings were found in the ten quadrats surveyed in the burnt area (total area = 100 m²), compared with 359 in an equivalent ten quadrats in the adjacent reference site. By September, 6 months after the fire, there were still three times as many seedlings in the reference area, with 376 and 109 seedlings in the reference and burnt plots, respectively

Table 1 – Soil surface temperatures measured at ten randomly located sites (ca. 70–120 m apart) during the prescribed burn at Woods Reserve using Thermochrom crayons

Temperature (°C)	No. of sites
100–150	4
150–200	1
200–250	1
250–300	1
300–350	3

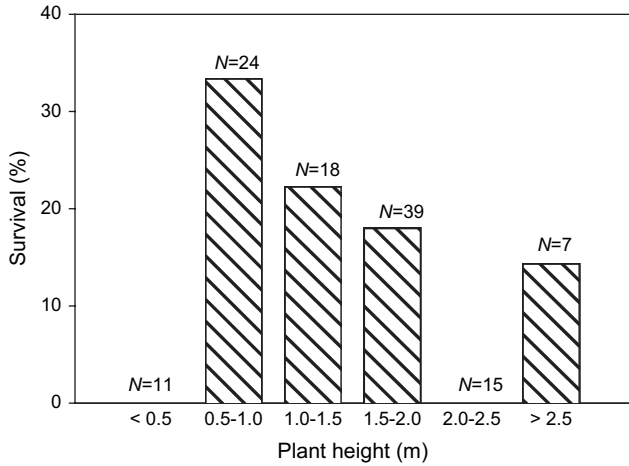


Fig. 2 – Number of *P. undulatum* plants in different height classes that survived a prescribed burn, as determined by the presence of new shoots 6 months after the fire.

(Table 2). The absolute increase in seedling number from autumn to spring was not significant, and probably represents a balance between mortality and new recruits (Table 2). There was a large variation in the number of seedlings in each plot (Table 2), consistent with the clumped pattern of invasion commonly observed in this species (e.g. Gleadow and Ashton, 1981; Gleadow, 1982). No seedlings of *P. undulatum* emerged from soil collected from the sites before the fire (data not shown), consistent with previous observations that this species does not have a soil seed bank (Gleadow, 1980, 1982).

3.2. Laboratory studies

The mean germination rate of control seeds, not exposed to elevated temperatures, was $79.6 \pm 5.8\%$ (\pm SE). Overall, germination was not significantly reduced by temperatures between 32 and 64 °C. Higher temperatures, however, significantly inhibited germination (Table 3; $P < 0.001$), especially with increased exposure time (i.e. the temperature \times exposure time interaction was significant, $P < 0.001$). At 94 °C, for example, germination was not significantly reduced with a 1 min exposure, but germination was reduced by almost half after 5 min and no seeds germinated after 10 min exposure. Seeds exposed to 118 °C only survived with the lowest exposure time (1 min).

Table 2 – Mean number of *P. undulatum* seedlings per m² (\pm SE) present in burnt and unburnt survey plots 2 months (May) and 6 months (September) after the prescribed burn (n = 10)

	Burn site	Reference site
May	3.8 \pm 2.6 ^a	35.9 \pm 10.0 ^b
September	10.9 \pm 10.5 ^a	37.6 \pm 12.9 ^b

Means with different superscripts are significantly different ($P < 0.01$) using ANOVA followed by Scheffé’s test.

Table 3 – Germination of *P. undulatum* after exposure to a range of elevated temperatures for 1–10 min

Temperature (°C)	Duration of heating (min)			
	1.0	3.0	5.0	10.0
32.1 \pm 1.9	75.0 \pm 4.0	85.8 \pm 5.0	80.0 \pm 6.5	77.5 \pm 7.6
41.9 \pm 0.3	73.3 \pm 2.4	65.8 \pm 4.2	75.0 \pm 6.2	68.3 \pm 5.2
49.6 \pm 1.7	83.3 \pm 3.6	77.5 \pm 5.2	82.5 \pm 4.4	75.8 \pm 7.4
64.4 \pm 0.9	79.2 \pm 3.7	81.7 \pm 6.5	65.0 \pm 3.5	85.0 \pm 6.5
94.1 \pm 2.6	69.2 \pm 2.8	73.3 \pm 2.4	43.3 \pm 2.9	0.0
118.8 \pm 1.1	16.7 \pm 9.9	0.0	0.0	0.0

Each germination value is the mean of four containers, each containing 30 seeds (\pm SE) (n = 4). Mean germination rate of control, unheated seeds was (\pm SE) was $79.6 \pm 5.8\%$ (n = 16). Temperature measurements are \pm SD.

The foliage of all *P. undulatum* seedlings was killed by the heat treatments. The proportion of seedlings that recovered, demonstrated by the presence of basal sprouts after 3 months, decreased with increasing temperature (Fig. 3; $P < 0.001$). Overall, 90% of seedlings exposed to 183 °C were killed, compared with 30% of those exposed to 83 °C, which is consistent with the field observations. Plants exposed to high temperatures for 10 min tended to show greater mortality at temperatures over 130 °C than those exposed for 5 min, although this was not significant ($P = 0.07$). Combining the 5 and 10 min treatments, a significant negative linear relationship was detected between temperature and survival rate ($P < 0.001$; $r^2 = 0.81$; $y = 115.1 - 0.62x$). Control plants, which had been kept at room temperature, showed no sign of die-back.

4. Discussion

Invasions by *Pittosporum undulatum* usually continue unchecked until this species becomes dominant (Gleadow and Ashton, 1981; Healey et al., 1993). The positive reinforcement

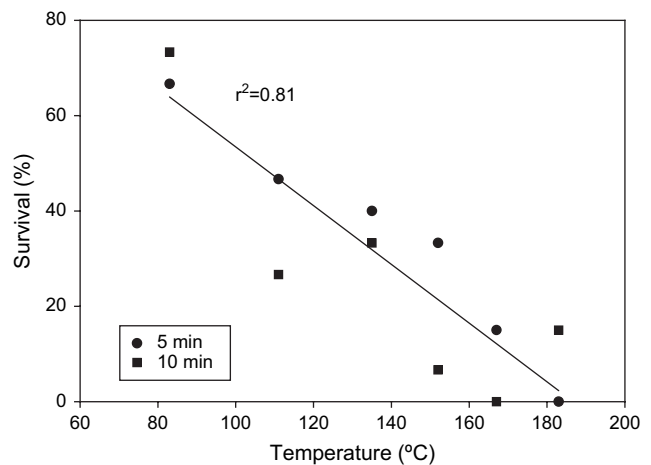


Fig. 3 – Proportion of *P. undulatum* seedlings that had resprouted 3 months after exposure to a range of temperatures for 5 min (circles) or 10 min (squares) (n = 15). The regression equation ($y = 115.06 - 0.62x$) was significant ($P < 0.001$; $r^2 = 0.81$).

inherent in the invasion cycle (see Fig. 1) makes management of this environmental weed in places such as southern Australia and Jamaica problematic (Gleadow and Ashton, 1981; Goodland and Healey, 1997). We conclude that fire, and the associated high temperatures, could disrupt this cycle at several key points. Firstly, the rate of invasion is curtailed after fire as around 80% of extant individuals are killed. Second, the competitive ability of *P. undulatum* and the suitability of the site for further invasion are reduced by the removal of the canopy. Third, the seed bank is effectively eliminated by high temperatures, as it is all held in the canopy.

Like many weeds, *Pittosporum undulatum* comes from a mesic habitat with a lower fire frequency than the open forests and woodlands that it typically invades (Melick and Ashton, 1991). In our field study, 80% of adults and all seedlings were killed in the prescribed burn, a similar proportion to that reported by Gleadow and Ashton (1981) (Fig. 2). By contrast, all adult *Eucalyptus* survived, resprouting from epicormic buds within 2 months. Moreover, temperatures required to kill *P. undulatum* seedlings determined experimentally were similar to those measured in this and other prescribed burns (e.g. Bradstock and Auld, 1995), which is consistent with the total removal of seedlings from the fire site. The complete removal of the youngest members of the population (i.e. seedlings <0.5 m tall, Fig. 2) must impact negatively on the invasiveness of *P. undulatum* in the short term. The removal of most reproductive adults must, in turn, reduce the availability of seed in subsequent years. Plants rarely flower until they reach 1 m, which in a field situation may represent 3–5 years growth in the shady parts of the dry open forests of southern Victoria (Gleadow, 1982).

Pittosporum undulatum has a dense canopy, with 8% and 24% penetration of full sunlight in winter and summer, respectively. Moreover, as invasions become more advanced the canopies coalesce to form a continuous stratum, resulting in light intensities of less than 1% full sunlight at ground level (Gleadow et al., 1983). It is this heavy shade that is primarily responsible for reduction in species richness in invaded areas (Gleadow and Ashton, 1981; Bradstock et al., 1997). The most obvious effect of fire is the removal of the canopy which must at least temporarily reduce *P. undulatum* growth rates due to the removal of the photosynthetic area. Further, roosting and nesting sites for avian vectors such as *Turdus merula* (European blackbird) are removed (see Gleadow, 1982; Kentish et al., 1995). Importantly, any newly recruited seedlings are likely to die in the ensuing summer as the survival rate of *P. undulatum* seedlings grown in exposed sites has been shown to be less than 5%, compared with the 75% survival rate of seedlings growing under an existing *P. undulatum* canopy (Gleadow, 1982), probably due to a low tolerance of water stress under high light intensities (Gleadow and Rowan, 1982).

Seeds of most plants are killed when exposed to temperatures of over 120 °C for several minutes (Auld and O'Connell, 1991; Bebawi and Campbell, 2002). Seeds of *P. undulatum*, by contrast, are more sensitive to heat, with a significant reduction in germination rates at 90 °C (Table 3). Seed held in the canopy would have been killed by the range of temperatures experienced in this study and in most prescribed burns. It is

more typical for fire tolerant species to re-establish from seed in the soil, rather than the canopy (e.g. Auld et al., 2000). In prescribed burns, soil temperatures rarely reach temperatures over 60 °C and so the soil seed bank is often not adversely affected anyway (Bradstock and Auld, 1995). Several studies have shown that *Pittosporum undulatum* does not store seed in the soil from one year to the next (e.g. Gleadow, 1982). Consequently, removing the seed in the canopy removes the seed bank.

The seedlings that emerged after the fire in this study were almost certainly from seeds transported to the quadrats from unburnt trees in the surrounding areas after seed fall in early winter (June–July; Table 2). Gleadow and Ashton (1981) studied the relationship between bird-distributed woody weeds into undisturbed forest (including *P. undulatum*) and distance from gardens. They found that for every metre of penetration into the forest, the number of weeds decreased by five (on a per hectare basis). No individuals were found more than 180 m from human modified sites. This would suggest that to prevent re-establishment of *P. undulatum* from seed, the area to be burnt should be a minimum of 4 ha, and preferably with a buffer zone of 200 m between the nearest seed sources and the reserve.

Leaf litter can be a source of allelochemicals that may inhibit germination and growth of other species. Gleadow and Ashton (1981) found that *P. undulatum* leaf litter inhibited seed germination of a range of species, while promoting germination of its own seed, consistent with the presence of saponins and other secondary metabolites in the leaves and fruit (Power and Tutin, 1906). A reduction in allelochemicals after fire has been observed in other woody species, such as *Cistus ladanifer* L. (Dias et al., 2005). The removal of leaf litter by fire, as was seen here in the prescribed burn, would thus be expected to eliminate any allelopathic effects of adult trees on newly recruited seedlings.

Fire is commonly prescribed to reduce the risk of high temperature, unplanned fires (although these are less common in remnant vegetation in suburban areas). Recent simulations of the effect of different fire regimes on natural vegetation suggest that the needs of conservation cannot be met by using methods employed primarily for hazard reduction (Morrison et al., 1996). Here we show that there can be positive benefits for conservation with prescribed burns by reducing the invasiveness of an environmental weed. A single fire such as the one described here is likely to delay the invasion by a number of years, depending on the proximity and number of surviving adult reproductive plants.

5. Conclusion

We conclude that fire can be used act as a circuit breaker in the invasions by *P. undulatum* by eliminating the local seed bank, reducing growth rates and reducing the probability of seed dispersal and seedling survival. The seeds are sensitive to temperatures as low as 90 °C, and are likely to be killed in most prescribed burns. As seed is not stored in the soil, this immediately removes the source of weeds. Fire not only kills most of the extant *P. undulatum*, it also reduces the number of roosting sites for avian vectors from neighbouring infested

sites. Moreover, high light intensities associated with canopy removal would decrease the probability of survival of new colonising seedlings. Prescribed burns in the temperature range described here would not eliminate *P. undulatum* from an area. They would, however, minimise the problem to a point where other control measures, such as poisoning and follow-up weeding could be used more economically.

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