

Changes over 46 years in plant community structure in a cleared brigalow (*Acacia harpophylla*) forest

ROBERT W. JOHNSON,¹ WILLIAM J. MCDONALD,¹ RODERICK J. FENSHAM,^{1,2*}
CLIVE A. MCALPINE³ AND MICHAEL J. LAWES⁴

¹Department of Science, Information Technology and Innovation, Brisbane Botanic Gardens, Queensland Herbarium, Toowong, ²School of Biological Sciences, ³School of Geography, Planning and Environmental Management, University of Queensland, Brisbane, Queensland (Email: r.fensham@uq.edu.au) and ⁴Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, Australia

Abstract Plant succession theory underpins the development of strategies for the conservation and regeneration of native communities. Current theory has been based largely on space-for-time rather than long-term monitoring data, which have known limitations. There is general consensus that more site-specific studies are needed to corroborate existing hypotheses. The target vegetation is a brigalow (*Acacia harpophylla*, Mimosaceae) forest in one of Australia's most endangered ecosystems, which was cleared and burnt in 1963. Forty quadrats were placed systematically within each of six 20 m × 20 m permanent plots. Presence, density and per cent canopy cover data were recorded for each species at 18 times over 46 years. Brigalow dominated the original vegetation, assumed dominance soon after clearing through massive root suckering and remained dominant throughout the study. It achieved maximum density within two years when severe intraspecific competition led to self-thinning. After approximately 30 years, vacant niches appeared. Woody understorey species were slow to recolonise. Species richness and other diversity indices increased rapidly to a maximum after 2–4 years, declined until the 30th year when they again increased. This was the pattern of the species-rich herbaceous layer; woody species showed a steady monotonic increase. The 'hump-shaped' relationship between cover (biomass) and species richness was confirmed. This example fits the inhibition model for which few examples have been described. While the long-term successional pattern is slightly confounded by climatic variability preceding sample surveys, this space-for-time study not only supports a bimodal pattern of diversity over time but also indicates that the relative species richness of the herbaceous and woody layers may explain the extreme variability reported in the literature.

Key words: brigalow forest, fire, inhibition, long-term monitoring, secondary succession, species richness.

INTRODUCTION

Successful strategies for the conservation and revegetation of our native communities must be based on sound plant successional theory. Current theory has arisen mainly through studies of space-for-time substitution

following disturbance (Peet & Christensen 1980). The limitations of these studies emphasize the need for more site-specific longitudinal studies to test existing theory (Austin 1981; Pickett *et al.* 2001; Guo 2003; Johnson & Miyanishi 2008; Cadenasso *et al.* 2009). The advantage of site-specific studies is that different, due to variation in habitat, species availability and different climatic conditions at similar points in the time sequence following the initial perturbation are removed providing a focus on directional change influenced only by climatic variation. The extent, intensity and type of perturbation, the biological characteristics of the target vegetation and climatic variability at a site all influence the outcome of succession. Accordingly, site-specific monitoring data are needed for a better understanding of successional processes.

We examine plant succession in a brigalow (*Acacia harpophylla*, Mimosaceae) forest. Brigalow is an endangered community in Australia and 86% of its original extent has been cleared (Johnson & McDonald

*Corresponding author.

Bob Johnson devoted much of his working life to the ecology of brigalow (*Acacia harpophylla*) and was for many years the Director of the Brigalow Research Station. Much of his research underpinned the development of the brigalow lands for cropping and sown pastures, but he also contributed to the reservation of representative areas including Dipperu and Palmgrove National Parks. This paper spans his working life and with an irony charts the potential for brigalow to recover after clearance. Bob passed away during the review of his manuscript, and the co-authors efforts to enhance the manuscript and see it through to publication were made difficult without his intimate knowledge of the brigalow community.

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2005). Brigalow open forests were extensive at the time of European settlement, occupying approximately 7 million hectare in north-eastern Australia, mainly in the 500–750 mm rainfall belt (Johnson 1964). With closer settlement and the expansion of agricultural and pastoral industries, brigalow communities were cleared and replaced by pastures and crops (Johnson 1964). Brigalow flowering intensity varies from year to year, and fruiting is a rare event (Johnson 1964). Seed is viable for a very short time and plays no part in the immediate re-establishment of brigalow after clearing and burning. However, brigalow produces suckers from its roots when damaged and following pulling, burning and sowing with seed of introduced pasture grasses (mainly *Chloris gayana*, *Megathyrsus maximus* var. *pubiglumis* and *Cenchrus ciliaris*), some brigalow regrowth usually occurs. In pulled and burnt areas, the density of suckers ha⁻¹ can vary between 30 and 29 000 (Johnson 1964; Anderson 1984). Pasture production declines after several years because of reduced nitrogen availability (Graham *et al.* 1981) and competition from regrowing woody plants, mainly brigalow. Understanding how succession after disturbance proceeds is key to conserving brigalow.

Classical theories of plant succession, such as the relay floristic and the initial floristic composition hypotheses (Egler 1954) have been shown to be too simplistic (Peet & Christensen 1980). Three alternative mechanisms that can bring about successional change, facilitation, tolerance and inhibition (Connell & Slatyer 1977) have also been shown to be simplifications of much more complex processes and interactions (Pickett *et al.* 1987; Walker & Chapin 1987). This has led to individualistic, though not mutually exclusive approaches, emphasizing resource availability and competition in plant succession (Tilman 1985; Walker & Chapin 1987) and population processes involving species life histories and differential longevity (Drury & Nisbet 1973; Pickett 1976; Noble & Slatyer 1980). However, these reductionist approaches have limitations too, for example, Finegan (1984) pointed out that facilitation, tolerance, inhibition and allogeneses are independent mechanisms, which may act successively or simultaneously on the same individual during its lifetime. In turn, the relative importance of these mechanisms may vary widely among environments.

Associated with succession are changes in community properties such as species diversity, biomass and productivity. The pattern of change in species richness during secondary forest succession has varied from study to study, and there is no single unifying concept to explain this variability. Odum (1969) proposed that richness increases monotonically towards a steady state (equilibrium), and this has been supported by numerous studies (Nicholson & Monk 1974), while others describe a steady increase until late succession followed by a

decline. An early post-disturbance peak in species richness followed by a decline has been commonly reported (Bazzaz 1975) but may only be supported at mesic sites (Auclair & Goff 1971). At more xeric sites, typically occupied by brigalow, depending on soil moisture, plant diversity may increase. A few studies (Habeck 1968; Peet 1978) have documented that declining species richness after an early post-disturbance peak may be followed by another increase, coinciding with the death of the initial cohort of dominant trees. The latter may be relevant to brigalow where recruitment pulses driven by favourable climatic conditions can result in an age or stage cohort stand structure.

Guo (2003) reviewed numerous studies of species richness and biomass along successional gradients with conflicting results. He assigned the latter to the absence of long-term studies at a single location. In nearly 70% of the studies, diversity increased initially and then declined, while many of the remaining studies that showed a continued increase considered only the early stages of succession. Guo (2003) did find support for a 'hump-shaped' relationship (Whittaker 1970) between species richness and cover during succession; however, it was not clear how they were related to each other over time at one location.

In this paper, we examine the successional pathway over 46 years at a single brigalow site. These site-specific longitudinal data are used to confront existing theories of succession (Walker *et al.* 2010). Our aim is to provide evidence-based insights to inform the ongoing conservation and revegetation of this threatened ecosystem. One of us (RWJ) measured changes in community attributes such as the structure, species composition and species abundance at this site. In addition, population processes such as the effects of conflicting life histories among competing species and the influence of resource availability on the trajectory of succession were examined.

METHODS

Study site

This study was conducted on the Brigalow Research Station, c.32 km north-west of Theodore in central Queensland (Johnson 1981) from 1963–2009. Rainfall at the site peaks in the summer months (MAR = 732.2 mm; 1903–1994; http://www.bom.gov.au/climate/averages/tables/cw_039090.shtml). The site experienced a relatively dry period from 1963 to 1971, a wet period from 1971 to 1989 and a dry period between 1989 and 2009 (Fig. 1). One hundred and fifty hectare of brigalow forest was cleared in September–October 1963. A soil and vegetation survey of the station was carried out prior to clearing (Webb 1970; Johnson 2004). Vegetation on the experimental site was classified as a brigalow forest with an understorey of *Eremophila deserti* and *Geijera parviflora* (Type-A1), and

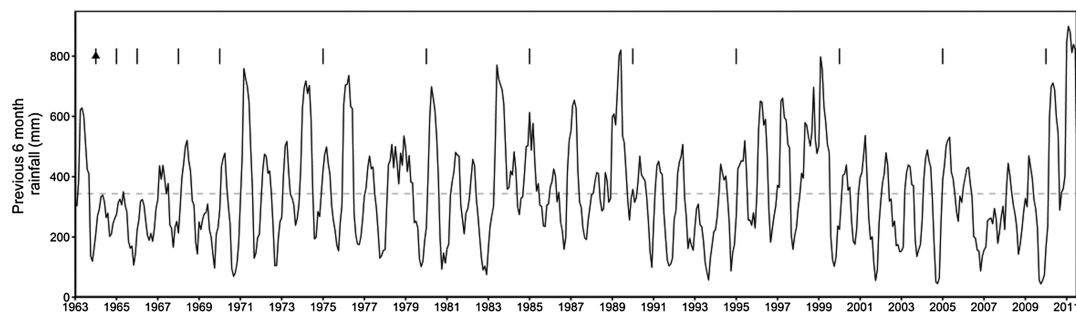


Fig. 1. Six-month rainfall prior to every month during the course of monitoring. Half the mean annual rainfall is identified by the horizontal line, and the time of clearing and burning (arrow) and monitoring records (vertical bars) are also indicated.

the soil is a heavy dark grey-brown vertosol (Isbell 2002) with some gilgai (natural depressions) development. A reference area was set aside that conserved most of the habitats occurring on the Research Station (Johnson 1980).

The study site was remote from disturbed areas harbouring exotic weed species, although introduced pasture species were sown into adjoining areas after clearing. Over the 46 years of the study, the nearest large stands of brigalow were 2–3.5 km from the study site, providing the main source of propagules. Cattle were excluded from the site, but on a few occasions cattle strayed onto the site. Native wildlife had access to the plots.

Initial burn

The trash remaining after pulling was burnt on 4 December 1963. The fuel load was estimated at about $250 \times 10^3 \text{ kg ha}^{-1}$ using the technique developed by Moore *et al.* (1967) on six plots in the same vegetation type in the reference area. During burning of the fallen trash, the spatial intensity of the burn varied considerably from very high to low intensity (Johnson & Purdie 1981). Three visual estimates of this intensity were made: white ash indicating the highest intensities, black areas of moderate intensity and scorched areas where surface temperatures were at their lowest. For some analyses, the first two categories were pooled under burnt as distinct from scorched areas.

Clearing and burning affects the available nutrients in the soil. Lawrence *et al.* (1993) measured changes in plant-available nutrients following the clearing and burning of another brigalow dominant community on the Research Station. They found that available nitrogen increased in the surface soil (0–10 cm) by 700%, available phosphorus by 225% and available potassium by 70%. Fire also changes the physical character of the surface soil. Cracking clay soils are not conducive to seed germination and establishment (Leslie 1965). Severe burning can fuse clay particles (Dyrness & Youngberg 1957; Ulery & Graham 1993), increase the sand-sized particle percent and decrease clay content in the upper layers, thus decreasing mechanical impedance and increasing the soil's water holding capacity. This enhances seed germination and seedling survival, but

the effect is short-lived. However, the thick ash left after burning logs becomes hydrophobic and, together with reduced water capacity in the upper soil and high temperatures at depth, areas subjected to intense fires can become unsuitable for immediate recolonization.

Experimental design

Following burning, six randomly selected $20 \text{ m} \times 20 \text{ m}$ experimental plots (four in the vicinity of -24.826 S , 149.766 E ; and two in the vicinity of -24.829 S , 149.766 E) were established. The areal extent of burnt area for each plot ranged from 60% to 97.5%, and the proportion of gilgais, which are largely devoid of brigalow regrowth, ranged from 6% to 41%.

Total counts of brigalow suckers were made at 3–6 weekly intervals from January to June 1964. Any suckers separated by more than 15 cm were regarded as individuals. Heights of individual suckers and the relative abundance of all species occurring in each plot were also recorded. Species presence in burnt or scorched areas was noted, as well as whether the species were regenerating from perennating organs and/or were present as seedlings.

In September 1964, 40 quadrats, each $0.76 \text{ m} \times 0.3 \text{ m}$, were placed systematically within each of the six replicate plots. The quadrats were marked as in Daubenmire (1959), and in each quadrat, the following data were recorded for each species: presence – both rooted and cover; density; and per cent canopy cover. This procedure was repeated eight times in the first 2 years and on a total of 18 different occasions between 1963 and 2010 (Fig. 1). The plant species were categorized by their life history traits (Table 1).

Although the height of brigalow was recorded regularly during the first 7 months, no heights were measured after this time until 1975. The average height of the canopy trees and the maximum tree height in each replicate were estimated. From 1980, five individuals were selected at random from the uneven canopy in each quarter of the plot, and their heights were measured. The height of the tallest individual in each replicate was also measured.

A quantified assessment of the plots prior to clearing is not available, but measurements from nearby similar

Table 1. Life history trait codes and their definition

Code	Life form	Comments
Perenniality		
LP	Long-lived perennials	commonly more than 10 years old
SP	Short-lived perennials	commonly less than 10 years old
AP	Biennials	semi-annuals which often persist for 2 years
A	Annuals	
Habit		
CT	Canopy trees	
UI	Understorey trees	
P	Epiphytes	
L	Lianas	
TS	Tall shrubs	commonly more than 2 m in height
LS	Low shrubs	
G	Grasses	
GS	Sedges	
GR	Other graminoids	
F	Forbs	
FF	Ferns	

vegetation serve as a reference to the original floristics and structure of the plots. Stem density data are presented from six 20 m × 20 m plots measured in 1996 located between 3.0 and 3.2 km from the cleared plots.

RESULTS

Initial assessment

Sixty-four species were recorded during the first summer. All but one were native species previously recorded in uncleared communities. The single exotic species was not recorded in subsequent years. Plants of 47 species survived on scorched areas, only 22 species survived in areas of moderate to high intensity burns and none in areas burnt at the highest intensity. Seedlings of 24 species were found on burnt areas while seedlings of only nine species were recorded on scorched areas.

The most abundant species were *Sesbania cannabina* and *Abutilon oxycarpum*, predominantly as seedlings. *A. oxycarpum* is a short-lived perennial, common in the original forest, which seeds prolifically in most years. By contrast, *S. cannabina* is occasionally found in uncleared forests, becoming common during wet periods particularly in and around gilgais. These seedlings occurred on burnt areas and only rarely were they recorded on scorched areas. In addition, resprouting *A. oxycarpum* did occur on occasions in scorched areas. These two species were the only species that produced seedlings in all six replicates.

Seedlings were uncommon on the scorched areas with only *Sporobolus caroli* ($n=2$) and *Portulaca filifolia* ($n=2$) recorded in more than one plot.

Some species regenerated in burnt areas, chiefly *Cyperus bifax* from tubers, brigalow from underground roots and *Paspalidium caespitosum* and *P. gracile* from butts, in less intensely burnt areas. All four species were abundant in all replicates. The next most abundant species were *Enteropogon acicularis* and *Brunoniella australis*, found mainly in scorched areas. Fifteen species, which survived the fire, were recorded in at least half the plots on scorched areas.

After six weeks, the density of brigalow suckers was 2642 ha⁻¹ and by week 24 reached a maximum of 30,250 ha⁻¹ (Johnson 1976). Then followed a slight decline in density into the winter and, although a few new suckers appeared, deaths greatly exceeded the number of new suckers (Table 2). Suckers reached an average height of 18 cm by March 1964, 15 weeks after burning, when the average height asymptoted. By the end of the first summer, the tallest suckers were 30–40 cm in height.

Brigalow density

Brigalow, which formed an almost monospecific canopy prior to clearing, grew rapidly from horizontal roots soon after burning and dominated the successional pattern over 46 years. The density of brigalow changed over time (Fig. 2a) from mean peak density of over 30 000 suckers ha⁻¹ in the second summer, followed by a slow but steady decline over the next 30 years, after which the decline became more pronounced. In plots with high maximum densities (1, 3, 4: greater than 40 000 suckers ha⁻¹), the decline in density occurred soon after the asymptote was reached and was linear until the last few years when the rate of decline increased slightly. In replicates with low maximum densities (5, 6: mean density approximately 20 000 suckers ha⁻¹), the density remained constant for almost 30 years before declining. After 46 years, the density of *Acacia harpophylla* remained substantially higher (2000–13 000 stem ha⁻¹) than in the reference plots where densities within one stan-

Table 2. Average density and average height of brigalow suckers during first 7 months after burn

Date	Weeks	Suckers (ha ⁻¹)	Av ht (cm)
15, 16 January	6	2642	11
18 February	11	17825	12
17, 18 March	15	25142	18
16 April	19	30058	19
20 May	24	30250	18
9, 10 June	27	28975	19

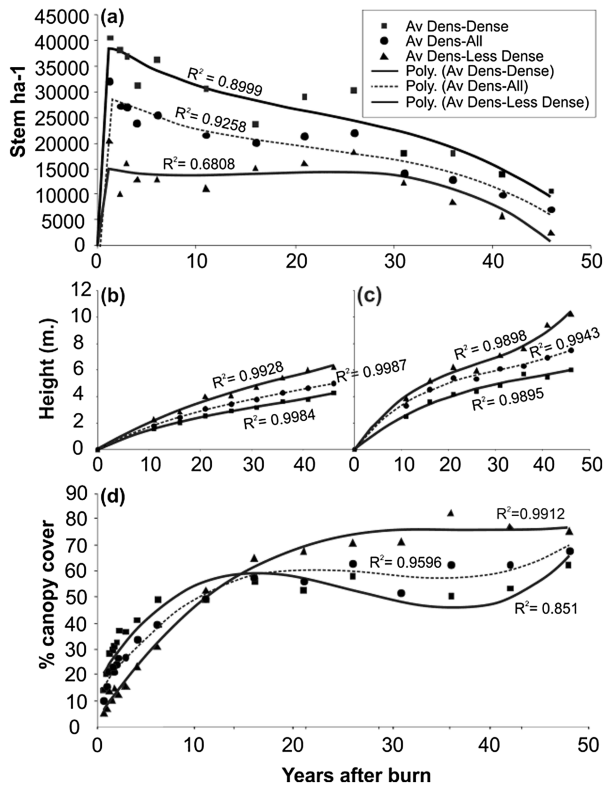


Fig. 2. Changes in properties of *Acacia harpophylla* over time. (a) density of individual stems, (b) canopy height, (c) maximum height, (d) per cent canopy cover, showing averages over all replicates, averages in dense replicates (1, 3 and 4) and averages in less dense replicates (5 and 6) with their respective polynomial trendlines.

standard error of the mean were 303 to 539 ha⁻¹ (Table 3).

Brigalow height

When height measurements were resumed in 1975, 11 years after the burn, the mean height in each plot ranged between 1.5 and 2.4 m (average 1.8 m), and the height of the tallest tree ranged from 2.4 to 4.3 m (mean 3.3 m) (Fig. 2c). The average height of the brigalow canopy showed a slight curvilinear increase ($R^2 = 99\%$) reaching a mean height of 5 m after 46 years (Fig. 2b). The increase in maximum height was also curvilinear ($R^2 = 98\%$). There was a density effect on mean height, with dense plots having a mean height of 4.3 m and the less dense 6.2 m (mean 5.0 m). Similarly, the heights of the tallest trees in dense and less dense plots reached 6 m and 10.3 m (mean 7.5 m).

Brigalow canopy cover

Within 9 months of burning, brigalow had a canopy cover of 10% (Fig. 2d) or almost 40% of the combined

per cent canopy cover of all species (Table 4). Initially, the increase was almost linear after which the rate of increase declined and stabilized. A change in the rate occurred after 11 years. By the 16th year, the canopy cover averaged 58%, but over the next 30 years, it increased to only 68%, although a temporary fall to 51% occurred in 1995 because of leaf drop and small branch death following extremely dry conditions. The shape of the curve was also influenced by stem density. In the dense replicates, the increase slowed markedly after 6 years, whereas in the less dense replicates, the initial linear increase persisted for 16 years. Higher stem densities resulted in a much higher initial canopy cover, but after 10 years, the canopy cover in the less dense plots, where competition was less intense, matched that of the dense plots. After 10 years, the rate of increase in canopy cover in dense plots had slowed markedly compared with the less dense plots, in which canopy cover after 30–40 years was more than 20% higher. After 46 years, the canopy cover in both dense and less dense plots converged on the average cover (68%).

Woody understorey

In the original stand, *E. deserti* was the most abundant understorey tall shrub or tree. Scattered trees of *G. parviflora* were also present. *Rhagodia spinescens* was the most common low shrub. Few understorey species were able to resprout following the burn.

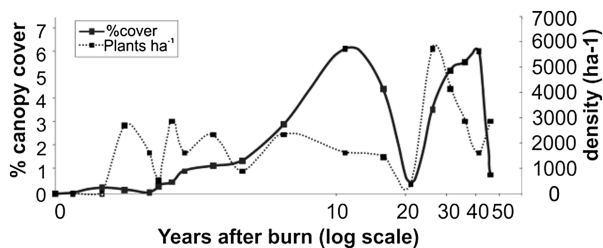
Understorey tree species and tall shrubs, prominent in mature brigalow forests, were very slow to establish, while their cover increased in fits and starts over time (Table 4). Woody understorey species only became prominent when the brigalow canopy cover reached 40% after 6 years, and by the 11th year, the combined understorey cover exceeded 9% (7% of the combined species canopy cover). Yet 10 years later, it was less than 2%, rising to 12%, 36–41 years after the burn, then dropping to 7% (about 8% of the combined canopy cover). The main contributor to the extreme fluctuations in cover was *E. deserti* with its cover reaching a peak of 6.3% after 11 years followed by a steep decline and a second peak of 5.6% in the 36th year followed by a similar decline (Fig. 3). These fluctuations reflected pulses in seed germination followed by deaths. *R. spinescens* showed a similar pattern of pulses of seedlings, establishment and death in the early years and only became prominent after 36 years. No plants of *G. parviflora* were recorded in the initial count. In plot 2, *G. parviflora* cover was recorded at 15 months and persisted until the 26th year after which the plants died. Very occasional *G. parviflora* survivors have persisted on the broader experimental site, but no plants or seedlings were recorded in the other replicates. This lack of *G. parviflora* contrasts with the reference site where it occurs at densities of about 250 stems per hectare.

Table 3. Average species canopy cover (%) of life form groups over 46 years after burn

	Years after burn																		
	0.8	1	1.3	1.6	1.8	2	2.3	3	4	6	11	16	21	26	31	36	41	46	
Total	26	61	91	51	58	123	114	104	118	116	131	105	133	131	96	152	145	164	
Woody	10	16	22	22	24	26	29	30	36	44	59	64	59	70	58	75	75	74	
<i>Acacia harpophylla</i>	10	16	22	21	23	24	26	27	34	39	49	58	56	63	52	62	63	68	
Others	0.1	0.7	0.9	1.1	0.7	2.3	3	2.8	2.8	5.1	10	6	2.6	6.9	6.6	12	12	6.8	
Herbaceous	45	68	29	34	98	84	75	82	72	73	42	75	61	38	77	70	90		
Graminoids	15	28	18	23	61	55	49	45	31	55	25	37	31	18	48	49	65		
Native	6.1	11	21	12	16	35	31	25	25	20	40	20	32	28	17	35	26	28	
Exotic	0.2	3.6	7.5	5.5	7.1	26	24	24	20	11	15	5.3	4.4	3	0.8	13	24	36	
Forbs	10	30	40	11	11	37	29	26	37	42	18	17	38	31	20	29	21	27	
Native	9.1	25	35	10	8.8	35	28	23	36	41	18	17	38	31	20	29	21	27	
Exotic	0.6	4.8	5.4	1.4	2.4	2.3	0.7	3.2	1.2	0.2	0.1	0.1	0.4	0	0.1	0.2	0.1	0.7	
Perenniality																			
A	0.7	5.3	6.1	2.4	3.4	8.5	7.7	5.4	5.8	10	0.5	7.4	1.9	0.2	0.9	0.2	0.7	8.4	
AP	0.8	5.7	7.8	1.1	1.2	7	5.8	4.3	5.2	5.7	5.4	4	9.2	2.3	4.5	3.2	4.8	7.5	
SP	14	34	54	26	29	83	71	66	71	57	67	31	64	60	33	77	66	75	
LP	10	16	22	22	24	25	29	29	36	44	59	63	58	68	58	71	73	73	
Habit																			
CT	10	16	22	21	23	24	27	27	34	39	49	58	56	63	52	63	64	69	
UT	0	0.1	0.3	0.1	0.2	0.7	1.5	1.1	0.9	1	2	1	1.4	1.4	0.4	0.7	0.7	0.8	
P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	1	1.1	
L	0.1	0.2	0.2	0.3	0	0.3	0.3	0.2	0.3	0.5	0.5	0.3	0.3	0.4	0.3	1.3	1.6	1.8	
TS	0	0.2	0.2	0.1	0.3	0.5	1	1.2	1.4	3	6.4	4.5	0.4	3.6	5.3	5.6	6.4	1	
LS	0.3	3.2	4.2	0.6	0.3	3.5	1.3	1.6	2.1	2.5	0.5	0.1	0.9	1.7	0.8	4.4	2.1	3.6	
G	4.3	12	23	16	21	53	51	46	43	29	53	24	32	28	17	45	47	58	
GS	1.8	3.4	5.6	1.7	1.6	7.4	3.6	3	2.1	1.6	1.9	1.2	4.4	2.2	0.4	2.7	1.1	4.1	
GR	0.1	0	0.3	0.1	0.2	0.3	0.3	0.2	0.2	0.2	0.6	0.2	0.5	0.4	0.3	0.5	0.7	2.2	
F	9.3	27	36	11	11	34	28	25	35	39	17	17	37	30	19	27	20	21	
FF	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0.1	0.2	0.2	0.7	0.5	1.4	

Table 4. Average species richness (number of species) using cover data over 46 years after burn

	Years after burn																		
	0.8	1	1.3	1.6	1.8	2	2.3	3	4	6	11	16	21	26	31	36	41	46	
Total	66	77	89	88	82	96	86	96	89	80	88	78	88	71	73	75	74	102	
Woody	6	11	13	14	9	10	15	12	14	12	17	11	13	14	13	18	18	18	
Graminoids	Herbaceous	60	66	76	74	73	86	71	84	75	68	71	67	75	57	60	57	84	
	19	25	29	26	26	31	31	28	30	28	32	31	30	26	24	30	29	35	
	Native	17	22	26	23	22	28	28	25	27	25	27	27	27	24	22	27	26	30
Forbs	Exotic	2	3	3	3	4	3	3	3	3	5	4	3	2	2	3	3	5	
	Native	41	41	47	48	47	55	40	56	45	40	39	36	45	31	36	27	49	
Perenniality	Exotic	37	36	41	41	40	47	36	48	42	37	37	35	39	31	35	26	43	
	Exotic	4	5	6	7	7	8	4	8	3	3	2	1	6	0	1	1	2	6
Habit	A	8	8	12	14	14	18	9	17	12	10	8	5	11	3	6	3	5	19
	AP	9	8	9	10	8	9	8	10	6	6	6	8	8	5	8	3	4	11
	SP	43	52	58	53	52	62	57	59	59	54	58	56	58	51	48	53	50	55
	LP	6	9	10	11	8	8	12	10	12	10	16	9	11	12	11	16	15	17
Habit	CT	1	1	1	1	2	1	2	1	2	1	2	2	1	3	4	3	4	4
	UT	2	4	5	6	3	3	6	5	6	6	9	4	7	5	4	6	4	5
	P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
	L	3	3	4	3	2	3	3	3	4	2	3	3	3	4	3	6	5	5
	TS	3	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	2	2
	LS	3	6	7	5	5	7	7	7	6	7	4	5	7	5	6	3	3	3
	G	15	23	24	23	22	27	27	24	27	25	27	26	24	22	19	26	23	27
	GS	3	2	3	3	3	3	3	2	2	2	3	3	3	2	3	2	3	4
	GR	2	1	3	1	2	2	2	2	2	2	3	3	4	3	3	3	4	5
	F	37	36	41	45	41	49	35	48	38	34	34	30	37	25	29	23	24	45
	FF	0	0	0	0	1	0	0	1	1	0	1	1	1	1	1	1	1	1

**Fig. 3.** Changes in per cent canopy cover and density of *Eremophila deserti* over time.

How *E. deserti* establishes after fire is fundamental to understanding succession in the developing brigalow community. There was no indication of *E. deserti* seedling establishment in vegetation gaps following rain. Plants were randomly distributed through the developing community, indicating that light is likely not an important factor in establishment and survival and that soil moisture might be more important. Brigalow is a clonal species, and stems arise from horizontal roots, which draw resources from a sizeable area around the parental plant. Although establishment and survival of *E. deserti* were not influenced by brigalow canopy cover, growth was greater in plants in more open areas.

Combined species canopy cover

The combined species per cent canopy cover rose sharply during the first two years (Table 4). Over the next 30 years, the increase was slight with fluctuations weakly correlated with rainfall in the months prior to sampling. After 36 years, there appeared to be a distinct increase in combined canopy cover, attributable to an increase in the woody understorey species, *E. deserti* and *R. spinescens* and in the exotic grass green panic (*Panicum maximum* var. *trichoglume*). This was maintained to the 46th year, although exceptional rain prior to the last count, following a severe drought, resulted in a substantial increase in the cover of annual plants, some never previously recorded at the site. During the first 2 years, the combined per cent canopy cover was dominated by herbaceous species, and by the second year, brigalow contributed only 19%. However, during the next 30 years, the proportion contributed by brigalow increased to 54%, while the herbaceous contribution declined from 79% to 39%. In subsequent years, this trend was reversed.

Apart from brigalow, the grasses and forbs provided most of the canopy cover, with the grasses

reaching a peak in the second summer followed by a slight but fluctuating decline until the 31st year with a small peak in the 11th year. Over the last 15 years, there was a marked increase in combined canopy cover due solely to the large increase in green panic grass, while the cover of native grasses stabilized. Similarly, forbs increased their cover until the 6th year, followed by a fluctuating decline that stabilized in the last 15 years. Together, by the second summer, forbs and grasses contributed almost 80% of the total combined cover; their relative decline over the next 29 years was correlated with a steady rise in the combined canopy cover of woody species, which after 11 years contributed approximately 50% of the combined cover.

The combined cover of perennials has always been much greater than that of the annuals and biennials, which have rarely exceeded 15% at any time. The latter reached their peak in the first few years and since have been in fluctuating decline as competition for moisture has increased. Only at the last count, when rainfall was at record heights and competition for available moisture was reduced, did the canopy cover of annuals and biennials reach levels attained in the first few years.

Native grasses and forbs have always provided more cover than exotic species. Exotic pasture species, green panic, buffel grass and Rhodes grass, common throughout the Research Station, increased steadily during the first 2–3 years comprising 40–50% of the grass composition, mainly due to abundant (20–25% of combined canopy cover) Rhodes grass. From the 16th to the 31st year, the contribution of exotic species to the combined canopy cover declined to about 1%. From the 31st to 46th year, there was a marked increase in the cover of exotic grasses, mainly green panic, to more than 20% of the combined canopy cover. Exotic forbs were never abundant, being only prominent (less than 8%) during the first year.

Species richness

Since the original count, 177 plant taxa were recorded. Of these, 30 taxa were recorded once while 24 were present at every sampling period. Total species richness increased sharply after clearing with 96 species recorded during the second and third summers (Table 5). Subsequently, there was a fluctuating decrease in richness with the relatively higher peaks associated with higher rainfall in 6 months prior to sampling. For example, total species richness was 78–96 species in the relatively wet years 1963–1971 and 71–74 species in the relatively dry years 1989–2009 (Table 5; Fig. 1). Species richness increased to a maximum of 102 species at the last count in 2010 after abundant rain (Table 5; Fig. 1),

Table 5. Average stem densities (and standard error) from six 20 m × 20 m plots in uncleared reference sites similar to the recovery cleared sites forming the subject of this study

	Stem density. ha ⁻¹
<i>Acacia harpophylla</i>	420.83 (118.22)
<i>Apophyllum anomalum</i>	41.67 (32.06)
<i>Lysiphyllum carronii</i>	8.33 (8.33)
<i>Psyrax johnsonii</i>	8.33 (5.27)
<i>Capparis loranthifolia</i>	29.17 (20.83)
<i>Casuarina cristata</i>	4.17 (4.17)
<i>Citrus glauca</i>	4.17 (4.17)
<i>Eremophila mitchellii</i>	75 (37.64)
<i>Geijera parviflora</i>	254.17 (48.05)
<i>Alectryon diversifolius</i>	12.5 (5.59)
<i>Eremophila deserti</i>	20.83 (13.57)
<i>Eucalyptus cambageana</i>	16.67 (12.36)
<i>Brachychiton rupestris</i>	12.5 (8.54)
Other species	4.17 (4.17)
Total	929.17 (82.01)

largely because of a 300% increase in annuals and very short-lived perennial species.

Different growth forms reacted differently over time. The number of potential canopy tree species remained low, largely because brigalow ultimately forms largely monospecific stands. Nevertheless, the highest tree species richness was recorded in the last five counts. The number of species in the tall shrub and understorey tree stratum increased rapidly over the first 2 years but then reached a plateau with a small peak 11 years after burning. Because of the small quadrat size, the low density of these woody species and slight variations in the placement of the quadrats, species, which occurred in the plots, may have been occasionally missed. This may account for fluctuations in species richness, but there was no evidence of an increase in understorey tree species over the last 35 years. However, during this period, the number of liana species increased. Forb species were quick to colonize the burnt area with the highest number of taxa recorded 2–3 years after burning, after which numbers declined with lowest numbers recorded during the 36th and 41st years. The number of species increased dramatically at the last count mainly because of an increase in annuals following high rainfall. Grasses showed a similar trend though species numbers persisted for much longer before declining to the 31st year after which there appeared to be a slight increase in species numbers. Annual species of grasses were never common.

Species with different life expectancy also responded differently. The pattern was similar for both annuals and biennials reaching maximum richness in the second and third years, with a much steeper decline after 3 years of annuals. Richness fluctuated during the latter period in response to rainfall conditions with peaks occurring

when rainfall was high, and competition for soil moisture was less severe. The number of short-lived perennials was greatest in the second year and remained relatively constant thereafter. However, the number of species of long-term perennials showed a slight but steady increase after the third summer and remained consistently high over the last 10 years.

Twenty five exotic species were recorded but only 13 of these were recorded in more than two sampling sessions. Poaceae with nine species and Asteraceae with eight species provided most of the alien species. Most were recorded in the first 3 years, but a few persisted. However, peaks also occurred at later times when rainfall was high. The Asteraceae were most species rich in the first 2 years but only occasionally appeared since then. Species richness of exotic Poaceae remained fairly constant with the three introduced pasture species becoming early colonizers and, except for Rhodes grass, persisting over time.

Species diversity

The overall trends shown by Simpson's and Shannon's Indices of Diversity were similar (Fig. 4). The diversity of canopy cover species increased during the first 2 years after which it was in fluctuating decline reaching its lowest level in 1995, 31 years after the burn. Diversity then increased over the next 15 years. Using Shannon's Index, forbs achieved high diversity in the second and third years followed by a fluctuating decline until the

31st year. Diversity then increased sharply to a second maximum at the last count because of very high rainfall prior to monitoring. The diversity of graminoids increased sharply in the first 2 years and peaked 9 years later, followed by a fluctuating decline. By contrast, the diversity of woody species increased steadily through the recording period. Using frequency data, the pattern was similar, but there was a lag in the initial peak values with maximum diversity occurring in the third and fourth years.

The Shannon Evenness Index of both species cover and frequency increased until the end of the second year when it peaked. Evenness then showed a slight fluctuating decline over the next 30 years, followed by an upward trend. In contrast, dominance was at a maximum in 1995, 31 years after the burn and a minimum in the 2-year to 4-year period after the burn. Since 1995, dominance has declined.

Species rank-abundance curves

A more complete picture of diversity can be obtained when the proportion of combined canopy cover (biomass) of each species is compared with its rank. Curves expressing the logs of relative cover against species rank for each of the 18 recording times were calculated, and seven selected curves are presented in Figure 5a. These curves approached a lognormal curve. Slopes of the curves were calculated, based on a linear model,

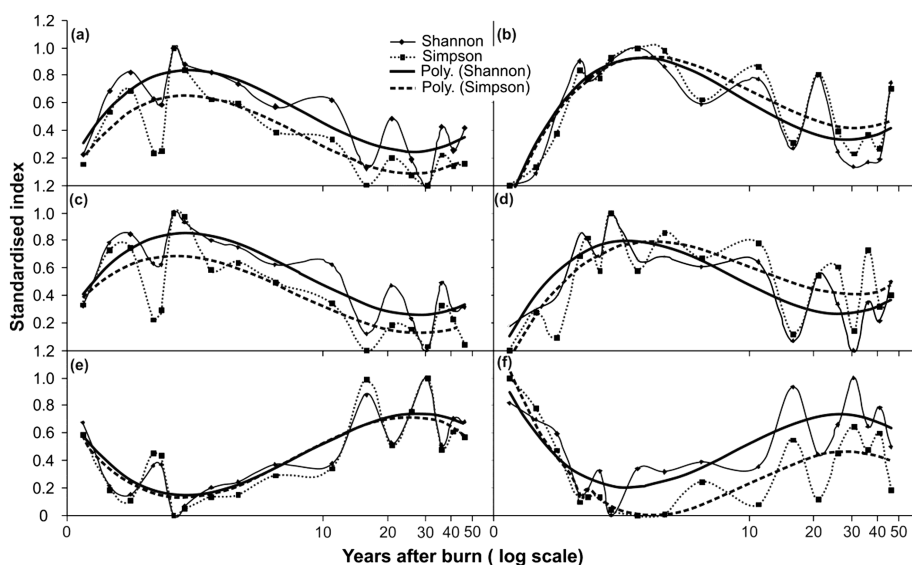


Fig. 4. Changes in Shannon and Simpson diversity indices (based on canopy cover and frequency data) over time, with their respective polynomial trendlines. All indices were standardized by subtracting the minimum value from each value and dividing by the range. (a) Indices of Diversity using cover data, (b) Indices of Diversity using frequency data, (c) Evenness Indices using cover data, (d) Evenness Indices using frequency data, (e) Indices of Dominance using cover data, (f) Indices of Dominance using frequency data.

showing that, after 2–3 years, the slope became steeper with time until the 36th years (Fig. 5b), then declined.

Species richness-cover relationship

Regression of species richness against combined species per cent canopy cover revealed a hump-shaped relationship (Fig. 6). The exceptionally high species

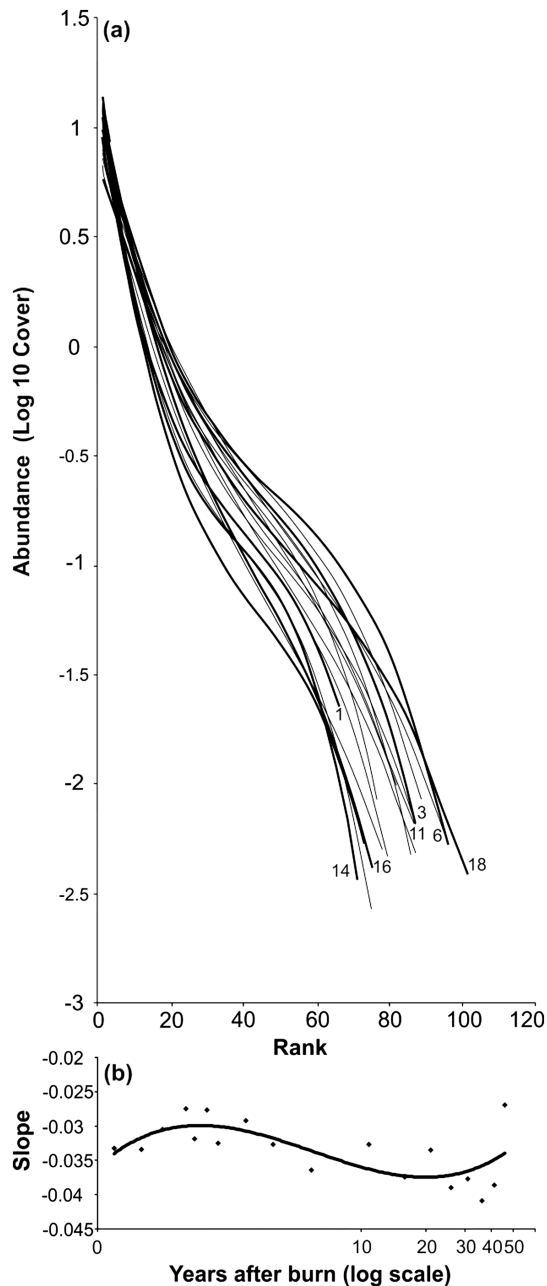


Fig. 5. Species rank-abundance curves. (a) Curves at each point in time with selected curves in bold and numbers representing the times of recording, (b) slope of species rank-abundance curves over time.

richness at the last count weakens but does not change this relationship. The graph highlights the problem with site-specific studies in that rainfall prior to each recording date can be very different, resulting in substantial variation in species richness. While in this study, the large number of recording dates overcomes this inherent variability; it does highlight the problems that may result from studies based on few points in time.

DISCUSSION

The path of secondary succession following the clearing of brigalow forest is influenced by many factors associated with the initial perturbation. The structure and composition of the original vegetation, weather and climatic conditions before and after clearing and the intensity of the burn can lead to different mosaics of burn intensity. This affects the initial density of brigalow suckers, which mainly determines the successional pathway (Johnson 1964). Where plant density is low, *Dichanthium sericeum* grassland with scattered brigalow can eventuate. In this study, the initial density following burning was very high.

Brigalow was dominant pre-clearing, assumed early dominance soon after clearing and dominated the

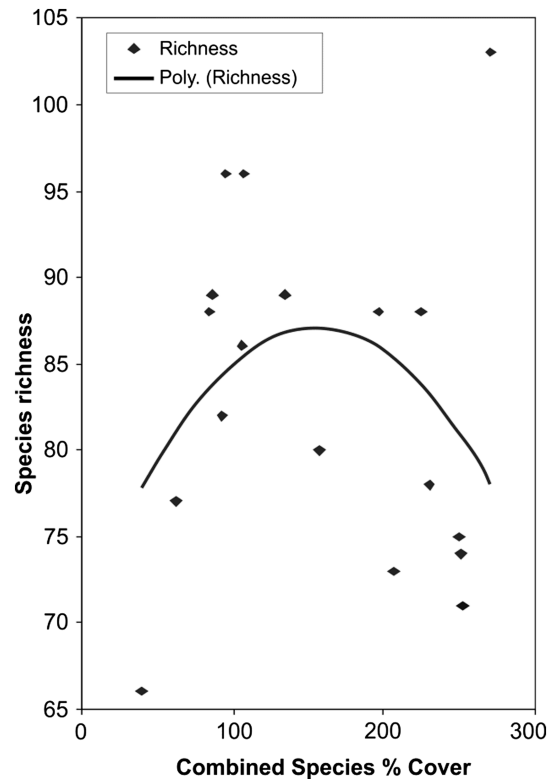


Fig. 6. Regression of species richness against combined species per cent canopy cover with polynomial trendline.

successional process over the next 44 years. It reached its maximum density in the second summer, and as the suckers increased in size, competition for resources resulted in self-thinning in the brigalow population, which steadily declined for the next 30 years followed by a slightly sharper decline. How long a regrowth stand takes to reach a density similar to stands at the time of clearing depends on the maximum density reached soon after clearing. In this study, the lowest density plot reached prefire density within 50 years, while the most dense plots may require 80 years (Fig. 2a; Table 3). The average height of the canopy showed a slight but steady curvilinear increase over time and after 46 years was about 60% that of the original stand (8.15 m), estimated from transect plots in similar adjacent habitat. However, the projected height was also density dependent with the least dense replicate exceeding 75% of predisturbance height, the limit set by current legislation for a regrowth stand to be protected, while the most dense plot only reached 50% of prefire height after 46 years (Fig. 2b and c). The canopy cover at the final count was still greater than that of the initial stand, and though there were density effects, the per cent cover of all plots appeared to be converging (Fig. 2d).

Species in the understorey tree and tall shrub layer were slow to colonize, and only *E. deserti* was prominent. Episodic germination events, establishment, followed by population crashes characterized its presence, which generally coincided with high soil moisture followed by dry periods. Competition with brigalow for available moisture was a controlling influence in the growth of its population over time. The common understorey tree, *G. parviflora*, whose seed is bird-dispersed, did not become established in the cleared area despite being an important component of the reference area (Table 3). *R. spinescens* the dominant low shrub in the original vegetation only became prominent after 36 years. Lianas were slow to establish.

The combined species canopy cover was initially dominated by the herbaceous species, and at the second year, brigalow contributed only 19%. Subsequently, brigalow strongly influenced the abundance and species composition of its competitors. While it inhibited all other species, their differential tolerance to varying degrees of inhibition determined their growth and survival and influenced community properties. Although for 30 years the combined cover of its competitors remained relatively constant, severe competition for resources, particularly moisture, led to the extinction of less competitive species. Intense self-thinning of brigalow eventually weakened its control, providing larger vacant niches leading to an increase in combined canopy cover during the last 15 years. Throughout periods of higher soil moisture, the relative contribution of the herbs increased, indicating competition for moisture under the controlling influence of brigalow was a limiting factor.

While various successional pathways were operating simultaneously in various strata of the regenerating community, the dominant successional pattern is most closely aligned with the inhibition hypothesis. Opinions are divided about the extent to which inhibition and tolerance are involved in secondary succession. Connell and Slayter (1977) contend that inhibition is more common, while Finegan (1984) suggested inhibition may be restricted to a small group of monospecific stands of clonally spreading shrubs. This study fits the narrow definition of Finegan, but the target vegetation is a widespread monospecific community of clonally spreading trees reaching more than 20 m in height, which prior to clearing occupied more than 7 million hectares. According to Finegan (1984), published examples (Niering & Egler 1955; Niering & Goodwin 1974) of this form of succession are rare. In the inhibition model, Connell and Slayter (1977) suggest the initial dominating colonists prevent any further succession until their damage or death releases resources allowing for a new phase to commence. They proposed two alternative models. In one, extremely long-lived and tolerant later successional species eventually replace the initial dominants, species not normally regarded as late succession species. In the other, the initial dominants may be replaced by the same species or species with similar life-history characteristics. In this study, the initial dominant, brigalow, is among the longest living species in the community. Rarely, when brigalow forests occur on better drained or less sodic soils does an understorey of semi-evergreen vine thicket species form, eventually displacing brigalow in the canopy to form a diverse semi-evergreen vine thicket. Mostly, because the inhibitor, brigalow, produces root suckers following damage, it has a competitive advantage and becomes self-sustaining. Having an ineffective sexual reproduction system, it relies on the production of root suckers following damage to persist. Processes such as ageing and episodic environmental events such as cyclones, drought and fire result in topkill (death of above-ground biomass), which stimulates suckering in clonal species such as brigalow. The complexity of interacting processes, demonstrated in this study, reinforces the views of many authors (Pickett *et al.* 1987; Walker & Chapin 1987; Callaway & Walker 1997) that succession involves complex processes and interactions.

There are divergent views on the pattern of change in species richness and diversity during secondary succession (Peet & Christensen 1988; Guo 2003). This study showed an early post-disturbance peak followed by a decline and then an increase after self-thinning of the initial dominant cohort. This study thus supports the bimodal hypothesis suggested by Peet and Christensen (1988), similar to that recorded by Habeck (1968) and Peet (1978). In this study, the late increase appeared about 30 years after the disturbance, whereas in the latter studies, it only appeared after more than 200–300 years. This

may reflect the life expectancy of the aboveground stems, which in brigalow is much less than that of the initially dominant *Pinus* spp. in their studies.

This study also demonstrates that simple comparisons of diversity over time are a simplification of the outcome of complex interacting processes. While the overall pattern reflected the pattern of the species-rich herbaceous layer, the woody element showed a steady overall increase in richness and judging from the original vegetation may not yet have reached species saturation. The relative richness of the woody and herbaceous elements in the original community must influence the overall successional pattern, and many studies in forest communities ignore the contribution of herbs. In the latter studies and where the species richness of the herbaceous layer is relatively small, such as in rainforests, the reported steady increase in species richness over time is paralleled by the pattern of the woody element in this study. This bimodal diversity pattern was confirmed by studying changes in species rank-abundance curves at each recording time. The curves fitted a log-normal distribution (Tokeshi 1993), while their slope indicated an initial increase in evenness followed by a protracted period of increasing dominance before returning to a more even state. The hump-shaped relationship between cover (biomass) and species richness (Whittaker 1970) was also supported and provides corroborating evidence from a study over time at one location, previously unreported (Guo 2003).

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