

Population Ecology of Waratahs, *Telopea speciosissima* (Proteaceae): Implications for Management of Fire-prone Habitats

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Waratah (*Telopea speciosissima*) post-fire floral displays are a prominent feature of the landscape in Royal National Park and elsewhere in southeastern Australia, but factors governing the persistence of the species are poorly known. We examined long term patterns of fecundity, recruitment and survival of waratahs in Royal NP in relation to two major wildfires. Flowering occurred mainly over 3 years following both the 1994 and 2001 fires, but fewer plants flowered, fewer seeds were produced and fewer seedlings established after the 2001 fire. After the 1994 fire, limited seed dispersal resulted in most seedlings establishing near fruiting individuals. Only 14% of the plants that established as seedlings after the 1994 fire survived the 2001 fire. At the time of the 2001 fire, these plants were 4-6 years old and post-fire survival was highest in older plants. A logistic model predicts that it would take 5.9 (95% CI 5.4-7.5) years of growth after germination for plants to have greater than 25% survival probability if burnt (equivalent to a fire return period of about 9 years). Waratahs are long lived, have long primary juvenile periods and occasional opportunities for recruitment. Each fire may not lead to successful recruitment. While recruitment failure after one or more fires may not be significant, understanding the proximate factors that limit recruitment is important to predict the impact of long term changes such as altered fire regimes under a changing climate.

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INTRODUCTION

The waratah (*Telopea speciosissima* Sm.) is a member of the Gondwanan family Proteaceae. As the New South Wales floral emblem, waratahs are an important conservation icon. Their post-fire floral displays are a prominent feature of the landscape in Royal National Park and elsewhere in the Sydney region, but our understanding of the requirements necessary to manage the species in the wild in perpetuity is still limited.

In contrast, our ability to cultivate waratahs for their bold red flowering spikes or confluences is more advanced (Harden et al. 2000). Development of cultivars for the cut-flower market and for domestic gardens has driven a considerable research agenda, leading to important knowledge of plant pathology, micro-propagation techniques and pollination biology

(e.g., Summerell et al. 1990, Offord et al. 1992, Offord and Campbell 1992, Offord 2004, Peterson et al. 2004). Patterns of fruit set and pollinator interactions have also been investigated by Whelan and co-workers, leading to improved understanding of flowering patterns, pollination syndromes and identifying the species as an obligate outcrosser (Whelan and Goldingay 1989, Goldingay and Whelan 1993, Goldingay 2000, Whelan and Denham 2009).

Given their occurrence in fire prone environments, it is clear that fires are likely to be a major influence on waratah demography and, hence, on their persistence in the landscape. Above ground parts of waratahs are killed and often consumed by fire, but individual plants survive fire by having dormant buds in underground lignotubers, from which new stems can resprout (Bradstock 1995). Waratahs do not have persistent long-lived seed banks, either on the plant

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or in the soil, and they rely on post-fire flowering for the establishment of new individuals (Denham and Auld 2002, Denham 2008). This establishment of new individuals is critical to the long-term survival of the species as these individuals can replace those mature plants that may die between or during fires. Thus waratahs are a part of the obligate pyrogenic flowering group of species. While such species occur in fire-prone habitats, they are less common, and their ecology is less well understood, than species with either a serotinous (canopy stored seed bank) or persistent soil seed bank (Auld and Ooi 2008). In the Sydney region, the functional group that the waratah belongs to also includes a number of monocotyledons (e.g. *Xanthorrhoea* spp Keith 1996, Tozer and Keith 2012; *Doryanthes excelsa* – Denham and Auld 2002), but only a few woody plants (e.g. *Angophora hispida* - Auld 1986; *Lomatia silaifolia* - Denham and Whelan 2000) including significant structural or functional members of several vegetation types.

To manage for biodiversity conservation (Bradstock and Kenny 2003) and to improve our ability to predict plant community responses (Pausas et al. 2004) a greater understanding of pyrogenic flowering species is critical. A key conservation issue for such species is what fire frequencies can be tolerated? Currently, for waratahs, the spatial and temporal patterns of recruitment, the time required for these recruits to become fire resistant and the time required for juveniles to become adults have not been well documented. To inform the management of fire in landscapes occupied by *T. speciosissima*, we quantified post-fire flowering, seed production, seedling recruitment and juvenile survival after two wildfires (January 1994 and December 2001) in Royal National Park, south of Sydney.

MATERIALS AND METHODS

Study sites

Three sites were selected within a 10 km radius in Royal National Park, approximately 35 km south of Sydney (34°03'151°03'). All sites had identical recent fire histories (all burnt in January 1994 and December 2001). Royal NP includes substantial habitat suitable for waratahs, on soils derived from Triassic Hawkesbury Sandstone Formation. Our Sites 1 and 2 occurred in Sydney Coastal Dry Sclerophyll Forest (Keith 2004) and Site 3 occurred in Sydney Coastal Heath vegetation (Keith 2004). For detailed descriptions see Denham and Auld (2002) for Sites 1 and 3, and Denham (2007) for Site 2.

Experimental methods

After the 1994 fire, a 30 m by 30 m plot was marked out within Sites 1 and 3. The area of the marked plot and a buffer zone of approximately 5 m beyond was surveyed and all *Telopea speciosissima* individuals were tagged and mapped. The reproductive effort of individuals was monitored annually until 2011 by scoring the number of flowering stems, the number of inflorescences and the subsequent infructescences and follicles. Seedling recruitment was monitored after flowering events by surveys from 1996 to 2001 and then subsequently after the 2001 fire. Seedlings were tagged and mapped and their survival monitored intermittently until the fire in December 2001. Post-fire survival of these juveniles was initially scored from February 2002. After the 2001 fire, an additional site (Site 2) was marked out and monitored for reproductive effort, seedling recruitment and survival until 2011.

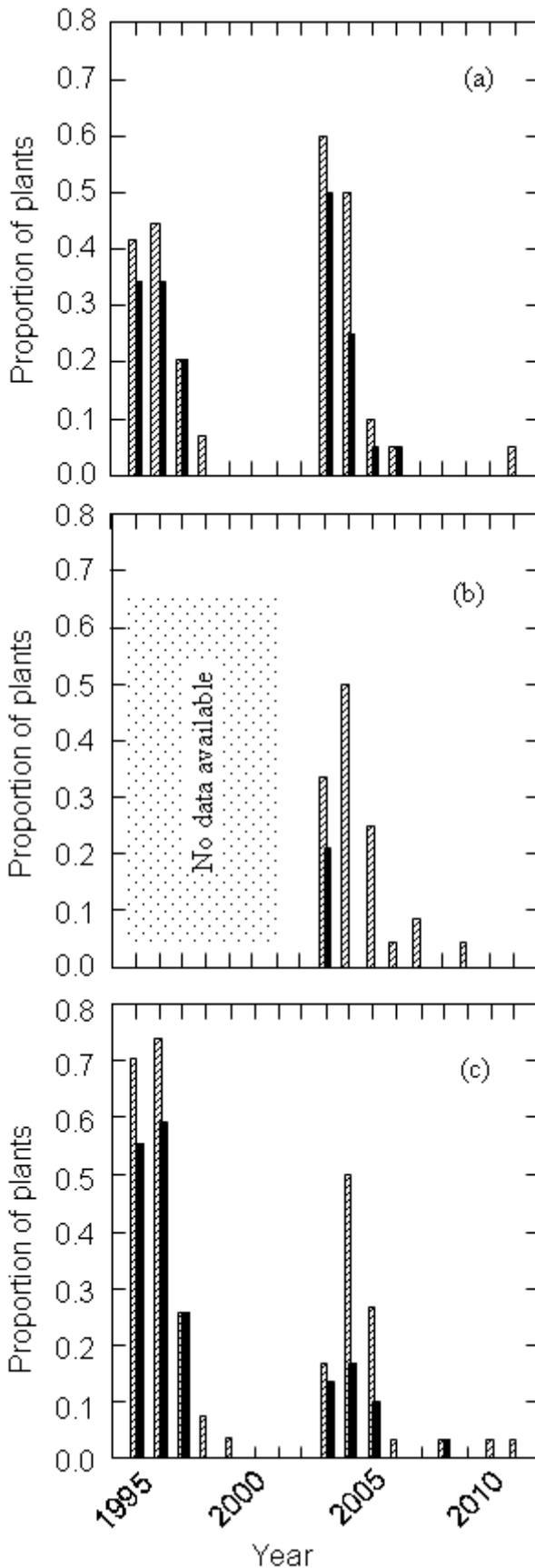
Analysis

The effects of juvenile age, site and distance from an adult on juvenile survival through the 2001 fire were assessed using logistic regression. The model with the best fit was obtained using backward stepwise regression. For calculation of survival quantiles with juvenile age, the distance from adults was fixed at 1.5m (the approximate median value for all seedlings). The distance from adults of surviving juveniles and those killed during the 2001 fire was compared with a t-test. These analyses were done with Systat 11 for Windows (SPSS 2004). Spatial patterns were assessed for departure from a random distribution by calculation of Moran's I and its z-normal derivative using Rookcase (Sawada 1999). Where $|z\text{-normal } I| > 1.96$, individuals were considered likely to be autocorrelated, either evenly distributed ($z\text{-normal } I < -1.96$) or clumped ($z\text{-normal } I > 1.96$).

RESULTS

Reproductive effort

Initial flowering after the 1994 fire occurred in spring 1995. Flowering effort at both study sites was concentrated in the first three flowering seasons (greatest in 1995 and 1996, reduced in 1997) and declined thereafter (Fig. 1). Fruiting success followed a similar pattern, with most flowering individuals maturing fruit in the first three flowering years, and no seed was produced after this period (Table 1). Total seed production was estimated to be 2.0 and 2.9 seeds per m² at Sites 1 and 3 respectively (Fig. 2). A similar pattern was found after the 2001 fire with



flowering effort also peaking soon after fire. The greatest proportion of plants flowered in the first 2-3 flowering seasons after the fire (2003, 2004 and 2005) and declined in subsequent years, with only sporadic flowering to the end of the study. At Site 1, the proportion of plants that matured fruit was similar after the 1994 and 2001 fires, but at Site 3 considerably fewer plants matured fruit after the 2001 fire compared to after the 1994 fire. There was little successful fruit production at Site 2, for which we have no pre-2001 data (Fig. 1). At all sites there were fewer infructescences and fewer follicles per fruiting plant after the 2001 fire than after the 1994 fire (Table 1), with total seed production post-2001 a third or less of the post-1994 production (0.74 and 0.67 seeds per m² at Sites 1 and 3 respectively and 0.44 seeds per m² at Site 2, see Fig. 2).

Seedling recruitment

Seedling recruitment was essentially confined to the first few years after a fire. The magnitude of recruitment varied across both sites and post-fire years (Fig. 2) but some patterns of recruitment were apparent. Recruitment was much greater at Site 1 compared to Site 3 after the 1994 fire with a density 0.29 seedlings/m² representing 14.5% of seeds establishing as seedlings at Site 1, but only 0.03 seedlings/m² (1.0%) at Site 3. Seedling recruitment after the 2001 fire was low at all sites, with 0.04 (5.3%), 0.01 (2.0%) and 0.03 seedlings/m² (4.6% of seeds produced) at Sites 1, 2 and 3 respectively (Fig. 2). Notably, at Site 3, a single adult plant produced fruit and subsequent seedlings in 2008, some 7 years after fire.

Young juvenile survival through the 2001 fire

Relatively few young juveniles that established as seedlings after the 1994 fire survived the 2001 fire. At Site 1, some 91 young juveniles were alive in the year prior to the fire, but only 18 (19.8%) resprouted subsequently. Survival was greatest in the oldest juveniles, such that none of the juveniles from the 1997 flowering survived (of 14 observed); 11% (3/28) of the juveniles from the 1996 flowering survived; and 31% (15/49) of the juveniles from the 1995 flowering survived. At Site 3, 71 seedlings were alive in the year prior to the fire, but only four (5.3%) survived and subsequently resprouted.

Figure 1. Proportion of adult *T. speciosissima* individuals flowering (hatched bars) and fruiting (solid bars) for the years 1994 to 2011 within the plot at (a) Site 1, (b) Site 2 and (c) Site 3. No data are available for pre-2001 flowering for Site 2.

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Table 1. Estimates of fruit production in *T. speciosissima* at sites in Royal National Park for the period 1994-2010. Data for infructescences and follicles are means per fruiting adult \pm SE.

Site	Year	Fruiting plants	Infructescences per fruiting plant	Follicles per fruiting plant
1	1995	10	2 (0.5)	8.6 (3.0)
1	1996	10	2 (0.4)	5.6 (2.8)
1	1997	6	1.8 (0.3)	2.3 (0.8)
1	1998-2002	0		
1	2003	10	1.1 (0.6)	3.8 (1.9)
1	2004	5	1 (0)	2.9 (1.1)
1	2005	1	1	1
1	2006	1	1	2
1	2007-10	0		
2	2002	0		
2	2003	5	1.6 (1.2)	4.4 (1.3)
2	2004-10	0		
3	1995	15	1.7 (0.2)	5.9 (1.0)
3	1996	16	2.4 (0.6)	8.4 (3.3)
3	1997	7	1.1 (0.1)	2.6 (0.6)
3	1998 – 2002	0		
3	2003	4	1 (0)	5 (1.9)
3	2004	6	1.2 (0.7)	2.5 (1.5)
3	2005	3	1 (0)	4 (2.1)
3	2006-7	0		
3	2008	1	1	7
3	2009-10	0		

Again, there was a pattern of greater survival in older juveniles, such that: none of the juveniles from the 1997 flowering survived (of 9 observed); 3% (1/40) of the juveniles from the 1996 flowering survived; and 14% (3/22) of the juveniles from the 1995 flowering survived. In the logistic model, survival probability was significantly affected by juvenile age and the interaction of age and distance from an adult, but Site and distance from an adult alone were not significant (Table 2, Fig. 3). The logistic model was considered to be a reasonably good predictor of outcomes with 2 and 14 % improvement over a random model for response and reference variables respectively (Table 3, Steinberg and Colla 2004). However, the absence of data in older age classes limits confidence in the model, as expressed by the widening confidence intervals beyond 6 years (Fig. 3).

Spatial patterns of flowering and seedling recruitment

Adult distribution was clumped at Sites 1 and 3, although not at Site 2 (Table 4, Fig. 4). Most adults flowered after one or both fires, with only a few failing to flower after either fire (Fig.4). With some exceptions, seedlings established in close proximity to fecund adults after the 1994 fire, reflecting a leptokurtic seed rain (Figs 4 and 5). Although there was also evidence of a clumped distribution of seedlings at the site scale (Moran's $I > 0$), it was only significant at Site 3 (Table 4). Similar patterns of seedling establishment in relation to adults were apparent after the 2001 fire (Figs 4 and 6), but there was no significant clumping (Table 4). Differential survival through the 2001 fire at Site 1 resulted in a more even pattern of seedlings but again, it did not

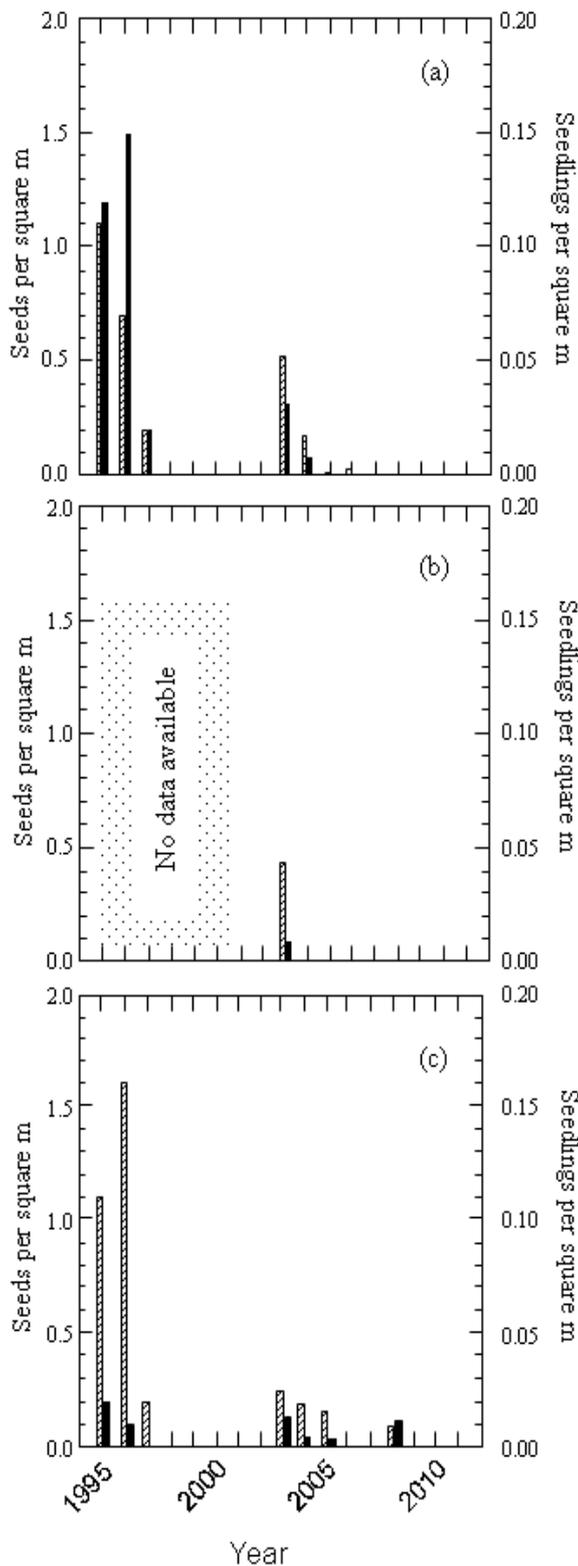


Figure 2. Estimated density of *T. speciosissima* seeds (hatched bars) and seedlings (solid bars) for the years 1994 to 2010 within the plot at (a) Site 1, (b) Site 2 and (c) Site 3. No data are available for pre-2001 flowering for Site 2. Note the different scales for seeds and seedlings.

differ from a random distribution. There were too few survivors at Site 3 to allow a statistical assessment. The proximity of surviving seedlings (post-fire resprouters) to adults at Site 1 was less pronounced after the 2001 fire (Fig. 5a). Although there was only weak support for proximity to adults to affect survival in the logistic model (Table 2), at Site 1 there was a significant difference in the mean distance between survivors and adults compared to mortalities and adults (3.69m cf. 2.21 m, $t=-2.08$, $P=0.034$). There was no evidence of this effect at Site 3, possibly due simply to the low number of survivors (Fig. 5b).

DISCUSSION

Pyrogenic flowering species such as *T. speciosissima* present difficulties for management because of their long life history stages, along with episodic recruitment linked to fire. Here we show how a long term study spanning consecutive fires can highlight key demographic parameters and provide insights into predictions about the likely tolerance of pyrogenic species to critical components of the fire regime, particularly fire frequency.

Recruitment linked to fire

Flowering and seed production in *T. speciosissima* is strongly linked to fire, with a pattern of increased flowering and fruiting in the years soon after fire and a subsequent decline (Pyke 1983). However, at the same time-since-fire, flowering effort, fruiting success and seedling recruitment all varied after different fires and at different locations. While a low level of flowering activity can be maintained up to a decade after fire, as previously observed by Goldingay (2000), recruitment of new plants was largely driven by fire, as observed previously (Bradstock 1995, Denham and Auld 2002). A similar proportion of plants flowered after the 1994 and 2001 fires. However, fewer fruits were matured after the 2001 fire, leading to a greatly reduced pool of seeds available for seedling recruitment. This was borne out by a much lower number of seedlings becoming established after the 2001 fire compared to the 1994 fire, although an increase in the relative intensity of seed predation may also have contributed to this difference (Denham 2008). Interestingly, many of the new recruits at Site 3 after the 2001 fire were established in 2009 from seeds released some 7 years after fire. This suggests that *T. speciosissima* has the capacity to establish seedlings long after the conventional post-fire recruitment period (of about 3 years – Denham et al. 2009), but the probability of these seedlings surviving the next fire is greatly

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Table 2. Results of logistic regression model for juvenile survival through fire. Only significant model parameters are shown, factors with odd ratios whose 95% CI do not include 1 make a meaningful contribution to the model.

Model parameter	Parameter estimate	SE	t-ratio	P
Constant	11.06	2.95	3.74	<0.001
Juvenile age	-1.66	0.56	-2.97	0.003
Juvenile age X distance from adult	-0.07	0.03	-2.55	0.011
	Odds ratio	Upper 95%	Lower 95%	
Juvenile age	0.19	0.57	0.06	
Juvenile age X distance from adult	0.93	0.98	0.88	

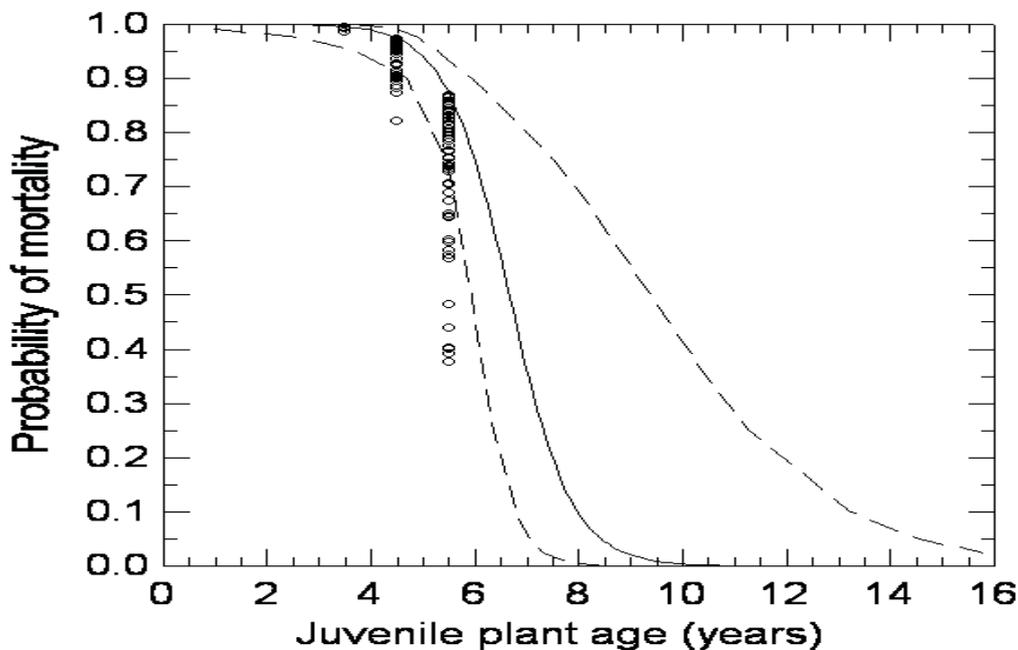


Figure 3. Logistic regression curve showing the predicted relationship between juvenile age and probability of mortality during fire (solid line) with 95% CI (dashed lines). Distance from an adult was fixed at 1.5m to generate these curves. Data points (open circles) are the predicted probability of mortality for each observed combination of age and distance from an adult. Regression equation is $y = (\exp(-1.66 \cdot \text{age} + 11.1)) / (1 + \exp(-1.66 \cdot \text{age} + 11.1))$, log likelihood ratio = -52.3, $p < 0.001$.

reduced, unless there is a fire free period long enough for them to become fire resistant (see below).

The 2001 fire caused no mortality of plants that had survived the 1994 fire, in contrast to Bradstock (1995) who described 2-17% fire mortality in juvenile and adult plants. However, Bradstock's data were after a severe wildfire in Brisbane Waters NP and fire intensity at our sites during the 2001 fire was moderate by comparison (A. Denham unpub. data). Young juvenile mortality in the 2001 fire was high, but

comparable to rates found by Bradstock (1995) and there was a pattern of greater chance of survival with increased age of the juveniles (Fig. 3). Examination of quartiles derived from the logistic model suggest 25% survival at 5.9 years (95% CI 5.4-7.5), 50% at 6.6 (5.9-9.4) years and 75% at 7.3 (6.4-11.3) years. Given that seedling recruitment generally occurs 2-3 years after fire, the model indicates that a 9 year fire frequency (January 1994 to December 2001 being almost 8 years) should allow a quarter of new juveniles

Table 3. Prediction success table for the logistic model of juvenile survival through fire. The success indicator shows the improvement in prediction that the model makes over a random model for both response and reference.

Actual Choice	Response	Reference	Actual total
Response	124	16.0	140
Reference	16	6.0	22
Predicted total	140	22	162
Correct	0.89	0.27	
Success indicator	0.02	0.14	
Total correct	0.80		

to be recruited into the adult population. The absence of data for older juveniles and the widening 95% confidence intervals when estimating larger quartiles, indicate that caution is required when predicting how long after fire the majority of new juveniles would be fire resistant (9-14 years for 75% survival). Similar requirements for fire free periods have been previously suggested for *T. speciosissima* (Bradstock 1995) and for other pyrogenic flowering species (e.g. *Angophora hispida* – Auld 1986, *Lomatia silaifolia* – Watson and Wardell-Johnson 2004), while for others such as *Xanthorrhoea resinosa* (Tozer and Keith 2012) shorter fire free periods may be more acceptable or even desirable.

Spatial patterns

There was evidence of clumped patterns in the arrangement of adult plants at Sites 1 and 3, while at

Site 2 the arrangement of adults was not significantly different from a random distribution. Seedlings were also clumped at Site 3, as well as being clustered around adult plants at all sites. It seems likely that these spatial patterns are largely driven by the patterns of seed dispersal that follow a classic leptokurtic shape (Denham and Auld 2002). However, the alteration of this pattern by differential fire survival of seedlings suggests that although establishment opportunities may be widespread within the sites (i.e., there is no microsite limitation), not all of these sites are suitable for fire survival. Indeed, we found some evidence that the adults may actually reduce fire survival of their offspring, possibly through altering the patterns of litter accumulation or reducing the capacity of seedlings to develop underground lignotubers. Experimentally establishing seedlings at a variety of locations within these sites prior to the next fire may provide insights into these mechanisms (see also Whelan et al. 2002; Denham 2008; Denham et al. 2011).

Conclusions

Telopea speciosissima is one of only a few woody pyrogenic flowering species (Keith 1996; Auld and Ooi 2008). This group has been considered to be highly resilient to frequent fire because adults usually survive fire and population declines may be difficult to detect. However, persistence of populations is also dependent upon recruitment and if frequent fire eliminates recruits (Bradstock 1995) then such species should be considered sensitive to frequent fire, rather than resilient (Watson and Wardell-Johnson 2004). The current fire return interval in the habitat of *T. speciosissima* is around 7-17 years (Bradstock and Kenny 2003), although fire

Table 4. Spatial statistics for adult and seedling distributions. For Sites 2 and 3 there were insufficient data for analysis of all variables. Moran's I values can be transformed to z-scores in which values greater than 1.96 or less than -1.96 indicate spatial autocorrelation that is significant at the 5% level.

Site	Variable	N	Moran's I	z-Normal I (variance)	Mean distance m (SD)
1	Adults	46	0.178	2.23 (0.008)	11.3 (8.9)
	Post-1994 seedlings	246	0.042	1.15 (0.002)	12.5 (7.0)
	Pre-2001 seedlings	182	0.076	1.75 (0.002)	12.5 (6.8)
	Post-2001 resprouters	36	-0.11	-0.79 (0.010)	12.3 (6.9)
	Post-2001 seedlings	58	-0.054	-0.45 (0.006)	12.0 (8.4)
2	Adults	50	-0.061	-0.47 (0.007)	19.1 (9.5)
3	Adults	74	0.220	3.26 (0.005)	16.4 (10.4)
	Post-1994 seedlings	150	0.229	4.61 (0.003)	17.5 (5.9)
	Pre-2001 seedlings	142	0.196	3.88 (0.003)	17.5 (5.6)
	Post-2001 seedlings	50	-0.043	-0.26 (0.007)	16.8 (6.2)

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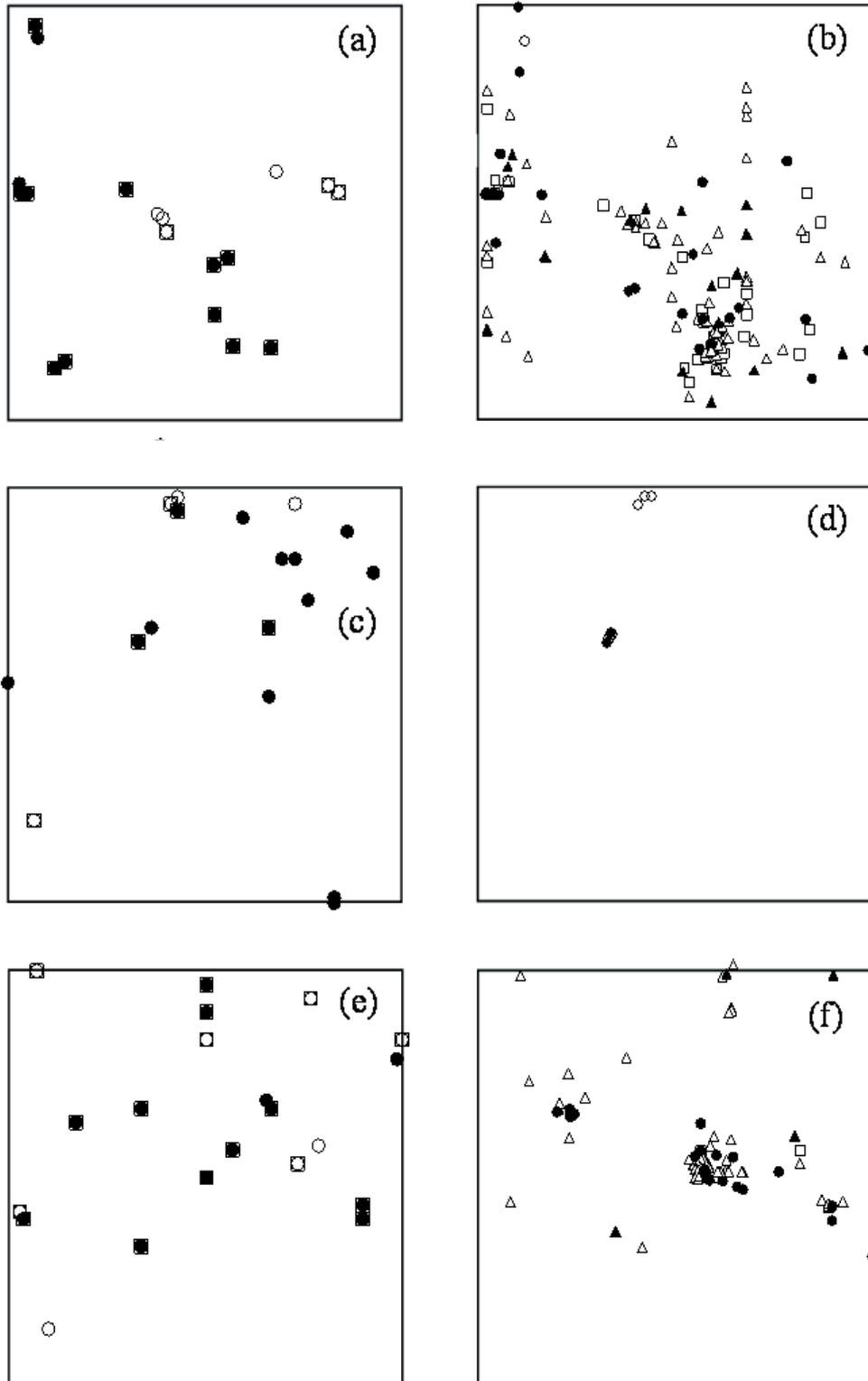


Figure 4. Maps of *T. speciosissima* adults (a,c,e) and seedlings (b,d,f) within the same 900 m² plots at Sites 1 (a and b), 2 (c and d) and 3 (e and f) in Royal National Park. For adults (a,c,e), filled circles represent plants that flowered after the 1994 fire, while open circles represent those that did not. Open squares represent those plants that flowered in the period 2002 to 2011 (after the 2001 fire). At Site 2, post-1994 flowering effort was estimated from old infructescences that remained after the 2001 fire. For seedlings (b,d,f), triangles and squares represent those that established after the 1994 fire. Open squares are those that died prior to the 2001 fire, open triangles those killed by the 2001 fire and filled triangles those that survived the 2001 fire. Circles represent seedlings that established after the 2001 fire, filled circles are those that were alive in September 2011.

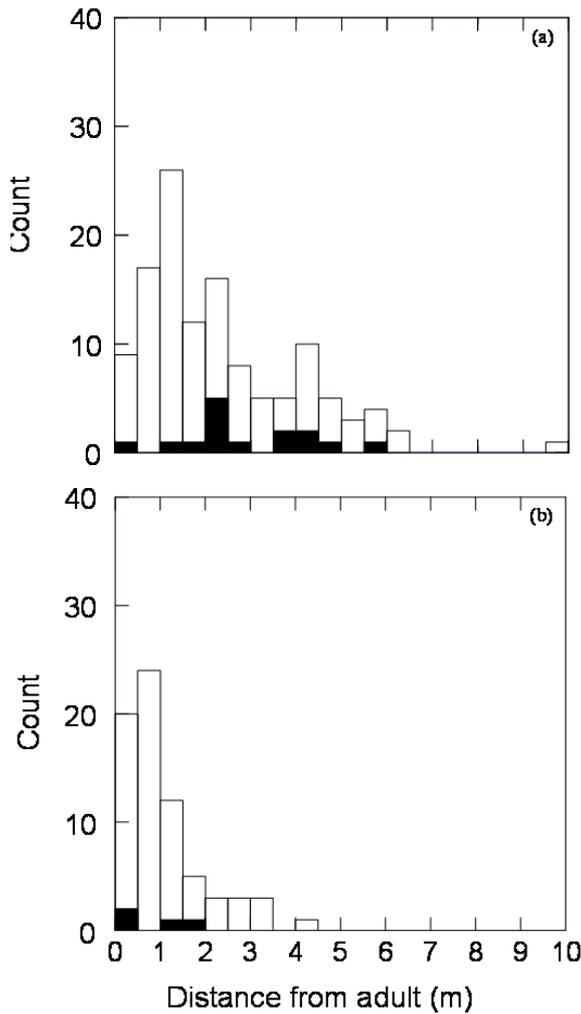


Figure 5. Frequency histogram of the distance between adult plants and seedlings established after 1994 at (a) Site 1 and (b) Site 3. Open bars represent plants that were present before the 2001 fire, filled bars represent those that survived the 2001 fire.

frequencies are likely to have increased greatly since European settlement (Mooney et al. 2011). Thus juveniles of *T. speciosissima* would need to become fire resistant within 7 years after fire to avoid the risk of fire frequency impacts. Bradstock (1995) also found that young juvenile survival through fire was a critical factor in the life history of *T. speciosissima*, and suggested that variable fire frequencies with occasional fire free periods of more than 10 years were likely to allow persistence. Our results of a long term study that allowed comparisons across two successive fires, and found a similar fire free period (in the order of 8-10 years) is needed to ensure that at least 25%

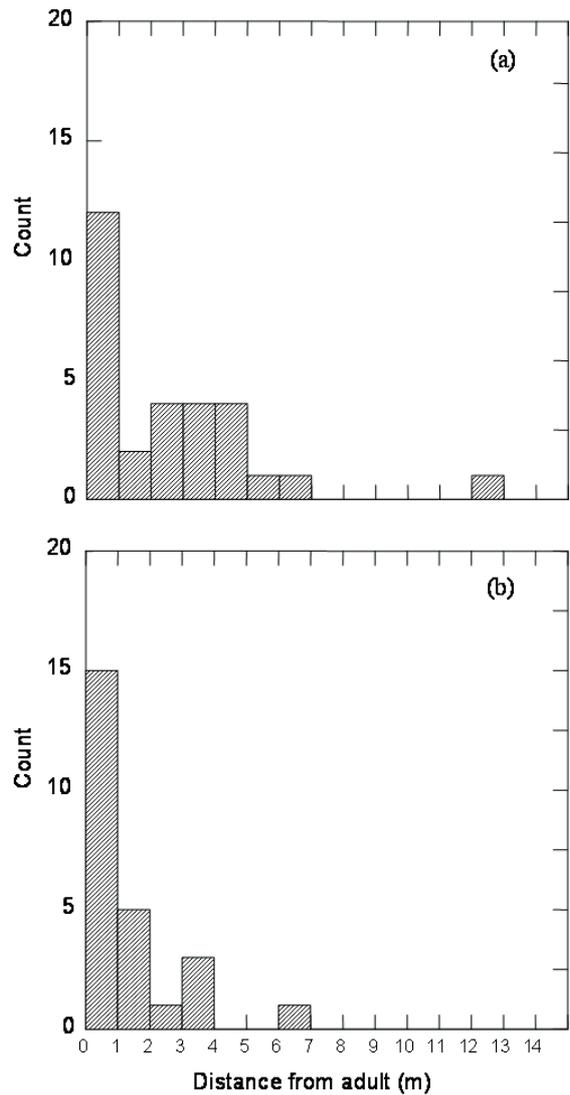


Figure 6. Frequency histogram of the distance between adult plants and seedlings established after the 2001 fire at (a) Site 1 and (b) Site 3.

of young juvenile plants can survive a fire. While recruitment failure after one or two fires is unlikely to significantly affect population persistence, on-going recruitment failure under a high fire frequency would lead to declines and possibly local extinction. Our study provides important insights into how fire drives both the factors controlling seedling recruitment and the mechanisms that may limit juvenile survival. Further changes to fire regimes, including expected increases in fire frequency with increases in extreme weather under a changing climate (Hennessy et al 2006; Bradstock et al. 2009; Clarke et al. 2011)

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will reduce the recruitment capacity of pyrogenic flowering species like *T. speciosissima*. This in turn will impact on the long-term persistence of this iconic species.

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