Population Dynamics of *Xanthorrhoea resinosa* Pers. Over Two Decades: Implications for Fire Management

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Tozer, M.G. and Keith, D.A. (2012). Population dynamics of *Xanthorrhoea resinosa* Pers. over two decades: implications for fire management. *Proceedings of the Linnean Society of New South Wales* **134**, B249-B266.

Fire has an important influence on the biota of Royal National Park and is a factor over which park managers exert some control. Fire management guidelines for biodiversity conservation are expressed as thresholds that define fire-regimes associated with elevated risks of extinction that management must aim to avoid. These thresholds strongly reflect fire-interval effects on fire-sensitive (non-resprouting) species. In contrast, the guidelines are less prescriptive about the characteristics of particular fire events (e.g. intensity, season, post-fire rainfall) or competition because the long-term importance of these factors is less well understood. On-going monitoring is required to determine if conservation goals will be met by management actions under these guidelines, or if they should be adapted to counter previously unidentified negative trends. In particular, populations of resprouting species which appear to be relatively resilient to interval-dependent effects must be monitored to detect subtle, but ultimately dangerous declines. We describe population trends in the iconic grass-tree *Xanthorrhoea resinosa* based on observations of over 3000 individual plants over a period of 23 years. We identify divergent population trends predicted to result in either local extinction within 200 years or slight declines depending on rates of mortality. Experimental evidence is presented for a strong impact of competition on survival which, at one of the study sites, led to local extinction following a single fire interval of 17 years. The relative importance of mortality associated with heat shock during fire, the effort of post-fire resprouting and flowering and other factors such as disease and competition are discussed. Our results suggest that a focus on minimum fire intervals alone will not guarantee the long-term persistence of key understorey species and that fire regime thresholds should more directly consider functional groups containing species with low potential for population growth.

Manuscript received 27 February 2012, accepted for publication 10 May 2012.

KEYWORDS: bushfire, fire intervals, fire management, park management, population dynamics, Royal National Park, *Xanthorrhoea resinosa*

INTRODUCTION

The structure and composition of heath communities in Royal National Park vary in time as a function of the interactive effects of fire, the environment and inter-specific interactions (Keith and Tozer 2012). In response, fire managers have adopted a flexible approach with the specific aim of avoiding the extinction of local populations (cf optimising the size of local populations; Bradstock et al. 1995). The key components of this approach are: i) defining groups of species which respond to fire regimes in similar ways (functional groups); ii) identifying fire regime thresholds beyond which species in certain functional groups are likely to decline; and iii) promoting variability in fire regimes in space and time as a means of managing conflicting requirements of different functional groups (Keith et al. 2002).

Central to this approach is a capacity to predict the cause, direction and magnitude of changes in population density. Population changes may be the result of: i) the length of the interval between fires (interval-dependent effects); ii) density-dependent feedbacks (self-regulation); iii) characteristics of individual fires and their timing in relation to seasonal population processes and weather (event-dependent effects); or iv) interactions with other species (Bond and van Wilgen 1996). The length of the fire interval is an important factor regulating the growth, reproduction and death of plant populations, thus interval-dependent effects are relatively easy to translate into management thresholds. In contrast, deriving management guidelines relevant to density-dependent or event-dependent effects is less tractable because the processes are less-well understood, inherently unpredictable or not amenable to management manipulation (Whelan et al. 2002). Dynamics driven by competitive interactions have been largely ignored (Bond and van Wilgen 1996), although recent studies have demonstrated that some understorey species decline in response to competition from overstorey shrubs in heath and shrubland communities (Cowling and Gxaba 1990, Keith and Bradstock 1994, Tozer and Bradstock 2002, Keith et al. 2007a, Keith and Tozer 2012).

The heath flora of Sydney may be classified into functional types based on life-history responses to fire (Keith et al. 2007a; Keith & Tozer 2012). Fire management guidelines for heath in Royal National Park assume that the plant functional type that includes serotinous obligate-seeder species is the most susceptible to local extinction due to interval-dependent effects on reproductive capacity. Fire-regime thresholds specified under the management plan (DECC 2009) nominate successive intervals of less than seven years and intervals greater than 30 years as incompatible with the conservation of these species (Short fire intervals eliminate populations before they reach reproductive age, while long intervals result in senescence and loss of both standing plants and the serotinous seed bank). In effect, the approach to fire management in Royal National Park assumes that on average, density and event-dependent effects on populations of other species are neutral under a variable fire regime and that competitive exclusion of understorey species by shrubs is prevented by recurring fire. Therefore, the risk of local extinction in resprouting species is low, at least for several fire intervals.

We established a demographic study in order to determine if the population dynamics of *Xanthorrhoea resinosa*, a long-lived, resprouting understorey species were consistent with these assumptions. We sought evidence for divergent population trends which may potentially arise as a result of contrasting fire regimes under the current management model. We compared growth, mortality and fertility in populations subject to two short inter-fire intervals (5 & 8 years) with populations subject to a short interval followed by an intermediate inter-fire interval (5 & 18 years) and computed population projections for a range of seedling establishment rates measured in field populations. Our aims were: i) to quantify the potential for population growth in populations subject to each fire regime; and ii) develop an understanding of the relative importance of factors inducing mortality (eg fire, competition). Our observations were augmented with an experiment in which we manipulated shrub cover in order to measure the effect of shrub canopy on survival.

METHODS

Species and study area

Xanthorrhoea resinosa is a common species occurring in heath and low sclerophyll woodland in seasonally wet sandy soils in the Blue Mountains and coastal sites south from Sydney (http:www.plantnet.rbgsyd.nsw.gov.au, Harden 1993). It has a terminal crown of up to several thousand leaves arising from a woody stem (caudex) which is typically subterranean but may grow up to 1 m above ground. Our study sites were located exclusively in heath on sandstone soils in Royal National Park, 20 km south of Sydney, Australia (Figure 1). Heath is characterised by a shrub stratum of variable cover up to 4 m tall with a semi-continuous groundcover of smaller shrubs and graminoids (Keith and Myerscough 1993, Tozer et al. 2010). Major bushfires occurred in the area in October 1988, January 1994 and December 2001. Study sites were burnt in either one (Garrawarra), two (Garie Trig, Bundeena Road and Jibbon) or all three fires (Wises Track, Maianbar Road and Crystal Pools).

Sampling methods

Six sites (Table 1) were established following a major summer wildfire in 1988, either on shallow, relatively well-drained soils (Wises Track, Crystal Pools, Maianbar Road, Bundeena Drive and Garie Trig) or deeper damp soils (Jibbon, Figure 1). Three sites were subsequently burnt in summer wildfires in January 1994 and December 2001 while the remainder were burnt only in 1994. A seventh site was established on deep, damp soil following the 1994 fire and remained unburnt thereafter (Garrawarra, Table 1). Sites subject to three fires (Wises Track, Crystal Pools, Maianbar Road) were burnt between 11 and 14 years prior to the 1988 fire and were structurally open at the time of the 1988 fire (Table 1). Sites subject to two fires (Bundeena Drive, Garie and Jibbon) were burnt between 8 and 22 years prior to the 1988 fire and ranged in structure from open heath to thicket at the time of the 1988 fire (Table 1).

Two transects (50 – 500 m apart) were established at each of the well-drained sites sampling contrasting scorch levels (high/low) assuming that

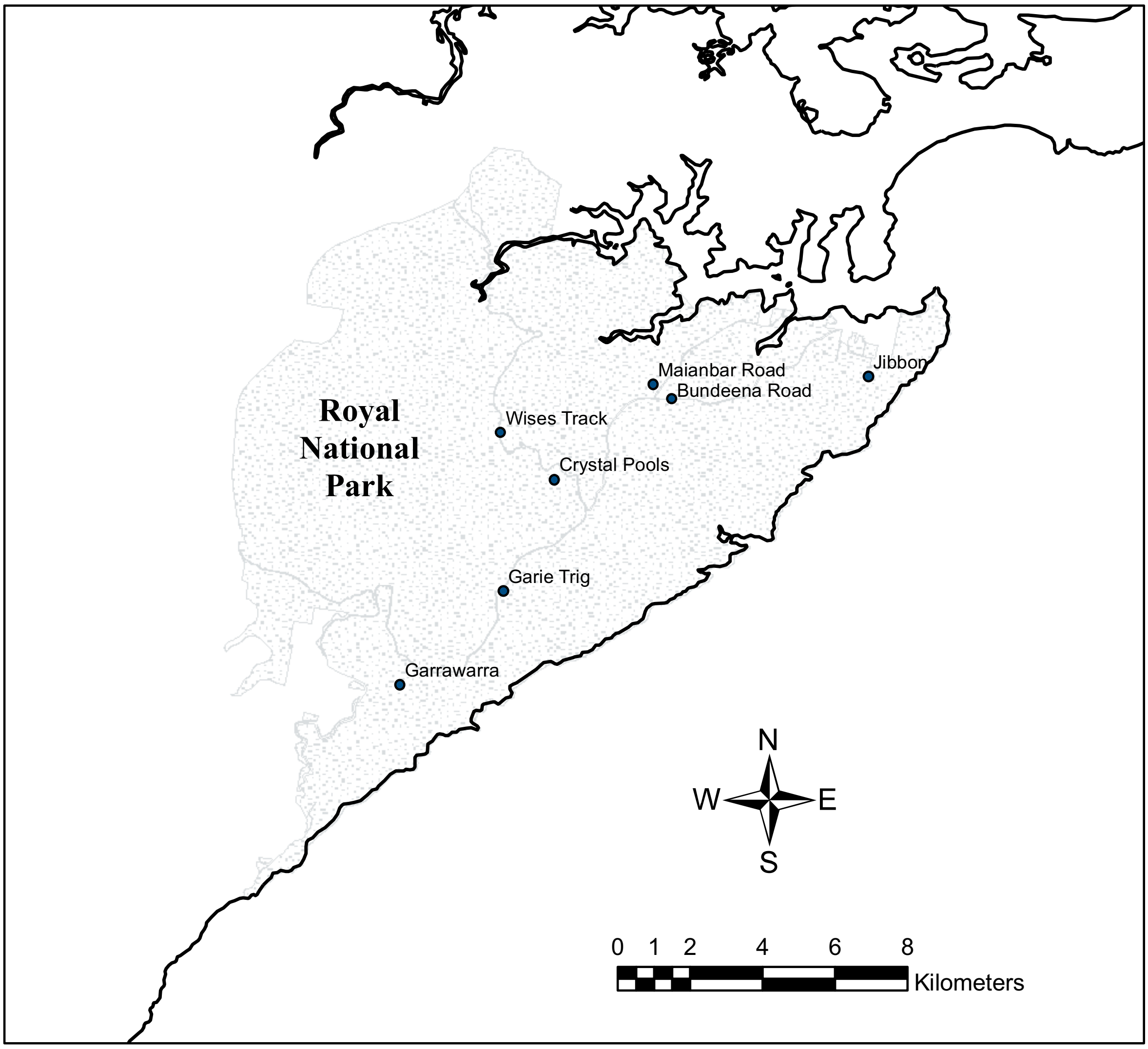

Figure 1: Location of study sites in Royal National Park.

Table 1: Location of study sites and their fire history and structural state prior to the 1988 fire

Site	Grid Reference (GDA)	Interval prior to 1988 fire (years)	State prior to 1988 fire	Burnt 1988	Burnt 1994	Burnt 2001
Wises Track	321085E 6223809N	11 (subpop. 1) 14(subpop. 2)	Open Heath	Yes	Yes	Yes
Crystal Pools	322345E 6222537N	11	Open Heath	Yes	Yes	Yes
Maianbar Road	324565E 6225205N	12	Open Heath	Yes	Yes	Yes
Garie Trig	321229E 6219446N	22	Shrub thicket	Yes	Yes	No
Bundeena Road	324997E 6224808N	20	Scattered shrub thicket	Yes	Yes	No
Jibbon	329486E 6225512N	8 (subpop. 4) 12 (subpops. 1-3)	Open heath and shrub thicket	Yes	Yes	No
Garrawarra	318912E 6216811N	-	Scattered shrub thicket	No	Yes	No

this represented variability in the above-ground heat output of the fire. At Jibbon a pair of transects (10 - 20 m apart) was established in each of four sites (200 – 500m apart) defining a (pre-fire) structural spectrum from open heath (no tall shrubs) to dense thicket. Two pairs of transects were established at Garrawarra. All tall shrub species were removed at the seedling stage from one transect of each pair, and seedlings left in the other to develop into a dense thicket. A minimum of 50 plants were sampled along each transect with the sample increased up to one hundred at most sites in order to increase the number of plants in size classes that were poorly represented. Plants were marked with uniquely numbered brass fire-proof tags attached to stainless steel stakes placed in the ground. A census of all populations was carried out approximately annually in summer from 1989 to December 2011 (Garrawarra was sampled in 2001, 2007 and 2011). Survival, crown size (number of living leaves), caudex height, flowering and fruiting data were recorded at each census except between 1990 and 1994 when crown size was measured on a subset of 15 plants at each transect). The number of capsules was counted on each spike except following the 1994 fire at Jibbon where a sub-sample of inflorescences was counted.

Seedling emergence and survival

Emergence, survival and growth of seedlings were measured at Jibbon in a seed-sowing experiment commencing in May 1990 after the first post-fire seed release. Clusters of 50 seeds were sown in five locations selected randomly at intervals of 1-5 m along each of the eight transects. Clear, square, perspex boxes (30 cm square and 10 cm tall, with open tops and bottoms) were used to reduce secondary dispersal of seeds by ants and surface water flow. The top edges of the boxes were smeared with tanglefoot to reduce access to the seeds by insect predators. Initially the seeds were monitored weekly. Additional seeds were sown to replace those in clusters that suffered high rates of seed removal or predation within 3 months of the initial placement. The perspex boxes were removed after 6 months. A total of 987 seedlings emerged. Survival of emergent seedlings was monitored at decreasing intervals, starting with weekly censuses for the first 3 months, reducing to monthly censuses until 2 years and 3-monthly censuses thereafter. All seedlings were burnt in the 1994 fire, 3.6 years after seeds were sown. Individuals that survived the fire were recorded in October 1994 and subsequently checked at approximately annual intervals.

Seedling establishment rates following the 1994 fire were estimated at the other six sites in 1996, approximately one year after seed release. Seedling density was estimated by counting seedlings in 0.25m^2 plots located at regular intervals along parallel transects through each population. Sampling continued until the coefficient of variation of the sampling error of the mean was below 0.3 (26-50 quadrats). The same method was used to estimate inflorescence density in 25m^2 plots (6-18 quadrats). Inflorescences were classified as fertile or non-fertile (no capsules). Capsule density on fertile inflorescences was estimated by measuring the length of the spike and counting the number of capsules on a representative portion (10 – 48cm) or the entire spike. Establishment rates per capsule were calculated by dividing the estimates for seedling and capsule density. Combinatorial errors were calculated as follows:

For $X = A + B$ or $X = A – B$, then $DX = \sqrt{\{(DA)^2 + (DB)^2\}}$

For $X = A.B$ or $X = A/B$, then $DX/X = \sqrt{\{(DA/A)^2 + (DB/B)^2\}}$

Where D denotes the sampling error associated with the respective measurements.

The resprouting capability of seedlings approximately 1.5 years old was investigated following a simulated fire at Garrawarra in May 1997. Plots (25m^2) containing 6-20 seedlings were randomly allocated to two defoliation treatments or a control (n=4). The first treatment simulated a moderate intensity fire using a hand-held propane gas torch (see Bradstock & Myerscough 1988). In the second treatment seedlings were defoliated using scissors. Seedlings were monitored weekly for two months then every three months until September 2000.

Population projections

Census data spanning the period 1988-2011 were used to construct a static life-table for each of two fire scenarios (two or three fires). Our preliminary appraisal of the data suggested that the rate of crown growth (leaf number) was geometric but very slow and that a significant proportion of individuals were either static or declined during the observation period. Furthermore, there was no apparent relationship between survival and reproduction and the location of the caudex (aerial or subterranean) and aerial growth in the caudex during the observation period was generally below the error of measurement. Therefore, we set our life-table time unit to the maximum possible (23 years) and used a stage structure based on leaf number alone. Stages were devised such that on average, individuals progressed by a single stage per unit of time (Krebs 2009). We calculated the average annual rate of crown growth for all individuals over 21 years (see below) then applied this to a hypothetical individual commencing with one leaf and growing for 400 years. Standardised to a 21 year time unit, this yielded 20 stages (Table 2) covering the variation in crown-size observed in the sample populations.

Table 2a: Static life table (part a) for a 23 year time step derived from census data for sites burnt, respectively, twice and three times, during the 23 year study period (see first column). Flowering data are Number flowering (%), number of failed infloresences, average capsule production (+ SEM) and range of capsule counts (Column totals are range with upper and lower bounds). NR = not recorded. Fertility data are seedlings produced per individual (observed range with upper and lower bounds (calculated from lowest rate – SEM and upper highest rate + SEM).

# Fires	Stage	# Leaves	N	Flowering (%) 1988	Flowering (%) 1994	Flowering (%) 2001	Dead (%)	Ann. Surv. (%)	Fertility
1	Sdl.		987	0	0	0	986 (99.999)	74.1	0
2	2	1	1	0	0	-	1 (100)	0	0
2	3	2	1	0	0	-	1 (100)	0	0
2	4	3	2	0	0	-	1 (50)	97	0
2	5	4-5	21	0	0	-	10 (47.6)	97.2	0
2	6	6-7	15	0	0	-	7 (46.7)	97.3	0
2	7	8-11	34	0	0	-	13 (38.2)	97.9	0
2	8	12-16	56	0	0	-	17 (30.4)	98.4	0
2	9	17-24	52	0	1 (2%) 0,NR(NR) NR-NR	-	15 (28.8)	98.5	0
2	10	25-35	45	0	0	-	19 (42.2)	97.6	0
2	11	36-50	56	0	3 (5%) 0,NR(NR) NR-NR	-	20 (35.7)	98.1	0
2	12	51-72	65	1 (2%) 0,48(-) 48-48	10 (15%) 1,102(-) 102-102	-	18 (27.7)	98.6	(0) 0 – 1 (1)
2	13	73-103	55	1 (2%) 0,5(-) 5-5	25 (45%) 0,NR(NR) NR-NR	-	11 (20)	99	(0) 2 – 24 (24)
2	14	104-148	57	4 (7%) 0,268(98) 5-480	22 (39%) 1,1156(-) 1156-1156	-	20 (35.1)	98.1	(0) 1 – 20 (20)
2	15	149-212	67	3 (4%) 0,399(95) 300-590	22 (33%) 0,1247(239) 22-2720	-	21 (31.3)	98.4	(1) 1 – 19 (35)
2	16	213-303	65	12 (18%) 2,869(176) 56-1785	24 (37%) 4,817(180) 56-1785	-	14 (21.5)	99	(1) 1 – 17 (29)
2	17	304-433	35	8 (23%) 0,1190(240) 76-1909	13 (37%) 0,1129(250) 80-2400	-	12 (34.3)	98.2	(1) 2 – 31 (51)
2	18	434-622	32	14 (44%) 1,1905(162) 1105-3080	15 (47%) 0,1412(101) 730-1700	-	7 (21.9)	98.9	(3) 4 – 65 (104)
2	19	623-886	12	5 (42%) 2,1145(718) 10-2280	4 (33%) 0,NR(NR) NR-NR	-	6 (50)	97	(1) 2 – 34 (57)

Table 2a continued

# Fires	Stage	# Leaves	N	Flowering (%) 1988	Flowering (%) 1994	Flowering (%) 2001	Dead (%)	Ann. Surv. (%)	Fertility
2	20	887-1266	3	0	3 (100%) 0,0(0)0-0	-	0 (0)	100	(3) 4 – 64 (118)
		Tot.	674	(111) 49 - 2213 (3297)	(381) 439 – 6539 (8153)	-	213 (32)	98.4	(1) 1 – 13 (13)
3	3	2	4	0	0	0	0 (0)	100	0
3	4	3	7	0	0	0	0 (0)	100	0
3	5	4-5	29	0	0	0	8 (27.6)	98.6	0
3	6	6-7	35	0	0	0	8 (22.9)	98.9	0
3	7	8-11	34	0	0	0	7 (20.6)	99	0
3	8	12-16	41	0	0	0	9 (22)	98.9	0
3	9	17-24	59	0	0	0	21 (35.6)	98.1	0
3	10	25-35	55	0	0	1 (2%) 0,0(-) 0-0	22 (40)	97.8	0
3	11	36-50	66	0	3 (5%) 0,NR(NR) NR-NR	0	24 (36.4)	98.1	(0) 0 – 1 (2)
3	12	51-72	81	3 (4%) 0,81(48) 4-170	3 (4%) 0,NR(NR) NR-NR	0	22 (27.2)	98.6	(0) 0 – 1 (2)
3	13	73-103	80	4 (5%) 1,412(225) 81-924	14 (18%) 0,NR(NR) NR-NR	0	20 (25)	98.8	(0) 0 – 5 (9)
3	14	104-148	69	6 (9%) 1,297(96) 21-516	19 (28%) 0,NR(NR) NR-NR	0	13 (18.8)	99.1	(0) 1 – 8 (14)
3	15	149-212	71	8 (11%) 0,569(129) 68-1173	18 (25%) 0,545(112) 210-880	1 (1%) 0,2(-) 2-2	12 (16.9)	99.2	(0) 1 – 9 (9)
3	16	213-303	59	9 (15%) 5,672(162) 353-1232	16 (27%) 0,975(156) 211-1720	9 (15%) 6,112(46) 13-210	8 (13.6)	99.4	(1) 1 – 14 (25)
3	17	304-433	80	15 (19%) 2,1017(136) 41-1740	32 (40%) 3,1061(97) 410-1920	8 (10%) 3,478(266) 20-1806	7 (8.8)	99.6	(1) 2 – 26 (42)
3	18	434-622	33	5 (15%) 0,1410(332) 396-2424	11 (33%) (1,343(122) 8-790	4 (12%) 1,227(171) 14-620	2 (6.1)	99.7	(1) 1 – 15 (25)
3	19	623-886	9	5 (56%) 0,3045(1176) 714-7020)	5 (56%) (0,3190(1197) 670-6000	0	1 (11.1)	99.5	(6) 11 – 157 (259)
3	20	887-1266	1	0	0	0	0 (0)	100	(0) 0 – 0 (0)
		Tot.	813	(104) 139 – 2075 (2964)	(237) 295 – 4396 (5911)	(5) 10 – 155 (270)	184 (23)	98.9	(1) 1 – 8 (8)

Table 2b: Static life table (part b) for a 23 year time step derived from census data for sites burnt, respectively, twice and three times, during the 23 year study period (see first column). Stage matrix specifies the final stage distribution (%, columns 11-29) by starting stage (column 2).

# Fires	Stage	# Leaves	N	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Sdl.		987							0.1												
2	2	1	1																			
2	3	2	1																			
2	4	3	2						50													
2	5	4-5	21			4.8	9.5	9.5	4.8	4.8	9.5	9.5										
2	6	6-7	15					6.7	33.3	6.7		6.7										
2	7	8-11	34					5.9	5.9	23.5	8.8	11.8	2.9	2.9								
2	8	12-16	56	1.8					5.4	17.9	25	8.9	5.4	5.4								
2	9	17-24	52							7.7	9.6	21.2	13.5	13.5	1.9	1.9		1.9				
2	10	25-35	45								8.9	13.3	8.9	17.8	4.4	4.4						
2	11	36-50	56								8.9	5.4	8.9	17.9	12.5	5.4	1.8	1.8	1.8			
2	12	51-72	65								3.1	4.6	9.2	18.5	12.3	15.4	4.6	3.1	1.5			
2	13	73-103	55		1.8		1.8				1.8	5.5	3.6	7.3	16.4	12.7	14.5	10.9	3.6			
2	14	104-148	57										1.8	1.8	9	14.4	7.2	14.4	14.4		1.8	
2	15	149-212	67										1.5	1.5	6	9	16.4	16.4	9	6	3	
2	16	213-303	65												1.5	6.2	12.3	18.5	12.3	15.4	4.6	7.7
2	17	304-433	35												2.9	2.9	5.7	14.3	20	14.3	5.7	
2	18	434-622	32														9.4	6.3	15.6	15.6	25	6.3
2	19	623-886	12													8.3			16.7	25		
2	20	887-1266	3																33.3	33.3	33.3	
		Tot.	674																			

Table 2b continued

# Fires	Stage	# Leaves	N	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
3	3	2	4	25		25	25		25													
3	4	3	7				14.3	28.6	57.1													
3	5	4-5	29		3.4			17.2	31	13.8	3.4	3.4										
3	6	6-7	35			2.9		17.1	14.3	22.9	14.3	2.9	2.9									
3	7	8-11	34				2.9	5.9	11.8	14.7	23.5	11.8	8.8									
3	8	12-16	41			2.4		7.3	2.4	17.1	14.6	24.4	2.4	7.3								
3	9	17-24	59					1.7	6.8	6.8	11.9	16.9	11.9	1.7	3.4		1.7	1.7				
3	10	25-35	55						5.5	5.5	5.5	16.4	12.7	9.1	5.5							
3	11	36-50	66						1.5		6.1	7.6	13.6	18.2	13.6	1.5	1.5					
3	12	51-72	81							1.2		4.9	11.1	12.3	19.8	14.8	6.2	2.5				
3	13	73-103	80						1.3			7.6	14	2.5	8.9	22.9	8.9	6.4	2.5			
3	14	104-148	69						1.4	1.4	1.4	5.8	1.4	4.3	14.5	11.6	20.3	14.5	2.9		1.4	
3	15	149-212	71						1.4			2.8	1.4	2.8	2.8	8.5	4.2	39.4	8.5	8.5	2.8	
3	16	213-303	59									1.7	1.7			1.7	6.8	10.2	28.8	23.7	10.2	1.7
3	17	304-433	80										1.3		1.3		5.1	7.6	25.3	27.9	19	3.8
3	18	434-622	33									3			3	3			12.1	18.2	24.2	30.3
3	19	623-886	9																33.3		11.1	44.4
3	20	887-1266	1																			100
		Tot.	813																			

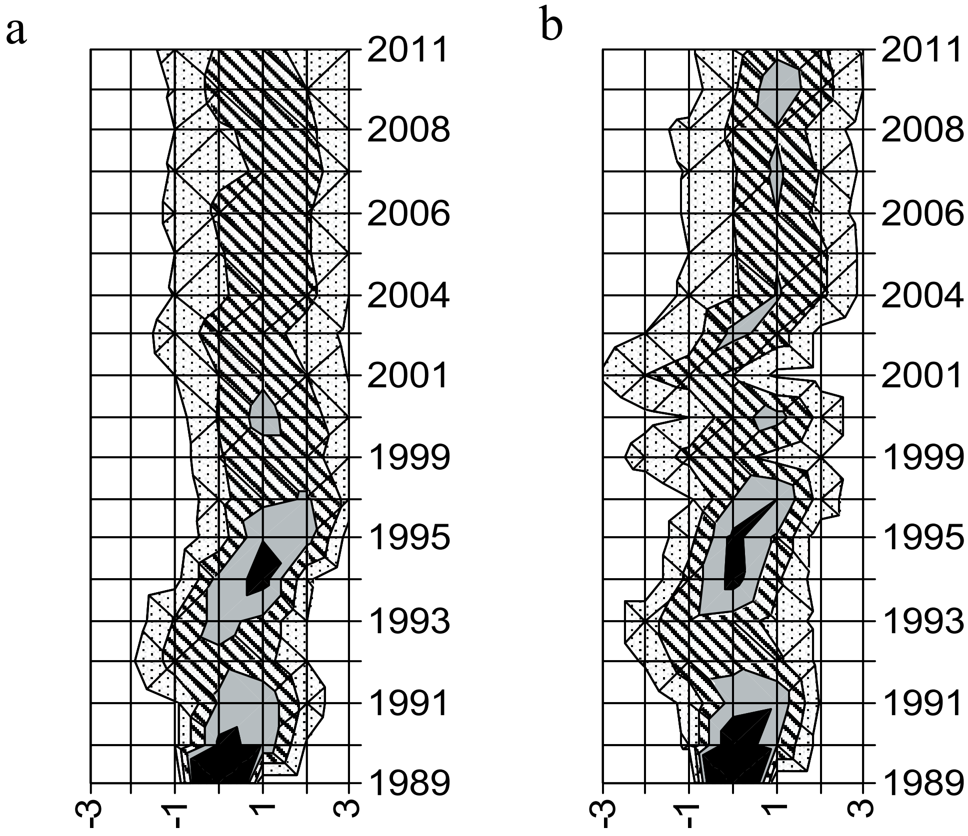

Figure 2: Growth stage relative to starting stage of populations subject to a) two fires and b) three fires. Shading indicates the percentage of individuals smaller than the starting stage (-1 to -3), static (0) or larger than the starting stage (1 to 3) at each census during the observation period 1988 to 2011 (no fill: 0-10%, stipples: 10-20%, diagonal stripes: 20-30%, grey fill: 30-40%, black fill: 40-100%).

The large number of stages meant there were insufficient individuals sampled to construct projection matrices for each site. Therefore sites were lumped according to the number of fires that occurred during the observation period. Transition probabilities were based on initial size recorded between October 1989 and April 1990 (12-18 months after the 1988 fire) and final size at December 2011. The probability of seedling transition to the first size class was estimated from the sample of 987 seedlings artificially established following the 1994 fire at Jibbon. Fertility rates (seedlings per individual) were calculated by multiplying total capsule output for the observation period by seedling establishment rates (as calculated above) and dividing by the number of individuals. Errors in the estimated parameters were combined as described above. Population projections were calculated for the lowest (non-zero) and highest establishment rates recorded across the seven sample sites as well lower (lowest rate – SEM) and upper (highest rate + SEM) bounds (where SEM is the standard error of the mean).

RESULTS

Growth

Crown recovery following fire occurred rapidly and individuals typically attained pre-fire size by the first year post-fire. Thereafter, crown growth became slower and more variable. The proportion of individuals in a stage higher than their starting stage increased through the study, although at any given point, some individuals were suppressed at or below their starting stage (Figure 2), generally those that were covered by shrub canopy (pers. obs.). Individuals burnt three times were more likely to progress to a higher stage than those burnt twice (Figure 3). The proportion of individuals suppressed below the starting size increased slightly with increasing size although this trend was more pronounced in individuals burnt twice compared with three times (Table 2). All but one of the seedlings raised in 1990 remained static with 1-3 soft short leaves characteristic of the juvenile form until death (< 20 years). The remaining seedling entered

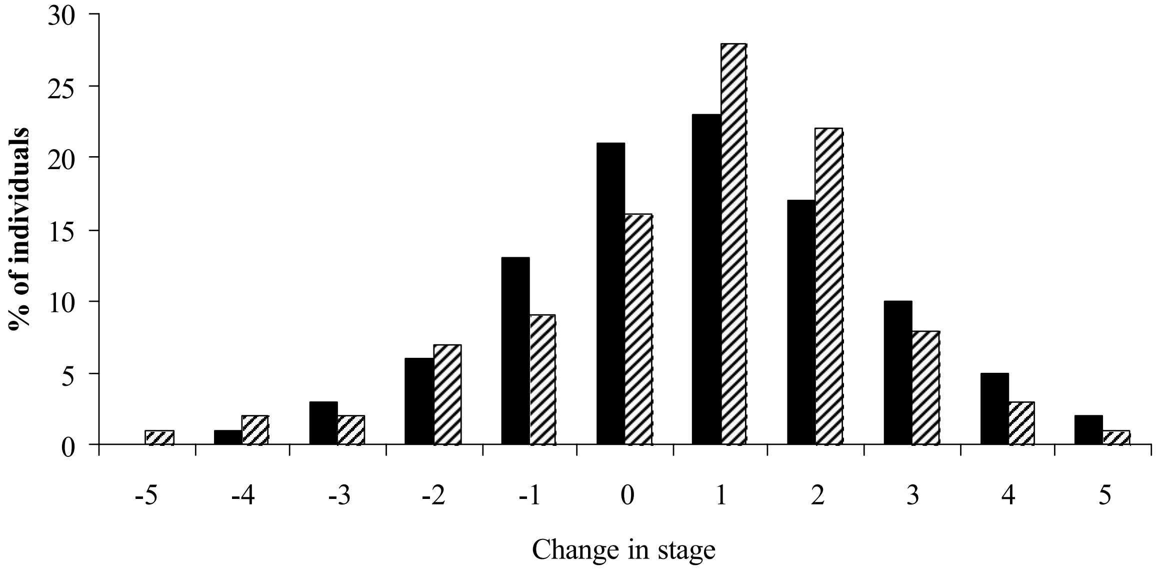

Figure 3: Histogram representing the growth of individuals over the course of the study partitioned by the number of times burnt (dark fill – two fires, diagonal shading – three fires). Data are the stage occupied at year 23 compared with the stage occupied at year one.

stage 1 in 2005 (15 years) and was at stage 8 at the end of the observation period, a rate of progression that was unmatched during the observation period.

Death

The survival rates for established plants over 23 years were 98.4%/year (two fires) and 98.9%/year (three fires), (Table 2). Survival varied among sites: Wises Track (3 fires) and Garie Trig (2 fires) were notable for higher mortality compared with the other sites (Figure 4). Within sites, individuals located under dense thicket were more likely to die than those located in gaps in the thicket (pers. obs.). Survival during fire was high: only 42 individuals failed to resprout and of these, 15 were in a state of senescence immediately preceding the fire. Survival of healthy individuals during fire ranged from 98.5% (1994 fire) to 99.6% (1988, 2001 fires, Table 3). Survival during the first year following fire was lower than the annual average (94.6 – 97.3%, Table 3, Figure 4). Fire-related mortality (heat shock combined with death following resprouting) affected up to 10% of

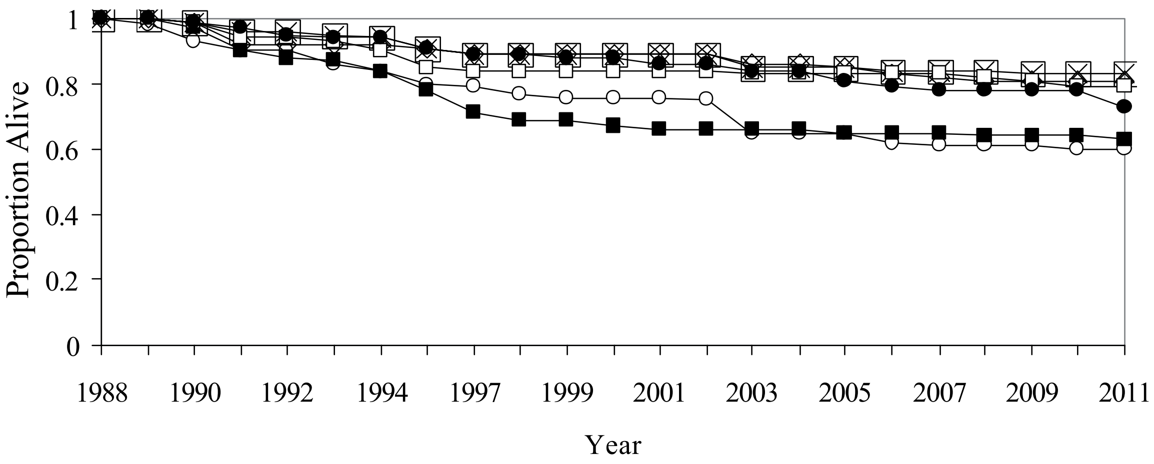

Figure 4: Survival of individuals at each site over the course of the study (○- Wises, X – Crystal Pools, ◊- Maianbar, ■ - Garie, □ - Bundeena, ● – Jibbon). Data are the proportion of the starting population surviving at each census.

Table 3: The number of individuals recorded alive and well prior to fire (N) and the number failing to resprout after the fire (killed). Post-fire survival applies to all individuals that were alive before the fire and survived up to the next census approximately one year later. The sizes of individuals killed in the 1988 fire were not recorded.

Starting stage	N	Killed	Post-fire Survival	N	Killed	Post-fire Survival	N	Killed	Post-fire Survival
	1988			**1994**			**2001**		
2	1	-	100	0	0	-	0	0	-
3	5	-	80	4	0	100	4	0	100
4	9	-	100	8	0	100	7	0	100
5	47	-	98	45	1	95	22	0	100
6	43	-	98	51	0	100	28	0	93
7	58	-	100	60	1	100	25	0	100
8	75	-	95	90	1	99	26	0	92
9	77	-	96	107	2	98	33	0	91
10	55	-	93	90	0	97	25	0	84
11	62	-	94	115	0	99	28	0	79
12	82	-	98	145	0	97	41	1	85
13	64	-	97	133	1	99	33	1	88
14	69	-	100	129	1	98	34	0	97
15	97	-	99	133	6	98	44	0	100
16	105	-	98	132	3	95	45	0	98
17	95	-	99	111	3	97	63	0	100
18	46	-	100	67	2	95	20	0	95
19	8	-	100	20	0	85	5	0	100
20	1	-	100	4	0	100	1	0	100
Total/ Average	999	4 (0.4%)	97.1	1444	21 (1.5%)	97.3	484	2 (0.4%)	94.6

the population in the 2001 fire (Wises Track, three fires), although the only other noticeable fire-related dips below background survival rates were 6% (Garie Trig, two fires) and 5% (Bundeena Road, two fires) following the 1994 fire (Figure 4). Mortality between fires (i.e. excluding the first post-fire year) varied among inter-fire periods (1989 – 1993; 1994 – 2001; 2002 – 2011) and stage classes (Figure 5). Mortality in sites burnt twice was generally higher than in sites burnt three times; the difference was generally greatest in the third inter-fire interval in small plants (stages 6 - 14) but the converse was true for plants in stage 5 and there was no trend for larger plants (stages 15 – 19, Figure 5).

At Garrawarra, 63% of seedlings burnt at age two years resprouted following simulated fire compared with 74% of those defoliated but not burnt. Survival rates over the subsequent year were 13% and 33%, respectively, compared with 74% survival in the control treatment. Of 141 four-year old seedlings alive immediately prior to the 1994 fire 53 (38%) were recorded alive eight months after the fire. There was no sign of the remainder, therefore they were probably killed by fire.

Fertility

Seedling establishment following the 1994 fire varied from zero to almost one seedling per four capsules produced (Table 4). A total of 2719 seeds were

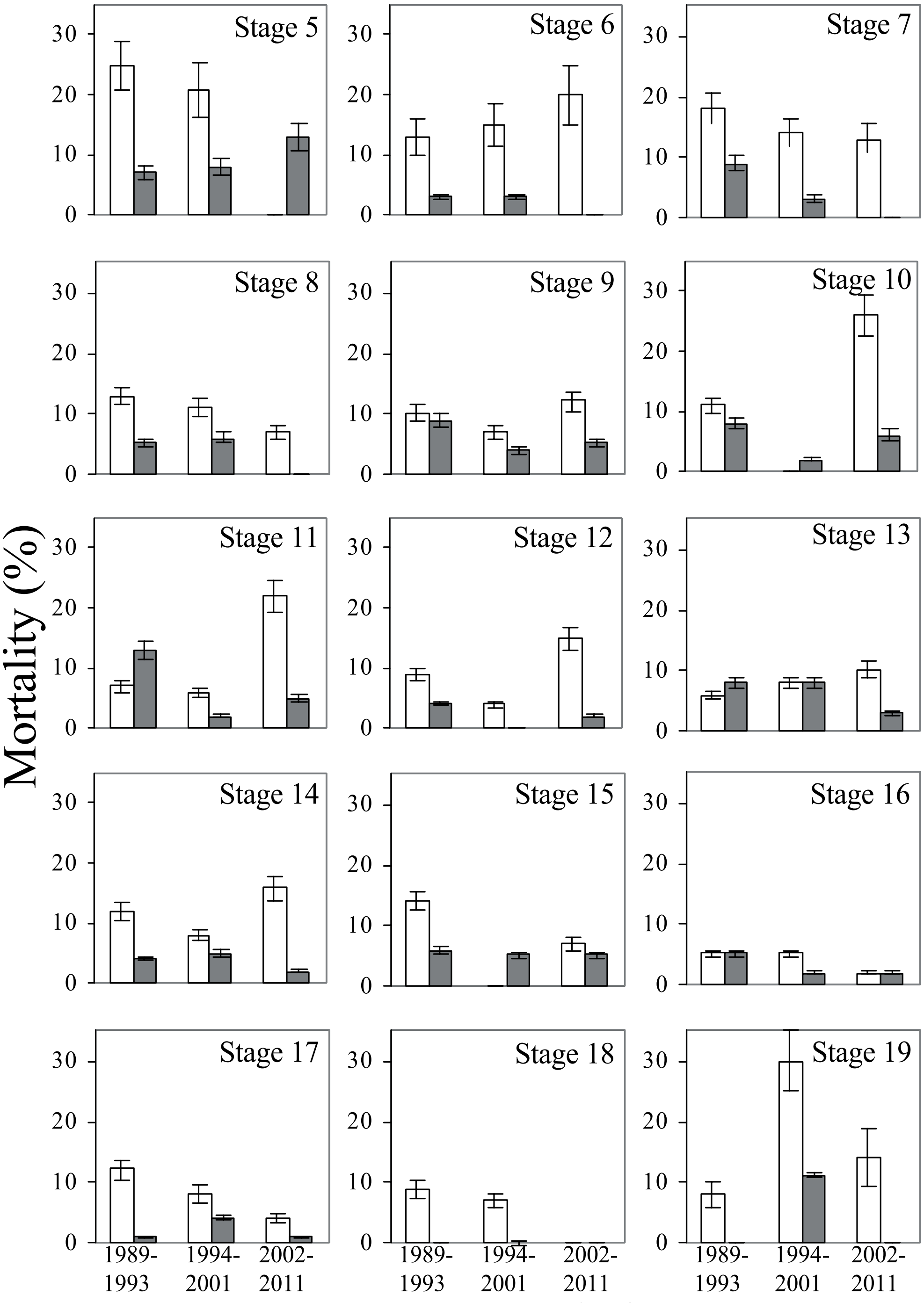

Figure 5: Mortality (%) partitioned by stage (stages 5-19) and fire-incidence (no fill – two fires, grey fill – three fires) during consecutive inter-fire periods during the study. Inter-fire periods (1989 – 1993; 1994 – 2001; 2002 – 2011) exclude the first post-fire year and mortality was calculated using the number of individuals alive at the start of each interval. Populations subject to two fires were not burnt prior to the third interval: in that case mortality for intervals two and three represents the early and later part of a single inter-fire interval.

Table 4: Seedling establishment as a function of capsule production following the 1994 fire (SEM).

Study Site	Seedling Density (m^{-2})	Capsule Density (m^{-2})	Establishment rate (sdl./foll.)
Crystal Pools	0.85 (0.28)	74(0.2)	0.012 (0.004)
Wises Track East	0	50 (0)	0
Bundeena Road	2.19 (0.99)	48 (0.7)	0.045 (0.038)
Garie Trig	0.57 (0.2)	187 (0.2)	0.003 (0.001)
Maianbar Road	1.04 (0.34)	116 (0.3)	0.009 (0.004)

required to raise 987 seedlings at Jibbon (1 seedling per 2.75 seeds), although more seeds were placed in sites with high rates of predation and following the first census measures to reduce predation were implemented. Reproductive output following the 1994 fire was more than double that of the 1988 fire, primarily because a higher proportion of individuals flowered, but also due to higher capsule production in some of the smaller size classes (Table 2). In comparison, reproductive output following the 2001 fire was negligible due both to the low proportion of flowering plants and the relatively high number of failed inflorescences. Individual fertility increased with plant size because flowering frequency generally increased with size and large plants produced larger inflorescences (Table 2).

Population projcetions

Populations declined to extinction following the projection of the two-fire population matrix through 18 cycles (414 years) under all but the highest of the four fertility schedules. Under the maximum fertility rate the population stabilised at a size of 275 individuals however these were dominated by seedlings with only a single individual occupying each stage from 8 to 20. Raising the highest fertility schedule by a factor of 35 was sufficient to stabilise the population at its current size. Despite having lower fertility overall, populations subject to three fires were predicted to grow, although the rate was sensitive to variation of the mortality rate in the highest stage class, especially when this was reduced below 0.99. Small reductions in survival of individuals in class 20 could plausibly be offset by increased fertility (1.5 – 6-fold), however this effect diminished rapidly as survival was reduced from 0.99 to 0.9, a plausible range based on survival in other classes (Figures 6, 7). In contrast, projections under the two-fire scenario were insensitive to increases in survival and growth of individuals in stages 15 to 20. The divergent trajectories were thus interpreted to be primarily caused by different mortality rates in the smaller stages. Life expectancy was consistently higher in individuals experiencing three fires compared with two (Figure 8).

Competition experiment

Survival of established plants in artificial clearings at Garrawarra was 98% from 2001 to 2011 with 60% of survivors progressing to a larger stage, 8% regressing and 32% static. Mortality in uncleared treatments was 44% in 2007 (comprising plants in stage 10 or smaller) and 98% in 2011.

DISCUSSION

Population Dynamics

Divergent population trajectories were predicted under the two fire regimes based on our 23-year census of multiple *Xanthorrhoea resinosa* populations. This was primarily due to contrasting patterns of survival which are attributable to at least three main sources: heat shock during fire, early post-fire mortality (probably associated with the effort of post-fire resprouting/flowering) and competition from overstorey shrubs. Relatively few deaths in our study were attributable to heat shock alone, although high rates of mortality have been observed in plants with a large aerial caudex at other sites as a result of caudex damage following very intense or repeated fires (author's unpublished data, Curtis 1998). Total fire-related mortality (heat shock combined with death following resprouting) was significant in isolated circumstances (e.g. 10% mortality at Wises Track following the 2001 fire) however overall, we observed higher mortality in populations burnt twice compared with those burnt three times.

Results from other studies suggest that overstorey competition affects the survival of understorey species such as *Xanthorrhoea resinosa*

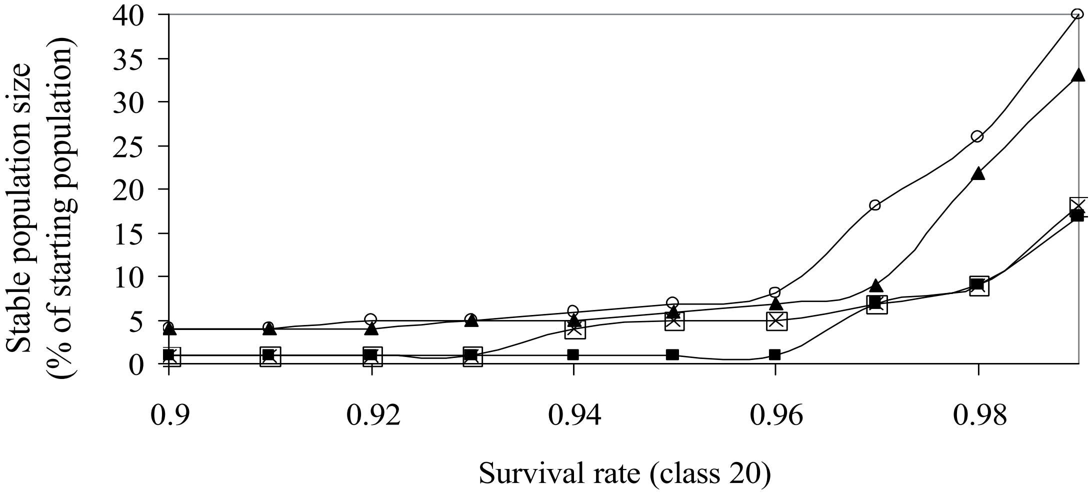

Figure 6: The size at which X. resinosa populations stabilize (as a percentage of the starting population) when projected over repeated 23-year intervals using survival rates derived from populations subject to three fires and the four different fertility schedules described in the text (○- maximum, ▲- high, X – low, ■ – minimum). The graphs show the decline in stable population size as survival of individuals in class 20 is reduced progressively from 99 to 99% (per cycle).

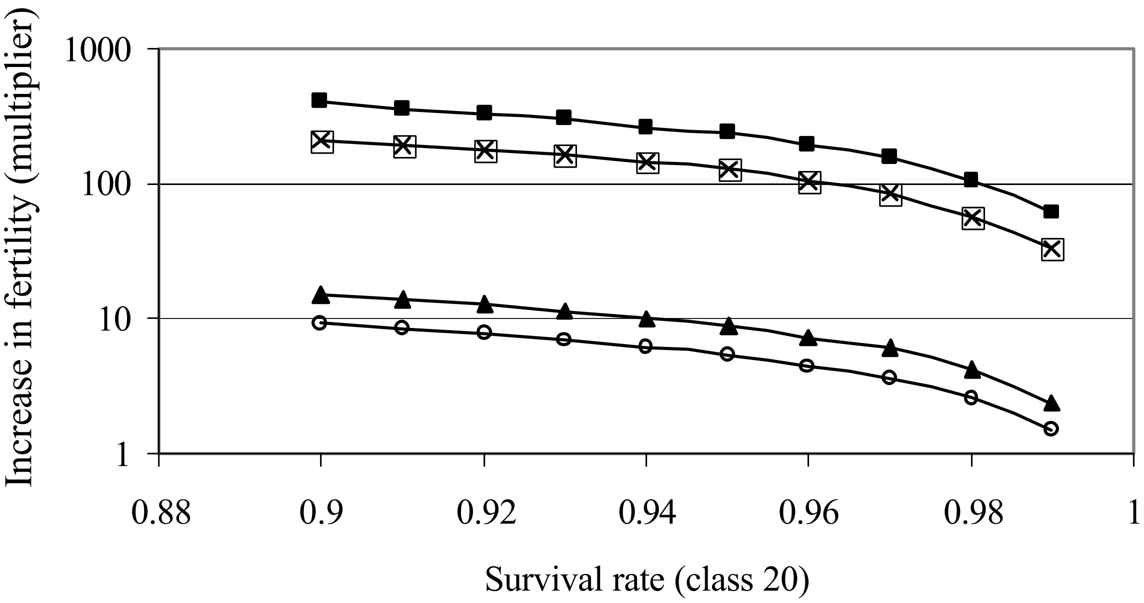

Figure 7: Increase in fertility (multiplier) required to maintain population growth when populations are projected over repeated 23-year intervals using survival rates derived from populations subject to three fires and the four different fertility schedules described in the text (○- maximum, ▲- high, X – low, ■ – minimum). The graphs show the increase on fertility required to maintain population growth as survival of individuals in class 20 is reduced progressively from 99 to 99% (per cycle).

(Keith & Bradstock 1994, Tozer & Bradstock 2002, Keith *et al.* 2007a), consistent with the dynamics of desmium starch storage in the caudex, as described by Lamont et al. (2004) for *X. preissii* in south-west Australia. Desmium starch serves as energy storage and is drawn down during the post-fire production of leaves and inflorescence. In the absence of fire, starch reserves fluctuate seasonally, accumulating over summer and depleting in late autumn (Lamont et al. 2004). Assuming a similar mechanism applies

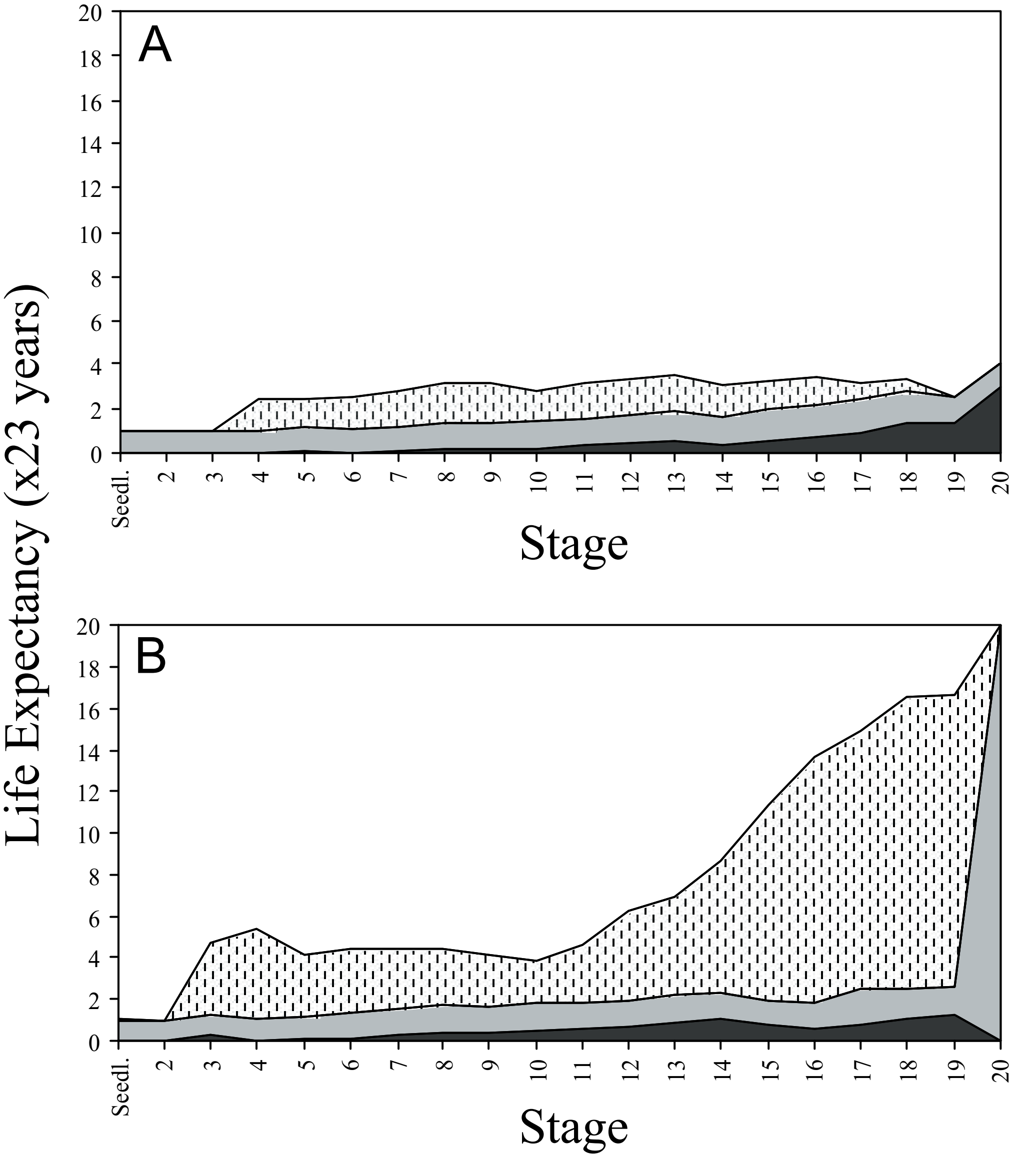

Figure 8: Life expectancy for individuals experiencing A) two fires and B) three fires as a function of starting stage (dark shading – time spent below the starting stage, grey shading – time spent at the starting stage, vertical dashes – time spent above the starting stage).

in *X. resinosa*, it seems probable that depressed crown growth under heavy shading is indicative of photosynthetic deficit, with the effect that progression through the size classes is slowed or reversed. In turn, this may render individuals less fit for resprouting and flowering following fire and more susceptible to death following pathogenic attack. Consistent with this model, we observed a lower overall risk of death among individuals that flowered.

Although the results of our experiment at Garrawarra provide a strong demonstration of the effect of competition on survival of *X. resinosa,* evidence in support of competition as the primary factor driving the dynamics of other populations is more equivocal. While survival patterns during the period 2002-2011 were consistent with patterns observed at Garrawarra (higher mortality in smaller size classes in sites not burnt in 2001), the response was much weaker and the higher overall mortality observed throughout the study in sites burnt twice can not be explained by competition during the period 1988 - 2001. Three factors can be identified which complicate the interpretation of our results. First, the pattern of shrub establishment following the 1994 fire was patchy as a result of lower recruitment due to the short inter-fire interval. Thus, competitive pressure on understorey species varied widely within sites, with some individuals subject to dense cover and others growing in open heath. Assuming patchiness was equal across sites then this factor is expected to diminish the expression of the competition effect. Second, our study sites had different histories prior to the commencement of the study: those in the three-fire treatment generally experienced a shorter fire-interval prior to 1988 and were free of thicket, while sites subject to two fires were subjected to a longer fire-interval and varying degrees of competition from thicket (Table 1). Sites subject to two fires were therefore more likely to have experienced the effects of competition prior to 1988 and higher mortality following the 1988 fire may have been a legacy of this competition. Third, attack from pathogens such as *Phytophthora cinnamomi* identified at some of our study sites (e.g. Wises Track and Garie Trig) may have contributed to higher mortality at heavily infected sites thus confounding any response to fire regimes. If sites subject to strong pathogenic attack were concentrated in the two-fire treatment then the argument for dynamics driven by competition is weakened. This does not appear to have been the case since the site with highest mortality was subject to three fires while that with second-highest was subject to two fires. However, it is likely that the presence of *P. cinnamomi* would exacerbate the effects of competition from overstorey species.

Our interpretation of the population dynamics of *X. resinosa* differs from that of Regan et al. (2011), primarily as a result of differing perspectives on mortality. Based on a stochastic model compiled from an earlier version of these population data, Regan et al. (2011) concluded that populations declined more slowly under lower fire frequencies because mortality induced by the combined effects of fire and disease outweighed higher fertility under higher fire frequencies. Our results corroborate this conclusion only when overstorey species are absent, but suggest that the opposite is true when competition from shrub species increases mortality. Regan et al. (2011) interpreted mortality differences among sites as a function of the presence of the pathogen *Phytophthora cinnamomi*, but did not incorporate the effects of overstorey competition into their model. Our observed rates of mortality were lower than in other disease-affected plant populations elsewhere in Australia (Keith 2004; Shearer et al. 2008), suggesting that the impacts of the disease are more subtle than elsewhere (see Keith et al. 2012). Nonetheless, in species such as X. resinosa, with slow population turnover, the effects of slow-acting disease on population persistence can be significant (Keith et al. 2007b). Disease effects manifest primarily by exacerbating the effects of fire early in the fire cycle and may also exacerbate effects of competition later in the fire cycle. Further experimentation is needed to resolve these interactions and their effects on population persistence.

On balance, increased mortality resulting from competition is a plausible explanation for the divergent population trajectories observed in our study sites because competition from overstorey shrubs is likely to have been less intense over the longer term (prior to and following 1988) and was more regularly interrupted by fire in the sites burnt three times compared with twice. Even allowing for the cumulative effect of fire-related mortality and strong inter-site variability in survival there exits a clear trend not easily explained by factors other than fire, although further analysis is required to examine the nature and implications of variation in survival among sites. Conversely, although survival appears crucial to population dynamics, fertility could also be important, especially if rare conditions that promote highly productive recruitment events were not observed during our study period. This hypothesis could explain why populations are apparently susceptible to decline despite having survival rates that are favourably high compared with other members of this long-lived genus (Lamont et al. 2004) and very similar (on average) among treatments.

Increased fertility may result from increased flowering frequency and fruit set, reduced predation and/or higher rates of seedling establishment. Among *Xanthorrhoea* species, flowering frequency increases with increasing plant size (Gill and Ingwerson 1976, Curtis 1998, Ward and Lamont 2000), is highest, and generates the greatest seed set following summer fires (Gill and Ingwerson 1976, Lamont et al. 2000, Taylor et al. 1998), and decreases with the length of the preceding inter-fire interval (Taylor et al. 1998). Flowering patterns in our populations were consistent with those observed in other species. We assumed that the timing of fires during our observation period was optimal for fruit production (authors' unpubl. data). Flowering frequency increased with plant size and experimental burning demonstrated a peak in flowering frequency in *X. resinosa* following summer fire (author's unpublished data). We observed flowering following inter-fire intervals of nine, six and 8 years. Although we observed a high proportion of individuals flowering in populations burnt in one short fire-interval, our data suggest this may not be repeated following two or more short inter-fire intervals, possibly due to the depletion of desmium starch.

Since our fertility estimates were based on seedling establishment following the most productive of three observed flowering events (1994), several arguments suggest that increased fertility is unlikely to offset observed mortality rates, particular under the two-fire scenario. First, following the analysis above, we consider that seed output is only likely to increase as a result of an increase in the proportion of plants flowering, and that a doubling of output (from 18% to 36% of all plants) is at the upper end of the plausible range. Second, given the intensity and scale of the 1994 fire (the entire park was burnt) and the large numbers of flowering individuals and undamaged capsules per inflorescence (authors' unpubl. data), we consider that satiation of both pre and post-dispersal predators was likely. Third, there were no obvious weather conditions (e.g. drought) to which we could attribute lower than average recruitment. We conclude that mortality is more important as a limiting factor than fertility because very large increases in fertility are required to offset relatively small differences in mortality. This interpretation is consistent with a strategy of longevity and repeated flowering events as a response to unpredictable reproductive success (Bond & Midgley 2001, Keith et al. 2007b, Krebs 2009).

Management implications

We conclude that local populations of *Xanthorrhoea resinosa* decline or grow depending on the level of competition from overstorey species and the extent to which seedling establishment varies both temporally and spatially. If temporal variation in seedling recruitment is similar to spatial variation in recruitment observed after the 1994 fire, then populations may stabilise or grow under a regime of frequent fires similar to our three-fire scenario (although lower densities are more likely). Conversely, if our measurements of spatial variation in recruitment are indicative of the relative suitability of different sites for seedling establishment then in the long term, the species is likely to contract in range to safe sites (sensu Harper 1977), or sites where overstorey is interrupted such as under *Eucalyptus* canopy, on rock shelves or areas of very shallow soil unsuitable for shrubs. More pessimistic projections may occur under a stochastic treatment of these data, because we have not factored in recruitment failure as observed in this study (although a stochastic treatment would also take into account higher recruitment, hitherto not observed).

This study provides an insight into the consequences for the population dynamics of a range of species known to be negatively impacted by competition from overstorey species (Keith and Bradstock 1994, Tozer and Bradstock 2002). Our results challenge central assumptions governing fire management of heath in Royal National Park in suggesting that a focus on minimum fire intervals alone will not guarantee the long-term persistence of key understorey species. To achieve this goal, fire management must also promote periods and places of low overstorey shrub density. This might be achieved by applying either very short fire-intervals (to interrupt shrub recruitment), under which serotinous obligate seeder species are the most obvious group affected, or very long fire-intervals (causing shrub senescence) under which resprouting shrubs, ferns and both rhizomatous and non-rhizomatous graminoids and herbs are likely to decline (Keith et al. 2007a). While one empirical study has suggested that populations of overstorey shrubs species may be more resilient under high fire frequencies than demographic studies suggest (Bradstock et al. 1992), the implications of local extinction caused by long fire-intervals for species such as *X. resinosa* are potentially more serious. For example, *Banksia ericifolia* has a similar dispersal capability to *X. resinosa* but a much higher capacity for population growth by virtue of rapid growth and maturation. In comparison, *X. resinosa* is likely to require 40 – 160 years to mature and from 120 – 240 years following germination before significant reproductive output occurs (Table 2). Nevertheless, proteaceous shrubs comprise an important habitat and food resource for nectarivores. Further studies are required to establish what spatial and temporal pattern of shrub density is required to promote coexistence of these contrasting species. Meanwhile, we argue that fire regime thresholds should more directly consider functional groups containing species with low potential for population growth.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of the following people in with field work: Elizabeth Ashby, Tony Auld, Ross Bradstock, Nicholas Carlisle, Janet Cohn, Andrew Denham, Richard T. Dutchman, Helga T. Dutchwoman, Murray Ellis, Cathy F. England, Meredith Henderson, Lisa Holman, Simon Hunter, Nathan Kearns, Karen Maling, Lisa Metcalfe, Ben Owers, Vicki Logan, Berin Mackenzie, Mark Ooi, Christopher Pennay, John Porter, Suzette Rodereda, Patsy Ross, Christopher Simpson, John Steer, Elizabeth Tasker, Dan Tindall, Ken Turner and several others (PG, MR, JD, PH, AP, and GN)

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