Plant Ecol (2016) 217:801–816
DOI 10.1007/s11258-016-0613-x

Regulation of seedling recruitment and survival in diverse ecotonal temperate forest understories

**Monica L. Campbell · David A. Keith ·
Peter J. Clarke**

Received: 5 August 2015 / Accepted: 6 May 2016 / Published online: 20 May 2016

Abstract Fire is an important factor driving the position and stability of ecotones between fire-prone and less flammable forest types. To better understand, the recruitment processes that mediate plant persistence in ecotonal systems, we used manipulative field experiments in Australian wet eucalypt forests to investigate factors that may be regulating seedling recruitment and survival in burnt and unburnt forest. We found no evidence that safe sites from predators or exposure regulated seedling recruitment in three of the four study species, but one species associated with less flammable rainforest systems had increased germination rates in response to soil scarification. Seedlings of all four study species experienced higher rates of mortality resulting from herbivory or water stress in the post-fire environment. We found that intact ground cover increased seedling survival by reducing exposure to dessicating conditions and providing refuge from vertebrate herbivores. Our results suggest that shrubs associated with mesic, low-flammability forests have fewer opportunities for recruitment with desiccation risks in post-fire environments limiting seedling survival. In contrast, shrubs associated with high-flammability forests were capable of recruiting and surviving in both burnt and unburnt forests. Post-fire recruitment is likely to be more abundant after fire than at other times, but we found that survival can be highly constrained by post-fire herbivory. The ability of these species to recruit in undisturbed conditions provides some insurance against recruitment failure under stochastic variation in herbivory and desiccating conditions. The capacity to spread risks could be important in maintaining boundary position and diversity in these ecotonal systems.

Keywords Regeneration niche · Fire regime · Recruitment syndromes · Seedling herbivory · Recruitment failure · Safe sites

Introduction

In humid regions of the world, vegetation with contrasting levels of flammability often co-occur

---

Communicated by Prof. Michael Lawes and Prof. Ross Bradstock.

M. L. Campbell (✉)
Ecological Survey and Management, Woombye,
QLD 4559, Australia
e-mail: monica.campbell@ecosm.com.au

M. L. Campbell · P. J. Clarke
Botany, University of New England, Armidale,
NSW 2351, Australia

D. A. Keith
Centre for Ecosystem Science, School of Biological, Earth
and Environmental Sciences, University of NSW, Sydney,
NSW 2052, Australia

D. A. Keith
NSW Office of Environment & Heritage, Hurstville,
NSW 2220, Australia

within the same landscape (Bond et al. 2005). For example, in tropical South America, Australia, Asia and Africa, low-flammability tropical rainforests adjoin high-flammability seasonally dry forests and savanna (Just et al. 2015). In Australia, juxtapositions of low- and high-flammability forests extend along the eastern ranges and coastal plains to temperate latitudes (Bowman 2000). The more flammable systems have an open tree stratum that enables drying of fuels and ready propagation of ignitions, whereas the low-flammability systems are characterised by a closed structure that maintains a humid microclimate and prolongs retention of fuel moisture, retarding the spread of fire. The structure and composition of litter fuels may also contribute to differential flammability (Sullivan et al. 2012).

The contrast extends to species composition and life histories of component plants: flammable systems are populated with species equipped with traits that enable them to regenerate vegetatively or from seed after fires (Pausas et al. 2004), while plants that regenerate independently of fire are more commonly encountered in low-flammability forests. More generally, these plant life histories form a continuum from those with fire-dependent recruitment to those with fire-independent recruitment (Keeley et al. 2012).

Fire-dependent recruiters in high-flammability vegetation typically produce many seedlings in the post-fire environment. Fire may play multiple roles through the recruitment process, by providing germination cues, enhancing resource availability, removing litter, reducing competition and releasing predation pressure in the post-fire environment, all of which may limit recruitment during inter-fire intervals (Auld and O'Connell 1991; Bell et al. 1993; Tang et al. 2003; Clarke et al. 2010; Tang et al. 2003; Williams et al. 2012). In contrast, fire-independent recruiters, typical of low-flammability vegetation, produce relatively few seedlings in the post-fire environment. For these species, seedling emergence is typically governed by seedfall and/or small-scale soil disturbance, and seedlings benefit from shelter, or at least tolerate shade associated with ground vegetation or deep litter (Poulsen and Platt 1989; Hoffmann 2000; Lusk et al. 2013; Metcalfe et al. 2014).

Ecotonal systems typically contain a mixed assemblage of species that are characteristic of each vegetation type (high- and low-flammability). However, these systems may be inherently unstable if positive feedbacks promote each of the alternate states (Harrington and Sanderson 1994; Folke et al. 2004; Warman and Moles 2009; Odion et al. 2010; Lindenmayer et al. 2011). If ecotonal systems are burnt, then the more open structure of regenerating vegetation promotes drying and increases the probability of recurring fire. If they remain unburnt, growth and inter-fire recruitment leads to development of a more closed canopy, more humid microclimate, sustained fuel moisture and a low probability of fire spread. The coexistence of species with fire-dependent and fire-independent recruitment could therefore be transient. Resolving this proposition requires an understanding of the ecological mechanisms underpinning recruitment in species from both flammable and non-flammable vegetation.

The wet sclerophyll forests of eastern Australia are an ideal system for investigating this problem. They typically occupy an ecotone between low-flammability rainforest and high-flammability dry sclerophyll forests (Fig. 1). These ecotonal communities are dominated by tall eucalypts, making them more open and more fire-prone than rainforests. However, their understories may support a number of rainforest species and retain moisture for long periods, making them less prone to frequent fire than dry sclerophyll forests (Keith 2004). Gradients in canopy openness, litter depth, soil pH, soil temperature and understorey solar radiation have been reported to influence the rates of germination and seedling establishment of rainforest and sclerophyllous taxa throughout the ecotone (Turton and Sexton 1996). Changes in these environmental gradients and community properties across the ecotone, particularly shifts in understory composition, have been linked to fire regimes and the length of fire-free periods (Ashton and Attiwill 1994; Turton and Sexton 1996).

We compared recruitment syndromes in two plant species from low-flammability rainforests and two from high-flammability dry sclerophyll forests that co-occur within ecotonal wet sclerophyll forests (Fig. 1). In previous work (Campbell et al. 2012), we evaluated the influence of seedbank properties on recruitment patterns in these species. In this paper, we report on a series of field experiments to examine the mechanisms limiting seedling emergence and establishment within the ecotonal forests. Specifically, we asked whether rates and timing of seedling emergence and survival differed between species from low- and high-flammability forest

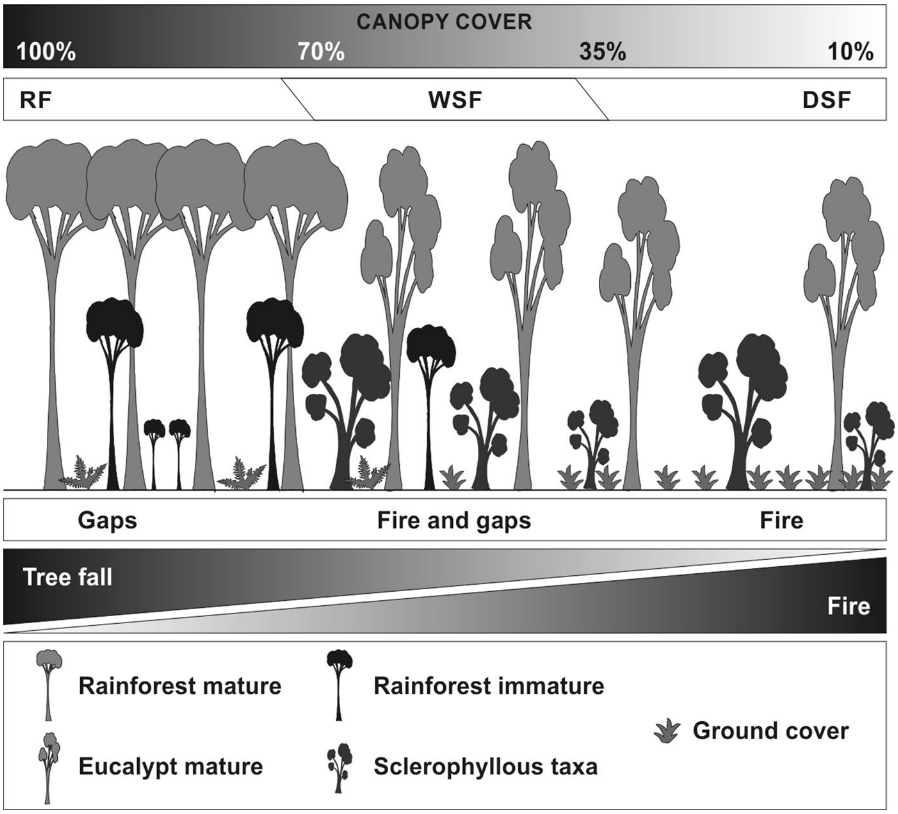

Fig. 1 Diagrammatic model of gradients in understorey conditions throughout wet sclerophyll forest (*WSF*) from the rainforest (*RF*) margin to the dry sclerophyll forest (*DSF*) interface. *Shaded triangle bars* at base of model are the relative importance and frequency of disturbance types in rainforest (low flammability), wet sclerophyll forest and dry sclerophyll forest (high flammability). *Dashed lines* indicate the boundaries of the ecotone with rainforest and dry sclerophyll forest. The layered understorey of wet sclerophyll forest is dynamic, where increased fire frequency will favour the persistence of fire-tolerant taxa and reduce the mesophyllous component; the DSF boundary will shift left into the ecotone. During extended fire-free periods, the sclerophyllous component will diminish from the ecotone and gap-phase rainforest taxa will become more predominant; the RF boundary will shift right into the ecotone. The persistence of understorey species will depend on their ability to regenerate under the prevailing disturbance regime, i.e. fire only, fire and gap formation, or gap formation only

in response to (1) burning; (2) manual removal of ground layer vegetation; (3) removal of surface litter; (4) surface scarification and (5) vertebrate herbivore exclusion. Where possible, we also diagnosed the cause of seedling mortality. We used this decomposition of the recruitment process to consider processes regulating population expansion and persistence across the wet sclerophyll ecotone.

Materials and methods

Study area

Our research was undertaken in montane wet sclerophyll forest along the eastern edge of the New England Tableland Bioregion, northern New South Wales, Australia. The New England montane wet sclerophyll forests are restricted to areas of high rainfall (>950 mm) on a rugged, mountainous escarpment exceeding 1200 m elevation. They are characterised by a eucalypt-dominated overstorey, typically exceeding 30 m in height, and a well-developed layered understorey of sclerophyllous species and cool or warm temperate rainforest taxa. In protected situations, these communities grade into cool or warm temperate rainforests (Hunter 1998; Benson and Ashby 2000). Many areas of montane wet forests on the New England Tablelands have been used for hardwood timber production and cattle grazing. Consequently they have been exposed to a regime of frequent, low-intensity fires that were applied to stimulate eucalypt germination after logging or to stimulate new growth for grazing. A high fire frequency, however, is thought to reduce the diversity of the understorey by removing the mesophyllous species and promoting growth of fire-tolerant grasses and forbs (Binns 1991).

Study sites

Field experiments were conducted along the edge of the New England Tableland escarpment at Cunnawarra National Park (Cunnawarra) and Mummel Gulf National Park (Mummel Gulf). Both parks had were partially burnt in spring (October) 2001, allowing comparison of burnt and unburnt sites in each park. The fire at Mummel Gulf was a back burn to contain a grass fire from a neighbouring property. This fire was of low intensity and resulted in complete removal of the understorey and ground strata, but most of the canopy remained intact. The burnt site at Cunnawarra was a wildfire that scorched the tree canopy and consumed the lower strata. The structure and composition of the unburnt forest was similar in the two parks, except that the Mummel Gulf site had greater cover of shrubs (<1.5 m in height) in the mid-stratum and grasses in the ground stratum than the Cunnawarra site (Table 1). In contrast, the litter layer was more prevalent at Cunnawarra but for both sites, the litter depth was deeper in unburnt forest (Table 1). Analysis of soil properties at Mummel Gulf indicated that soil moisture and organic carbon content was similar in in burnt and unburnt forest (Table 1).

Study species

Recruitment processes were investigated in two understorey shrub species characteristic of fire-prone open eucalypt forests *Banksia integrifolia* subsp. *monticola* K.R.Thiele (*Proteaceae*) and *Goodia lotifolia* Salisb. (*Fabaceae*), and two species characteristic of low-flammability rainforest vegetation, *Trochocarpa laurina* (Rudge) R.Br. (*Ericaceae*) and *Tasmannia stipitata* (Vickery) A.C.Sm. (*Winteraceae*), hereafter *Banksia*, *Goodia*, *Trochocarpa* and *Tasmania.* All four species are widespread and relatively in abundant ecotonal wet sclerophyll forests on the New England Tablelands: The four species differ in their dispersal modes, seed traits and recruitment syndromes (Table 2), but their combinations of life-history traits are representative of other understorey taxa in the New England wet sclerophyll forests. Field observations on all four species indicated that the structure of most populations was skewed towards adult life-stages, suggesting that seedling recruitment was uncommon (Campbell 2004).

Seed germination and emergence

The field germination experiment was factorial in design with two levels of habitat (burnt vs. unburnt forest) and four levels of substrate treatment replicated at each study site. Substrate treatments were designed to test for the independent effects of litter, competition with surrounding live vegetation and soil disturbance, relative to a control. The effects of removing litter and ground vegetation were examined individually because each dominates different patches of the heterogeneous floor of unburnt forest. In litter removal plots, bare ground was exposed prior to planting seeds. In the ground layer, removal treatment biomass less than 1 m in height was clipped at ground level with secateurs and discarded outside of the plot. Litter and biomass of competing ground cover species were removed repeatedly from their respective plots throughout the experiment. The soil scarification treatment involved excavating the soil to a depth of 10 cm and manually turning and then replacing the soil prior to seed sowing. In each habitat, there were three randomly placed replicate experimental plots of each treatment, giving a total of 12 replicate plots in each habitat type. Experimental plots measured approximately 70×70 cm^2 and were enclosed by a polythene mesh cage (approx. 1 m in height and with a mesh aperture of approx. 0.5×0.5 cm^2) to exclude vertebrate herbivores from access to emerging seedlings. Field experiments were set up in habitat types (burnt vs. unburnt forest) that were at least 50 m apart, with experimental plots being located at least 5 m apart within each habitat type. The spatial separation between habitat types and experimental plots was constrained by the spatial pattern of the fire and the remote locations of our study sites. However, the experimental layout used is considered to be a reasonable approximation of random sampling in relation to the spatial scale of the processes under investigation. Seed germination and seedling emergence vary on highly localised spatial scales in the order of centimetres (e.g. Lamont et al. 1993),

Table 1 Characteristics of burnt and unburnt forest at each study site (approximately 6 months after fire)

	Cunnawarra		Mummel Gulf	
	Unburnt	Burnt	Unburnt	Burnt
Canopy cover (%)	50–55	40–45	35–40	25–30
Understorey cover (%)	35–40	5–10	60–65	10–15
Ground cover (%)	5–10	10–15	75–80	15–20
Litter depth (cm)	4.8 (0.2)	1.1 (0.2)	2.7 (0.1)	1.3 (0.2)
Height of fire scars (m)	n.a.	13.1 (1.9)	n.a.	8.2 (1.1)
Lithology	Metasediment		Metasediment	
Soil moisture (%)	n.a.	n.a.	32.1 (0.7)	30.7 (0.7)
Organic content (%)	n.a.	n.a.	21.4 (1.0)	21.8 (1.1)

Data are ranges or mean (±s.e.); *n.a.*, not available. Canopy, understorey and ground cover were estimated visually, litter depth measured with standard ruler at ten random points within the experimental area, height of fire scars estimated visually on ten randomly selected trees. Soil analysis conducted on 12 replicate soil cores taken to 5 cm in depth in burnt and unburnt forest. Organic content determined using loss on ignition method

n.a. not available

indicating that fine-scale spatial variation has a larger influence on the germination and emergence outcomes than variation over larger distances. The factorial design of our experiment is therefore considered to have sufficient independence and power to detect differences between habitat and treatment types, given the spatial resolution of experimental plots is appropriate for the processes being measured and frequent-repeat sampling has been used to measure experimental outcomes over time.

Seeds/fruits of each species were collected from field populations at Cunnawarra, Mummel Gulf and an additional site Guy Fawkes River National Park. Pre-experiment viability tests indicated that greater than 80 % of seed rain produced by each species was viable (Table 2). Ten seeds/fruits of each species were sown per replicate plot in mid-autumn (April) 2002, approximately 6 months after fire. Seeds/fruits (depending on their size) were planted at a maximum depth of 1 cm, at a randomly allocated planting depot on a grid of 5 × 10 total depots. Planting depots were at least 2 cm apart in order to reduce the possibility of density-dependent effects on germination (Bergelson and Perry 1989). Each planting depot was marked with a species-specific colour-coded bamboo skewer so that germination, emergence and survival could be followed for each individual seed. As seeds and intact fruits are both diaspores in *Tasmannia*, both were sown separately in this experiment. Seed coat dormancy of *Goodia* seeds was broken by manual scarification prior to planting. Plots were watered for the first 2 days after planting of seeds and then at each census event.

The field experiment ran for a total of 12 months with germination, emergence and survival assessed monthly for 7 months and then at two-month intervals for a further 4 months. Germination and emergence was scored when the cotyledons had emerged above the soil surface. The condition of emerged seedlings was noted for the duration of the experiment, and where possible the most likely cause of mortality recorded. Germination data were analysed using orthogonal logit-linear models (analysis of deviance) with binomial error distributions in GLMStat$^{\text{TM}}$ (Beath 2001). The assumption of homogeneity of variances was validated for all samples using the Cochran's test on the binomial variances. The binomial denominator was defined by the number of seeds planted for *Banksia*, *Goodia* and *Tasmannia* ($n = 10$). For *Tasmannia* (fruits) and *Trochocarpa*, the average number of seeds per fruit (Table 2) × 10 (fruits planted per replicate) was used as the binomial denominator, therefore $n = 80$ and $n = 30$, respectively. Significance of the models was determined by Pearson's Chi-square function in GLMStat$^{\text{TM}}$ (Beath 2001). When a significant difference between factors was detected, pair-wise contrasts with a Bonferroni correction were used for multiple comparisons between means.

Table 2 Life-history traits of study species

Family/species	Growth form	Foliage type	Dispersal mode	Fire response	Post-fire recruitment	Annual seed/fruit rain per plant	Proportion of seed rain viable	No. seeds/ fruit	Dry mass (mg)	Seed bank half-life (yearrs)
Proteaceae Banksia itegrifolia subsp *monitcola*	Small tree	L, Sc	Wind	I, VI	+	536 (102.6)	0.9 (0.02)	n.a.	5.9 (0.2)	<1
Fabaceae *Goodia lotifolia*	Shrub	S, Me	Invertebrate	IV, V	+	41.1 (7.9)	1.0 (0.01)	n.a.	24.0(0.5)	5.2
Winteraceae *Tasmannia stipitata*	Shrub	L, Me	Vertebrate	V	–	424.6^a (75.6)	0.8 (0.06)	8.2 (1.6)	92.9 $(3.2)^a$ 2.1 (0.04)	0.7
Ericaceae *Trochocarpa laurina*	Small tree	L, Me	Vertebrate	V	–	255.8^a (35.1)	0.8 (0.05)	3.1 (0.1)	134.5 $(5.6)^a$	0.8

Foliage types: *L*, Large leaf; *S*, Small leaf; *Sc*, Sclerophyllous; *Me*, Mesophyllous; *n.a.* not applicable. Fire responses from Campbell and Clarke (2006): I, fire killed with a canopy seed bank; IV, responds via root suckers; V, resprouts via basal stems; VI, resprouts via stem bud bank. Data are means (standard error in parantheses). Mean weight obtained from 100 seeds/fruits of each species. Mean number of seeds per fruit for *Tasmannia* and *Trochocarpa* were calculated from 50 fruits. Annual seed rain and seed bank half-life data from Campbell et al. (2012)

[a] Fruit

Seedling survival

The seedling survival experiment was carried out in burnt and unburnt forest at Mummel Gulf during spring (October) 2002, approximately 1 year after the fire had occurred at the burnt site. Due to logistic constraints (access and seedling availability), the experiment could not be replicated at Cunnawarra. The field experiment was factorial in design with the three factors each having two levels: habitat (burnt vs. unburnt), vertebrate herbivory (plots caged vs. uncaged) and ground stratum manipulation (ground cover intact vs. ground cover removed). There were three replicates of each combination of the treatments, giving 12 replicate plots within each habitat (24 plots in total). Cages were constructed out of portable fences, three of which were wired together to form triangular exclosures, $2 \times 2 \times 2\ \text{m}^3$ in dimension and 1 m high. The experimental areas of uncaged plots were the same size and shape as caged plots and were marked with star pickets. Habitat types were at least 50 m apart and experimental plots were located at least 5 m apart within each habitat, which was considered sufficient to ensure independence while allowing for efficient set up and monitoring of the experiment. Manipulation of the ground stratum involved physically removing all live vegetation to 1 m in height or leaving the ground cover intact. In plots where groundcover had been removed, new growth was continually clipped off with secateurs for the duration of the experiment.

Seedlings were grown in the glasshouse from seed collected from study populations at three different sites. Seeds of *Banksia* and *Goodia* (seeds were scarified prior to planting due to seed coat imposed dormancy) were directly planted into tubes filled with sterilised potting mix and germinated and raised in the glasshouse until 3 weeks of age. *Tasmannia* and *Trochocarpa* seeds were germinated first in an incubator set at 12-h light/12-h dark with a corresponding temperature regime of 25/15 °C. Young seedlings were transplanted into tubes of sterilised soil and subsequently grown on a heat and mist bed for at least 1 week to aid establishment. Due to slower growth rates, *Tasmannia* and *Trochocarpa* seedlings were then grown under glasshouse conditions until 5 weeks of age. To reduce the risk of death induced by transplant shock, seedlings were grown outside the glasshouse for at least 3 weeks prior to planting in the field.

Six seedlings of *Banksia*, *Goodia* and *Tasmannia* were planted per replicate (144 seedlings per species). Due to low levels of emergence, there were only five *Trochocarpa* seedlings per replicate plot (115 seedlings in total). At the time of planting, all seedlings had at least three pairs of true leaves. Seedlings were planted in random positions on a triangular shaped grid within the experimental area of each plot. To enable relocating the seedlings, each seedling was marked with a steel pin and numbered metal tag and the position of each seedling within each plot mapped. Seedlings were watered in (10 L per plot) for 2 days following initial planting and then at each census of seedling survival.

The survival and condition of each seedling was recorded at 1, 2, 4, 8, 16 and 28 weeks from original planting date. A seedling was considered dead if the shoot was no longer green and stems were not malleable to gentle pressure. Where possible, a cause of mortality was assigned to dead seedlings. The condition of surviving seedlings was also monitored and allocated to one of six pre-defined categories, which were defined as follows: good, shoot green and flexible to touch; low-grade water stress, minor wilting of leaf edges and tips; high-grade water stress, most leaves and parts wilted and brown; lightly grazed, some nibbling of leaf/shoot parts; heavily grazed, complete defoliation or seedling uprooted; and resprouting, new shoots or regrowth from damaged plants. Given the warm and dry climatic conditions preceding and during the experiment, wilting of transplanted seedlings was attributed to water stress rather than factors such as pathogens or disease.

The proportion of seedlings surviving 28 weeks was analysed with logit-linear models (analysis of deviance) with binomial error structures in GLMStat$^{\text{TM}}$ (Beath 2001). The assumption of homogeneity of variances was validated for all samples using Cochran's test on the binomial variances. The binomial denominator was defined as the number of seedlings planted per replicate plot ($n = 6$ for *Banksia*, *Goodia* and *Tasmannia*; $n = 5$ or 4 for *Trochocarpa*). Significance of models was determined by Pearson's Chi-square function in GLMStat$^{\text{TM}}$ (Beath 2001). When a significant difference between factors was detected, pair-wise contrasts with a Bonferroni correction were used for multiple comparisons between means.

Variation in seedling survival between treatment combinations was also examined using survival

Table 3 Significance of habitat treatment effects on proportion of seeds germinating and emerging after 12 months (analysis of deviance)

Factor	*Banksia*		*Goodia*		*Tasmannia* (fruits)		*Tasmannia* (seeds)		*Trochocarpa*	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Site	0.1	n.s.	0.6	n.s.	3.2	n.s.	0.2	n.s.	1.3	n.s.
Habitat (H)	2.7	n.s.	1.7	n.s.	0.6	n.s.	1.2	n.s.	0.0	n.s.
Treatment (T)	1.8	n.s.	0.1	n.s.	0.5	n.s.	0.3	n.s.	5.0	**
H × T	2.8	n.s.	1.3	n.s.	2.0	n.s.	2.0	n.s.	0.7	n.s.

n.s. not significant

** $P < 0.01$, * $P < 0.05$

analysis (based on failure-time analysis; Fox 1993). Cox's proportional hazards models, in Statview™ (SAS Institute Inc. 1998), were used to investigate whether treatments increased or decreased the survival hazard (death) of transplanted seedlings compared to seedlings in control plots. Time (since initial planting) of recorded death was the event variable used in the models. Seedlings that were still alive at the conclusion of the experiment were right-censored in the analysis (Fox 1993). Right-censored individuals contribute information to the survivor function, but do not provide statistical information about hazard or age at death, hence their use in proportional hazards models was appropriate (Cox and Oakes 1984; Crawley 1993). Plots of log cumulative hazard versus time for different treatment pairs (e.g. burnt vs. unburnt, caged vs. uncaged) were used to validate the assumption of proportionality for hazard functions.

Results

Seed germination and emergence experiment

There was no significant difference in germination and emergence of any species between our two study sites (Table 3). Data were therefore pooled and analysed for habitat and treatment effects. There were no significant effects of habitat or treatment on the proportion of seeds germinating in *Banksia*, *Goodia* or *Tasmannia* (fruit or seed) (Table 3; Fig. 2). However, significantly more seed germinated from *Trochocarpa* fruits in plots where the soil had been scarified than in control plots (Table 3; Fig. 2). *Goodia* had more experimentally buried seeds germinate than any other species (Fig. 2). Overall, germination was higher in *Banksia* and *Goodia* than in the two species from low-flammability forests (Fig. 2). The majority of *Banksia* and *Goodia* seeds germinated within 2 months of planting, whereas *Tasmannia* and *Trochocarpa* showed delayed germination until 10 months after planting. Germination events for the latter two species were therefore restricted to the final two census dates and span a period of only 4 months as opposed to the 12 months for *Banksia* and *Goodia*.

Mortality rates of emerged *Banksia* and *Goodia* seedlings were similar over the six-month period and water stress (indicated by wilting of the plant body) was consistently the major cause of death in emerged *Banksia* (64 %) and *Goodia* seedlings (69 %). Other factors limiting survival of emerged seedlings were smothering by litter, 11 % in *Banksia* and 4 % in *Goodia*, and grazing by invertebrate herbivores 3 and 11 %, respectively. Mortality rates in *Tasmannia* and *Trocahocarpa* were negligible at the end of the experiment.

Seedling survival experiment

After 28 weeks, there was a marked difference in the overall survival of planted seedlings of between species from more flammable forests and those from more mesic systems. Around 56 % of *Banksia* seedlings and 57 % of *Goodia* seedlings were still alive at the last census date. In comparison, *Tasmannia* and *Trochocarpa* seedlings experienced high rates of mortality with only 6 and 8 % (respectively) of seedlings surviving at 28 weeks. In most cases, survival curves approached Type III survivorship

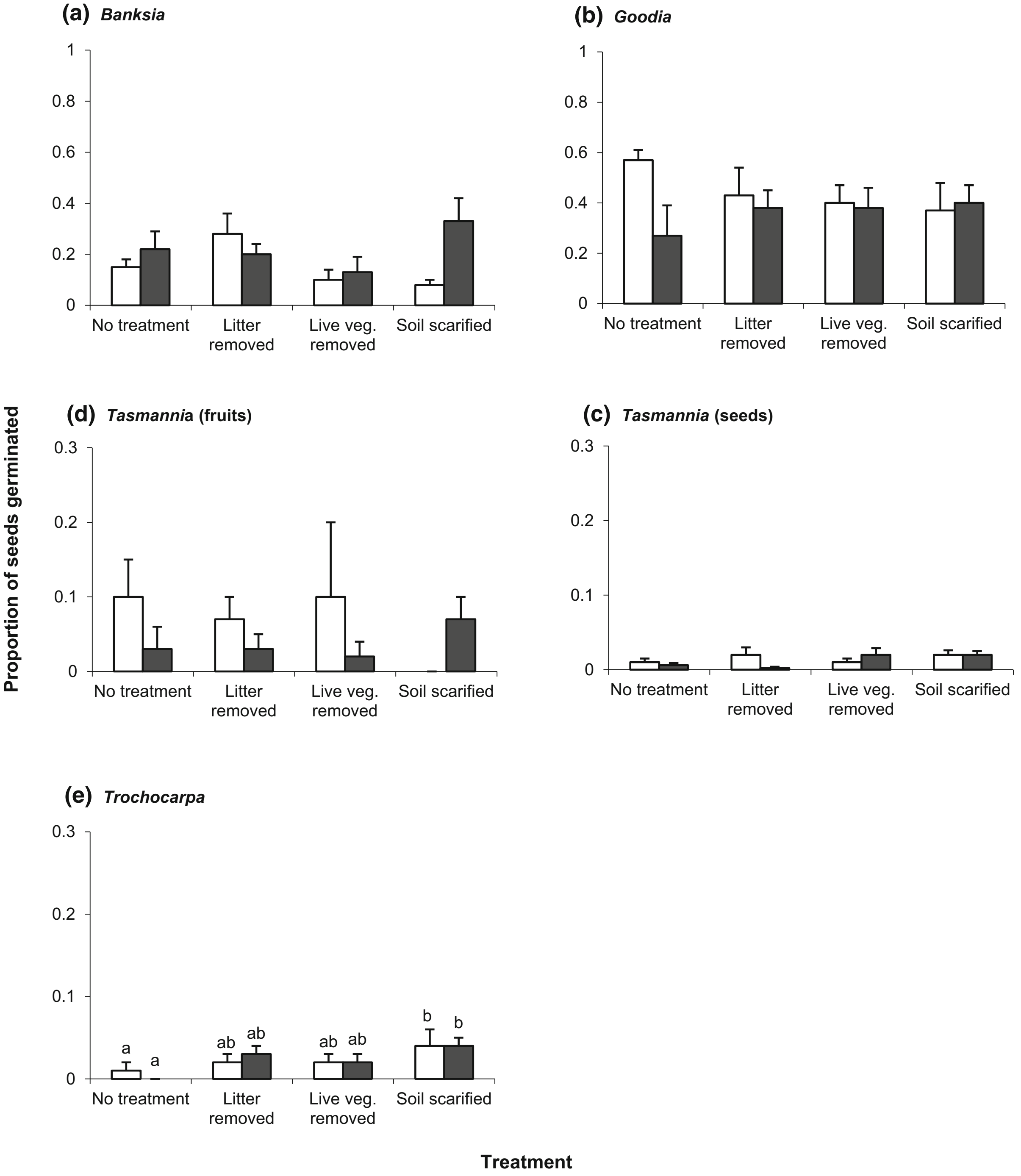

Fig. 2 Mean (+ s.e.) proportion of experimentally sown seeds that germinated within 12 months of planting in four treatments in unburnt (*unshaded bars*) and burnt forest (*shaded bars*) at Cunnawarra and Mummel Gulf. Data are pooled across sites as no significant site effect on germination was found in any species. For **e** *Trochocarpa* different letters denote a significant difference (Bonferroni test, $P < 0.05$). No significant effects of habitat or treatment on germination were found in the other three species. Note that y-axis differs between species

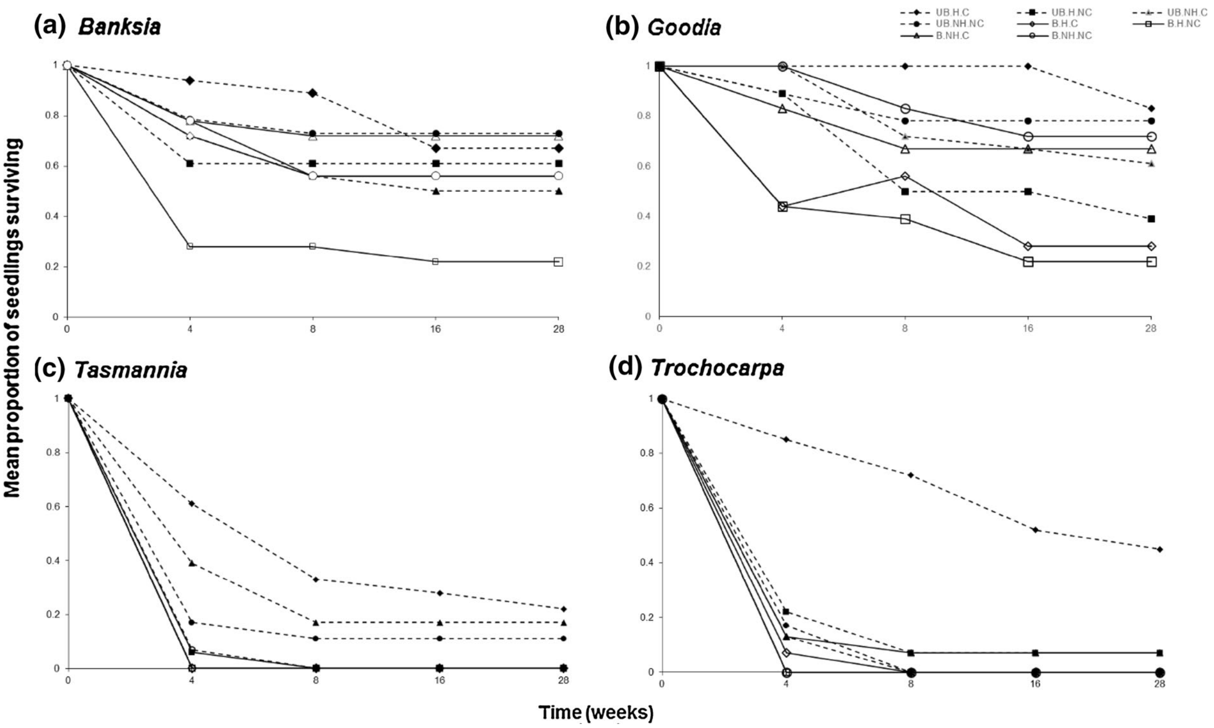

Fig. 3 Seedling survival over 28 weeks in unburnt and burnt forest at Mummel Gulf. *UB*, Unburnt; *B*, Burnt; *NC*, No competition (*groundstorey removed*); *C* (*groundstorey left intact*), Competition; *H*, Herbivory (*uncaged plots*); *NH*, No herbivory (*caged plots*)

Table 4 Significance of habitat treatment effects on proportion of seedlings surviving after 28 weeks (analysis of deviance)

Factor	*Banksia*		*Goodia*		*Tasmannia*		*Trochocarpa*	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Habitat (H)	1.5	n.s.	3.1	n.s.	25.8	***	9.7	**
Caged (C)	1.5	n.s.	6.8	*	0.3	n.s.	8.2	*
Groundcover removal (G)	0.9	n.s.	0.5	n.s.	6.7	*	9.4	**
H × C	2.3	n.s.	3.0	n.s.	$1.9e^{-6}$	n.s.	10.8	**
H × G	3.6	n.s.	0.5	n.s.	$9.7e^{-5}$	n.s.	0.3	n.s.
C × G	1.6	n.s.	3.5	n.s.	5.9	*	$3.9e^{-5}$	n.s.
H × C × G	0.1	n.s.	1.5	n.s.	$6.3e^{-4}$	n.s.	$5.4e^{-4}$	n.s.

n.s. not significant

*** $P < 0.001$,
** $P < 0.01$,* $P < 0.05$

(Deevey 1947), where mortality decreased with time since planting (Fig. 3).

Seedling survival in burnt and unburnt forest

Goodia, Tasmannia and *Trochocarpa* seedlings experienced significantly greater mortality in burnt than unburnt forest (Table 4; Fig. 3). No seedlings of *Tasmannia* and only 2 % of *Trochocarpa* seedlings survived more than 28 weeks in burnt forest. Survival analysis confirmed that the survival hazard was significantly greater in burnt conditions relative to unburnt conditions for *Goodia*, *Tasmannia* and *Trochocarpa* seedlings (Table 5; Fig. 3). There was no significant difference in survival of *Banksia* seedlings between burnt and unburnt sites after 28 weeks (analysis of deviance, Table 4; Fig. 3).

Table 5 Summary of significant proportional hazards models for effects of experimental factors on seedling over 28 weeks

Experimental factors	Beta coeff.	*df*	*P* (Wald)	Biological interpretation
Banksia				
Burnt—caged versus uncaged	−0.8	1	*	Survival hazard decreases 22 % when herbivores are excluded
Burnt, uncaged—gc intact versus gc removed	−1.0	1	*	Survival hazard decreases 3 % when ground cover left intact
Goodia				
Burnt versus Unburnt	0.9	1	***	Survival hazard increases 13 % in burnt forest
Burnt—caged versus uncaged	−1.6	1	***	Survival hazard decreases 53 % when herbivores are excluded
Unburnt, uncaged—gc intact vs. gc removed	−1.8	1	***	Survival hazard decreases 79 % when ground cover left intact
Tasmannia				
Burnt versus Unburnt	1.0	1	***	Survival hazard increases 4 % in burnt forest
Unburnt, uncaged—gc intact versus gc removed	−1.2	1	**	Survival hazard decreases 20 % when ground cover left intact
Trochocarpa				
Burnt versus Unburnt	0.6	1	**	Survival hazard increases 42 % in burnt forest
Unburnt—caged versus uncaged	0.8	1	**	Survival hazard increases 17 % in caged plots
Unburnt, uncaged—gc intact versus gc removed	−1.5	1	**	Survival hazard decreases 52 % when ground cover left intact

A negative beta coefficient denotes a decrease in survival hazard (i.e. death)

n.s. not significant, *gc* ground cover

*** $P < 0.001$, ** $P < 0.01$

Herbivory and seedling survival

Overall, exposure to herbivores increased the mortality of *Banksia* and *Goodia* seedlings, with herbivory significantly decreasing the survival of seedling in burnt forest (analysis of deviance, Table 4; Fig. 3). Survival analysis further demonstrated that for both of these species exclusion of herbivores in burnt forest plots significantly decreased the survival hazard for *Goodia* seedlings by 53 % and for *Banksia* seedlings by 22 % (survival analysis, Table 5). In *Tasmannia*, there was no significant effect of herbivore exclusion on seedling survival in either burnt or unburnt habitat (analysis of deviance, Table 4; Fig. 3). Interestingly, exclusion of herbivores increased the survival hazard for *Trochocarpa* seedlings by 17 % (survival analysis, Table 5; Fig. 3). Both mesic species experienced extremely high rates of mortality in the burnt forest, which may have left too few survivors to detect whether herbivory was having a significant effect of seedling survivorship.

Competition and seedling survival

In this experiment, evidence of reduced seedling survivorship associated with competition with the ground stratum was not detected in any of the species (analysis of deviance, Table 4; Fig. 3). On the contrary, an intact ground stratum had a positive effect on seedling survival particularly in unburnt forest plots where herbivores had not been excluded (i.e. uncaged plots). Survival analysis confirmed that leaving the ground cover intact in the unburnt forest reduced the survival hazard for seedlings in *Goodia* by 79 %, *Tasmannia* by 20 % and *Trochocarpa* by 52 % (survival analysis, Table 5; Fig. 3). In contrast, in burnt forest plots with herbivore access intact ground cover reduced the survival hazard only marginally for *Banksia* seedlings by 3 % ($P < 0.05$) (survival analysis, Table 5; Fig. 3) but had no effect for *Goodia*, *Tasmannia* or *Trochocarpa*.

Causes of seedling death

There were two main factors causing seedling mortality in this experiment: vertebrate herbivores and water stress. Vertebrates caused seedling death either through direct consumption of live biomass or by uprooting the seedling. In *Banksia* and *Goodia*, grazing was the most common cause of death in burnt forest, accounting for 57 % and 54 % of seedling mortality, respectively. For both species, water stress was the main cause of death in caged plots in burnt and also in unburnt forest. Around 37 % of *Banksia* and 35 % of *Goodia* seedlings that had been severely grazed were able to resprout and return to a healthy condition. No *Banksia* seedlings survived severe water stress, but 36 % of *Goodia* seedlings in unburnt forest and 11 % in burnt forest resprouted after defoliation through resulting from water stress. The high rates of mortality in *Tasmannia* and *Trochocarpa* were caused by water stress in both burnt and unburnt forest. No seedlings of either species resprouted after defoliation through water stress.

Discussion

Recruitment and fire

Recruitment syndromes varied among the four species that we studied, although there was a broad dichotomy between species from low-flammability rainforest (*Tasmannia* and *Trochocarpa*) and those from more flammable systems (*Banksia* and *Goodia*). Seedlings of *Tasmannia* and *Trochocarpa,* successfully emerged in both burnt and unburnt forest, consistent with expectations for fire-independent recruitment. However, these seedlings had low survival rates in the harsher environmental conditions in the post-fire environment, suggesting that they may be unable to persist and transition to juvenile plants when the ecotonal forest experiences recurring fire.

In contrast, *Banksia* and *Goodia*, demonstrated risk-spreading recruitment strategies that potentially provide more opportunity for persistence and expansion throughout the ecotone. Our results indicate that successful emergence and persistence of *Goodia* seedlings in post-fire environment is strongly consistent with fire-dependent recruitment patterns often observed in species from high-flammability vegetation. Like other legumes, *Goodia* has the potential to develop a long-lived soil seed bank (Table 2; Campbell et al. 2012) and post-fire episodes of recruitment have previously been observed in wet sclerophyll forests of the New England region (Campbell and Clarke 2006). However, when physical dormancy was broken *Goodia* seedlings emerged in unburnt forest. This and the high seedling survival rates that we observed in unburnt forest suggest that *Goodia* is capable of recruiting from seed during fire-free periods. This could occur either if some non-dormant seed is produced in each crop or if a fraction of the persistent soil seedbanks is released from dormancy spontaneously over time (Auld et al. 2000). *Goodia* is apparently able to spread risk of recruitment failure by having some capacity for fire-independent recruitment, albeit at lower rates than may occur after fire.

Banksia showed similar levels of seedling emergence and survival in burnt and unburnt forest, suggesting a capacity for both fire-dependent and fire-independent recruitment. Unlike other *Banksia* species in the New England region, our focal species does not retain seeds in its canopy for multiple years, suggesting fire-stimulated seed release is not critical to the recruitment dynamics of this species (Campbell et al. 2012). Moreover, the reliance on regular production of non-dormant seed is consistent with reproductive strategies of species that depend on large-scale disturbances such as fire for seedling recruitment. However, like *Goodia*, pulses of seedling recruitment in *Banksia* have been observed post-fire (Campbell and Clarke 2006), and cohorts of seedlings have been recorded in unburnt forests that have been exposed to some form of disturbance (i.e. road verges; Campbell 2004). The low and patchy occurrence of seedlings in unburnt forest may be explained by factors operating at the seed production phase, as less than 30 % of inflorescences have been observed to develop into infructescences (Campbell 2004). The ability of *Banksia* to recruit seedlings either in the absence of or following fire events may offset risks posed by variability in seed production.

Recruitment and small-scale processes

We found no evidence that either litter or gaps in the litter layer created safe sites for seedling recruitment in any of our four study species, contrary to previous studies in a range of other systems (Facelli and Pickett 1991; Vazquez-Yanes and Orozco-Segovia 1993; Lamont et al. 1993; Christie and Armesto 2003). Litter was expected to have some influence on germination and emergence of the small-seeded *Tasmannia* and *Trochocarpa*, as litter depth has been shown to negatively influence the abundance of small-seeded species in rainforest communities (Molofsky and Augspurger 1992; Christie and Armesto 2003). Germination and emergence in *Trochocarpa* was, however, increased by soil scarification. Positive effects of soil scarification on the emergence of woody understorey species have also been observed in Victorian wet sclerophyll forests (Ashton and Chinner 1999) and small-seeded temperate tree species (Willis et al. 2015). Clarke and Davidson (2001) attributed an increase in temperate grassland shrub recruitment following scarification of the soil to refuge from seed predators and improved water relations. Elevated safe sites, such as logs, have also been found to increase germination and emergence of small-seeded shrub and tree species in temperate and tropical rainforest by providing refuge from burial in the litter layer (Molofsky and Augspurger 1992; Christie and Armesto 2003; Lusk and Kelly 2003).

The presence of neighbouring plants has also been reported to limit germination and emergence of a wide range of plant species (Winn 1985; Tripathi and Khan 1990; Williams 2000), but we found no evidence of this relationship in our study species. It is possible that the live ground cover in our experimental plots was not dense enough to suppress germination and emergence of sown seed.

Seedling survival

Mammalian browsing was a significant factor limiting survival of *Banksia* and *Goodia* seedlings in burnt forest. The post-fire abundance and foraging behaviour of herbivores could therefore influence the future distribution of adult plants in the established community. Previous studies in wet sclerophyll and other forest communities have found that increased levels of herbivore activity following fire had a substantial effect on the composition and structure of the post-disturbance community (e.g. Cremer and Mount 1965; Leigh and Holgate 1979; Parsons et al. 2007; Dexter et al. 2013). More work is needed to understand the variability in post-fire herbivory to identify safe sites that promote seedling survival. However, fire patch size may influence the activity of herbivores in the post-disturbance community (e.g. Dickinson and Kirkpatrick 1986; Whelan 1995). Low-intensity, patchy fires (such as the burn Mummel Gulf) may be expected to promote more herbivore activity than broad-scale, high intensity fires that result in higher mortality of herbivores and provide fewer post-fire refuges from their predators. To test this hypothesis, future studies will need to compare rates of post-fire seedling survival across a range of fire sizes and intensities.

At the landscape scale, the ability to recruit seedlings during fire-free periods may provide some bet-hedging capacity against recruitment failure under high levels of post-fire herbivory. Our data suggest that intact ground layer vegetation promotes the survival of herbivore-limited species, *Bansksia* and *Goodia* (Fig. 3). The strength of this effect would depend on the spatial scale of fire mosaics in relation to herbivore movement and behaviour (Parr and Anderson 2006). Such effects, if they exist, could be stronger in *Banksia* populations than *Goodia*, due to its greater capacity to recruit between events. However, Price and Morgan (2003) attributed skewed age structures and a lack of recruitment in long unburnt coastal populations of *B. integrifolia* subsp. *integrifolia* to seedling predation by vertebrate herbivores.

Water stress, not herbivory, was found to be the critical factor limiting seedling survival in *Tasmannia* and *Trochocarpa*. Overall, rates of seedling survival of these mesic species were substantially lower than in *Banksia* and *Goodia*, particularly in the burnt forest. The temperatures and solar radiation associated with large gaps have been found to inhibit germination, stunt growth and reduce seedling survival of shade-tolerant species in tropical forests (Denslow 1987). Bowman and Panton (1993) concluded that edaphic factors and harsh microclimate conditions limited recruitment of monsoon-rainforest tree species in open savanna habitat, while Gray and Spies (1996) determined that the high surface temperatures, desiccation and soil moisture loss associated with exposed environments accounted for conifer seedling mortality in gaps of varying sizes.

Our data suggest that intact groundcover provides safe sites for seedling survival in *Tasmannia* and *Trochocarpa* by reducing exposure to desiccation. Facilitation or ‘nurse’ plant effects have been reported in a range of different forest systems (Bertness and

Calaway 1994; Hoffmann 1996, 2000; Eccles et al. 2001; Price and Morgan 2003). The mechanisms of facilitation relate to both the amelioration of desiccating microclimate conditions and protection from herbivores The lack of facilitation in burnt forest appears to be a major barrier to recruitment of *Tasmannia* and *Trochocarpa* seedlings in burnt forest and hence a driving factor in their event-independent recruitment response.

Conclusions

The coexistence of rainforest and dry forest plant species in the wet sclerophyll ecotone appears to be supported by differentiation of their regeneration niches through alternative recruitment syndromes. Overall, our results suggest that the shrubs typically associated with mesic, infrequently burnt forests (*Tasmannia, Trochocarpa*) may be able to recruit from seed in the post-fire environment but constraints on seedling survival in open, desiccating post-fire environments may limit the distribution and abundance of adult populations through the ecotone. In contrast, the shrubs associated with more flammable open forest environments (*Banksia, Goodia*) appear capable recruiting after fire and during fire-free periods. Mechanisms that regulate seed availability (physical dormancy, fire-stimulated seed release) suggest that post-fire recruitment in *Banksia* and *Goodia* is likely to be more abundant after fire than at other times. However, the ability of these species to recruit in undisturbed conditions provides some insurance against recruitment failure under stochastic and uncertain post-fire conditions, particularly in relation to varied levels of herbivory and desiccating conditions. The capacity to spread risks in this way could be important in their persistence within infrequently burnt wet sclerophyll forests, and hence the position and stability of the ecotone and floristic diversity of these systems. The contrasting mechanisms and sensitivities we have observed suggest that multiple mechanisms at different stages through the recruitment process sustain species and functional diversity of ecotonal vegetation across the flammability gradient.

Acknowledgments This research was funded by an Australian Research Council Linkage grant with the New South Wales National Parks and Wildlife Service and University of New England. We thank Richard Willis and Shanti Virgona for their invaluable assistance with field and laboratory work. We also thank the anonymous reviewers who provided comments on drafts of this manuscript. This manuscript is dedicated to Peter J Clarke, a mentor, colleague and friend who will be missed.

References

Ashton DH, Attiwill PM (1994) Tall open-forest. In: Groves RH (ed) Australian vegetation. Cambridge University Press, Cambridge, pp 157–196

Ashton DH, Chinner JH (1999) Problems of regeneration of the mature *Eucalyptus regnans* F. Muell. (the Big Ash) forest, in the absence of fire at Wallaby Creek, Victoria, Australia. Aust For 62:265–280

Auld TD, O'Connell MA (1991) Predicting patterns of post-fire germination in 35 eastern Australian *Fabaceae*. Aust J Ecol 16:53–70

Auld TD, Keith DA, Bradstock RA (2000) Patterns of longevity of soil seedbanks in fire-prone communities of south-eastern Australia. Aust J Bot 48:539–548

Beath KJ (2001) GLMStat Version 5.5. User Manual. Sydney Australia

Bell DT, Plummer JA, Taylor SK (1993) Seed germination ecology in southwestern Western Australia. Bot Rev 59:24–73

Benson JS, Ashby EM (2000) Vegetation of Guyra 1:100 000 map sheet New England Bioregion, New South Wales. Cunninghamia 6:747–872

Bergelson J, Perry R (1989) Interspecific competition between seeds: relative planting date and density affect seedling emergence. Ecology 70:1639–1644

Bertness MD, Calaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Binns DL (1991) Vegetation dynamics of *Eucalyptus microcorys—E. saligna* wet sclerophyll forest in response to logging. Masters thesis, University of New England

Bond WJ, Woodward FI, Midgley GF (2005) The global distribution of ecosystems in a world without fire. New Phytol 165:525–538

Bowman DMJS (2000) Australian rainforests: Islands of green in a land of fire. Cambridge University Press, Cambridge

Bowman DMJS, Panton WJ (1993) Factors that control monsoon-rainforest seedling establishment and growth in north Australian *Eucalyptus* savanna. J Ecol 81:297–304

Campbell ML (2004) Population dynamics of montane wet sclerophyll forest understorey species. PhD Thesis, University of New England

Campbell ML, Clarke PJ (2006) Response of montane wet sclerophyll forest understorey species to fire: evidence from high and low intensity fires. Proc Linn Soc NSW 127:63–73

Campbell ML, Clarke PR, Keith DA (2012) Seed traits and seed bank longevity of wet sclerophyll forest shrubs. Aust J Bot 60:96–103

Christie DA, Armesto JJ (2003) Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile. J Ecol 91:776–784

Clarke PJ, Davison EA (2001) Experiments on the mechanism of tree and shrub establishment in temperate woody grasslands: seedling emergence. Aust Ecol 26:400–412

Clarke PJ, Knox KJE, Butler D (2010) Fire intensity, serotiny and seed release in 19 woody species: evidence for risk spreading among wind-dispersed and resprouting syndromes. Aust J Bot 58:629–636

Cox DR, Oakes D (1984) Analysis of survival data. Chapman and Hall, London

Crawley MJ (1993) GLIM for ecologists. Blackwell, Oxford

Cremer KW, Mount AB (1965) Early stages of plant succession following the complete felling and burning of *Eucalyptus regnans* forest in the Florentine Valley, Tasmania. Aust J Bot 13:303–322

Deevey ES (1947) Life tables for natural populations of animals. Q Rev Bio 22:283–314

Denslow JS (1987) Tropical rainforest gaps and tree species diversity. Annu Rev Ecol Syst 18:431–451

Dexter N, Hudson M, James S, Macgregor C, Lindenmayer DB (2013) Unintended consequences of invasive predator control in an Australian forest: overabundant wallabies and vegetation change. PLoS ONE 21:8. doi:10.1371/journal.pone.0069087

Dickinson KJM, Kirkpatrick JB (1986) The impact of grazing pressure in clearfelled, burned and undisturbed eucalypt forest. Vegetatio 66:133–136

Eccles N, Lamont B, Esler K, Lamont H (2001) Relative performance of clumped vs. experimentally isolated plants in a South African winter-rainfall desert community. Plant Ecol 155:219–227

Facelli JM, Pickett STA (1991) Plant litter: its dynamics and effect on plant community structure. Bot Rev 57:1–32

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581. doi:10.1146/annurev.ecolsys.35.021103.105711

Fox GA (1993) Failure time analysis: emergence, flowering, survivorship, and other waiting times. Integrative Biology Faculty and Staff Publications, Paper 71

Gray AN, Spies TA (1996) Gap size, within gap position and canopy structure effects on conifer seedling establishment. J Ecol 84:635–645

Harrington GN, Sanderson KD (1994) Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. Pac Conserv Biol 1:319–327

Hoffmann WA (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. J Ecol 84:383–393

Hoffmann WA (2000) Post-establishment seedling success in the Brazilian Cerrado: a comparison of savanna and forest species. Biotropica 32:62–69

Hunter JT (1998) Vegetation and floristics of the Washpool National Park Western additions. NSW National Parks and Wildlife Service, Glen Innes

Just MG, Hohmann MG, Hoffmann WA (2015) Where fire stops: vegetation structure and microclimate influence fire spread along an ecotonal gradient. Plant Ecol. doi:10.1007/s11258-015-0545-x

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012) Fire in Mediterranean ecosystems: ecology, evolution and management. Cambridge University Press, Cambridge

Keith DA (2004) Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT. Department of Environment and Conservation, Hurstville

Lamont BB, Witkowski ETF, Enright NJ (1993) Postfire litter microsites— safe for seeds, unsafe for seedlings. Ecology 74:501–512

Leigh JH, Holgate MD (1979) The responses of the understorey of forests and woodlands of the Southern Tablelands. Aust J Ecol 4:25–45

Lindenmayer DB, Hobbs RJ, Likens GE, Krebs C, Banks SC (2011) Newly discovered landscape traps produce regime shifts in wet forests. P Natl Acad Sci USA 108:15887–15891

Lusk CH, Kelly CK (2003) Interspecific variation in seed size and safe sites in a temperate rain forest. New Phytol 158:535–541

Lusk CH, Kelly JWG, Gleason SM (2013) Light requirements of Australian tropical vs. cool-temperate rainforest tree species show different relationships with seedling growth and functional traits. Ann Bot 111:479–488 **(London)**

Metcalfe D, Liddel M, Bradford M, Green P (2014) Tropical rainforests of eastern Australia. In: Lindenmayer D, Burns E, Thurgate N, Lowe A (eds) Biodiversity and environmental change: monitoring, challenges and direction. CSIRO, Melbourne, pp 111–165

Molofsky J, Augspurger CK (1992) The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73:68–77

Odion DC, Moritz MA, DellaSala DA (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. J Ecol 98:96–105

Parr CL, Anderson AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conserv Biol 20:1610–1619

Parsons MH, Rafferty CM, Lamont BB, Dods K, Fairbanks M (2007) Relative effects of mammal herbivory and plant spacing on seedling recruitment following fire and mining. BMC Ecol 7:13. doi:10.1186/1472-6785-7-13

Pausas JG, Bradstock RA, Keith DA, Keeley JE (2004) Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85:1085–1100

Poulsen TL, Platt WJ (1989) Gap light regimes influence canopy tree diversity. Ecology 70:553–555

Price JN, Morgan JW (2003) Mechanisms controlling establishment of the non-bradysporous *Banksia integrifolia* (Coast *Banksia*) in an unburnt coastal woodland. Aust J Ecol 28:82–92

SAS Institute Inc. (1998) Statview Reference Guide. SAS Institute Inc., Cary

Sullivan AL, Wl McCaw, Cruz MG, Matthews S, Ellis PF (2012) Fuel, fire weather and fire behaviour in Australian ecosystems. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: The fire regimes and biodiversity of a continent. Cambridge University Press, Melbourne, pp 51–78

Tang Y, Boulter SL, Kitching RL (2003) Heat and smoke effects on the germination of seeds from soil seed banks across forest edges between subtropical rainforest and eucalypt forest at Lamington National Park, south-eastern Queensland. Aust J Bot 51:227–237

Tripathi RS, Khan ML (1990) Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a Subtropical Wet Hill Forest. Oikos 57:289–296

Turton SM, Sexton GJ (1996) Environmental gradients across four rainforest-open forest boundaries in northeastern Queensland. Aust J Ecol 21:245–254

Vazquez-Yanes C, Orozco-Segovia A (1993) Patterns of seed longevity and germination in the tropical rainforest. Annu Rev Ecol Syst 24:69–87

Warman L, Moles AT (2009) Alternative stable states in Australia's wet tropics: a theoretical framework for the field data and a field-case for the theory. Landscape Ecol 24:1–13

Whelan RJ (1995) The Ecology of fire. Cambridge University Press, New York

Williams PR (2000) Fire-stimulated rainforest seedling recruitment and vegetative regeneration in a densely grassed wet sclerophyll forest of north-eastern Australia. Aust J Bot 48:651–658

Williams PR, Parsons M, Jensen R, Tran C (2012) Mechanisms of rainforest persistence and recruitment in frequently burnt wet tropical eucalypts forests. Aust Ecol 37:268–275

Willis JL, Walters MB, Gottschalk KW (2015) Scarification and gap size have interacting effects on northern temperate seedling establishment. For Ecol Manag 347:237–246

Winn AA (1985) Effects of Seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. J Ecol 73:831–840