Regeneration of spinifex (*Triodia* spp.) grasslands after burning or harvesting

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Abstract

This project examined the effects of burning (summer/winter) versus harvesting (hand harvest/mechanical) on spinifex grasslands dominated by *Triodia pungens* or *T. longiceps*, two dominant spinifex species in north-west Queensland. Factors influencing germination of spinifex seeds were examined in controlled experiments to assess if germination can occur in the absence of fire. Floristic composition and species abundance of regenerating vegetation were assessed, and species composition and abundance analysed across treatments. Burning and harvesting significantly increased species diversity when compared to mature (control) vegetation at all sites. Species composition and abundance differed significantly between control and harvested sites, and harvested and burnt sites in *T. pungens* grassland. Season (dry or wet) of disturbance occurrence significantly changed composition of regenerating vegetation at harvested but not burnt sites in *T. pungens* grassland. Method of harvest (mechanical versus hand) did not change species composition in regenerating *T. longiceps* grassland. Results from germination studies showed *T. pungens* had a significant positive response to treatment with 5% and 10% smoke water solutions. Together the results show that the effects of fire and harvesting on regenerating species composition and spinifex seedling establishment are distinct in two spinifex alliances. If harvesting of spinifex is to occur, it is hypothesised that the most sustainable landscape management plan would consist of: a mosaic of dry season harvest events after good wet seasons and intermixed with wet season burning events.

Introduction

Grasslands dominated by grasses in the tribe *Triodiae* form one of Australia's dominant vegetation types covering ~27% of the continent (Griffin 1984). The common names 'spinifex' or 'porcupine grass' refer collectively to ~70 endemic species across three genera *Triodia*, *Monodia*, and *Symplectrodia* (Poaceae). This study focuses on species in the genus *Triodia* (referred to as 'spinifex'). Spinifex dominates grasslands in the semi-arid and arid regions of inland Australia, and also forms the dominant understorey in some savannahs and woodlands (Allan *et al.* 2002). Spinifex is found on a variety of land forms including rocky slopes of mountain ranges, sandplains and dry salt lake systems (Griffin 1990). Spinifex grasslands are characterised by soils of low fertility and water holding capacity, usually sands and red clayey sands with underlying sandstone or limestone.

Spinifex species are long lived, perennial xerophytes that are hummock-forming and often stoloniferous. Typically with an aerial cover of 20-80%, spinifex grasslands can accumulate 3000-8000 kg biomass/ha in mature communities (Winkworth 1967; Beadle 1981). Small dispersed trees and shrubs are also characteristic of spinifex grasslands with *Eucalyptus* species being the common association in the north and *Acacia aneura* (mulga) widespread in the southern and eastern zones (Griffin 1984). Leaf anatomy allows grouping of spinifex species into 'hard' and 'soft' categories (Burbidge (1946). 'Soft' taxa lack stomata and associated photosynthetic tissues on the abaxial leaf side whereas 'hard' taxa have stomata on adaxial and abaxial surfaces (Mant 2000). Further distinctions lie in the higher fibre content and relative stiffness of hard species, while soft species exude resin from leaf bases (Mant 2000).

Considering the vast expanse of spinifex grasslands and presence as a main understorey species in other ecosystems, it has attracted surprisingly little attention. There is much uncertainty about the effects of climate change on spinifex communities but also interest in the potential to sustainably harvest spinifex as a source of biomaterials. Spinifex grasslands are a potential source of fibre and resin for use in bio-composite materials and could form the basis for sustainable housing to replace materials currently used in remote Australian communities. Our study focussed on the effects of burning versus harvesting spinifex in the context of regeneration of spinifex and associated species, and the removal of nutrients in order to understand the impacts of these disturbances.

Vegetation processes in Australia's arid zone are driven by interactions of three main factors: variable and pulsed rainfall, nutrient availability and fire (Wright & Clarke 2007). Of these factors fire has received the most attention in spinifex grasslands (Wright & Clarke 2007). Spinifex grasslands, like most grasslands, have evolved and coexisted with fire. Most investigations have examined species composition with time- since- fire (Burbidge 1944; Suijendorp 1981; Jacobs 1984; Griffin 1990; Wright & Clarke 2007), and it is widely accepted that species richness increases in spinifex grasslands during early stages of post fire succession.

Recently burned communities are associated with a higher diversity of resprouting perennials, short-lived grasses and ephemeral forbs, which, during later successional stages, are being replaced by spinifex (Wright & Clarke 2007). Of the fire regime components, including time-since-fire, frequency, intensity and seasonality, time since fire proved to be the strongest influence on the floristic composition of regenerating vegetation (Wright and Clarke 2007). Comparatively little is known about regeneration biology of spinifex in relation to fire. The extent to which regrowth after fire is vegetative, ie. from existing stool or runners, or from seed, appears to vary both within and between spinifex species (Bogusiak *et al.* 1990). The distinction between fire-killed and resprouting species is fundamental for understanding the ability of spinifex grasslands to tolerate fire regimes (Rice & Westoby 1999), and important if harvesting was to replace fire. No definitive relationships have been detected between regeneration strategy of spinifex and site attributes, and it is unknown which factors limit seed production and seed survival (Rice & Westoby 1999). Conditions during and after fire are known to enhance seed germination, and *Triodia* seeds not exposed to such physical or chemical conditions, display germination rates of ~10 % (Davidson & Adkins 1997).

Spinifex grasslands dominate areas with oligotrophic soils with very low phosphorous (P) and nitrogen (N) contents. Nutrient relations in spinifex grasslands are directly related to fire and rainfall. The availability of nutrients is restricted to wet periods when microbial activity is stimulated (Ford *et al.* 2007), and spinifex grows when resources are available. Wildfires induce chemical changes in the soil and are responsible for recycling of nutrients bound in live biomass and litter. Intense fire is responsible for volatilising nitrogen (N) and sulphur, and increases the availability of nutrients in the resulting ash (Orians & Milewski 2007).

Little is known about the effects of harvesting on spinifex grasslands. Traditional Aboriginal uses of spinifex were limited to small-scale harvesting for materials including biomass for shelter construction and resin extraction (Bird *et al.* 2008). Use of spinifex by pastoralists involves grazing of cattle on juvenile spinifex (Letnic 2004). There is uncertainty about how best to manage spinifex grasslands as changes in climate and invasion by exotic plants threaten the integrity of Australia's arid zone ecosystems. The majority of spinifex grasslands exist on vacant crown land and receive no organised management (Allan *et al.* 2002). Desert ecosystems may become a greater carbon sink because increasing atmospheric CO_2 levels will result in increasing water use efficiency of desert vegetation and enhanced growth (Nowak *et al.* 2004). This potential increase in biomass accumulation could cause an increase in frequency and intensity of large wildfires and hence harvesting could be employed to lessen this fuel accumulation.

The aim of this study was to increase our understanding of fire and regeneration ecology of spinifex grasslands. This information will aid in the assessments of the potential to sustainably harvest spinifex for use as a biomaterial in remote aboriginal communities. Currently there is no knowledge of the effects of spinifex harvesting on local plant species diversity and long term ecosystem health. Research into regeneration ecology and germination triggers is limited as studies that have explored this topic have produced variable findings for a limited number of spinifex species, and these suggest that seed germination is species and environment specific. This project analysed existing experiments in north-west QLD to improve the knowledge of spinifex regeneration in the context of fire regimes and harvesting. To quantify the effects of these disturbances on regeneration and species diversity in *T. pungens* and *T. longiceps* grasslands, we analysed floristic composition and nutrient relations. Germination of three *Triodia* species was also examined in controlled experiments using chemical treatments to simulate fire.

Methods

Field Sites

This study was conducted in two locations with summer wet – winter dry climates in north-west Queensland; Camooweal (19°57' S, 138°27' E) and Dajarra (21°42' S, 139°30' E) (Figure 1). Previously established experimental plots in both locations were studied; in each location a single species of *Triodia* dominates the vegetation community.

Figure 1. A) Photograph of control site at Camooweal. B) Photograph of dry season harvest site at Camooweal. C) Photograph of wet season burn site at Camooweal (Photographs taken by author June 2010)

Mean annual rainfall in Camooweal is 398 mm per annum with sites located on a flat plain of lateritic red sandy soil. The dominant vegetation type is *T. pungens* grasslands with low open woodland of *Eucalyptus leucophloia* (Snappy gum) and a sparse shrub layer of *Acacia* spp. (e.g. *Acacia elachantha*). The experimental sites in Camooweal consisted of 25 plots of 10 m x 10 m (Appendix 1) each with a two metre fire break around each plot. Two fire and two harvesting regimes with five replicates were implemented including dry season burn (DSB), dry season harvest (DSH), wet season burn (WSB), wet season harvest (WSH) and unburnt/unharvested control. Dry and wet season treatments were carried out in August 2008 and February 2009, respectively. Intermittent stock grazing also occurred throughout this site which belongs to a larger cattle property.

With a mean annual rainfall of 450 mm per annum, the field sites near Dajarra were characterised by a landscape of red lateritic soil with sites located on flat zones surrounded by a low ridgeline of rocky hills. The dominant vegetation type is a *T. longiceps* grass understorey in low open woodland of *E. leucophloia*. The Dajarra sites consisted of five separate sites (site A, B, C, D and E) within an area of approximately 10 km² (Appendix 2).

Within sites B and E there was one 10m x 20m control and mechanical harvest treatment applied (Figure 2). For sites A, C and D there were three treatments applied: 10m x 20m control and mechanical harvest and a 10m x 10m hand harvest, harvested in September 2009.

Figure 2. A) Photograph of control site E at Dajarra. B) Photograph of mechanical harvest treatment site C at Dajarra (Photographs taken by author June 2010).

Floristic Studies

In Dajarra sampling was conducted in June 2010. In Camooweal sampling was carried out in May and again in June 2010. The importance-score method was used for sampling alpha diversity (Morrison *et al.* 1995; Uys *et al.* 2004) which provided measures of both species diversity and abundance. This method involved an expanding quadrat design whereby sub-quadrats increased in cumulative size geometrically 1 x 1, 1 x 1, 2 x 1, 2 x 2, 4 x 2, and fit in a 4 x 4m total quadrat (Appendix 3). Quadrats were set up in the south western corner of every treatment site at both field locations. Each sub-quadrat was searched consecutively, starting with the smallest of the sub-quadrat and proceeding to the largest. Scores were awarded to the smallest of the sub-quadrats in which a species was first encountered. Abundance scoring was based on the number of sub-quadrats in the design (5) with the highest scores being awarded to the smallest sub-quadrat. That is, the inverse of the sub-quadrat number in which a species was first encountered equalled the species abundance score for that treatment site.

This method assumed that common species require a small area to be included in the sample. May and June data sets for Camooweal were combined into one data set using the highest abundance values for each species between the sampling times. Voucher specimens were collected and lodged at the Queensland Herbarium (Mt. Coot-tha, Queensland) for identification.

Spinifex Foliar Element Analysis

Foliar nutrient analysis was carried out for the dominant *Triodia* species at both field locations. Mature *T. longiceps* was collected from all five control sites at Dajarra and *T. pungens* was collected from all five control plots at Camooweal during the dry season in June 2010 (Appendix 1, 2). For each sample approximately 15 healthy mature leaves were collected from the crown of three individual hummocks within a treatment site. These were oven-dried at 60°C for one week and ground using a migratory ball mill to achieve a homogenous particle size. This procedure was repeated for juvenile *T. longiceps* in all mechanical (five sites) and hand harvest (three sites) treatment plots and for *T. pungens* in all burn and harvest treatment replicates.

Samples were analysed for total carbon and nitrogen via combustion (LECO CNS 2000 autoanalyser). To determine total foliar elemental concentrations of Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, S and Si an acid digestion was run using CEM MDS 2000 Microwave digester. For all elements excluding silicon nitric acid and hydrogen peroxide were used in digestion. For silicon, a separate microwave digestion was used.

Soil Sampling and Nutrient Analysis

Soil sampling was undertaken at both field locations. In Camooweal soil was collected from three of the five replicate plots for each treatment totalling 15 samples. Within each 10m x 10m plot soil was collected from the top 5cm at three locations, pooled and then a subsample was taken sieved (20mm mesh) and air dried in the laboratory. The same protocol was undertaken in Dajarra in four of the five sites (site B not sampled) totalling 11 samples.

Total carbon and nitrogen were determined via combustion (LECO CNS 2000 autoanalyser). Total soil macro nutrient concentrations (Al, Ca, Fe, K, Mg, Mn, Na, P, S) where determined by acid digestion of nitric acid and hydrofluoric acid (CEM MDS 2000 Microwave digester). Elemental concentrations in the digest were then determined using Inductively Coupled Plasma-Optical Emission Spectroscopy (ICPOES). Plant available phosphorous was calculated using the Colwell method, a bicarbonate extraction involving a colourimetric assay. Plant available sulphur (in the form of sulphate anions SO_4^{2-}) was determined via calcium monophosphate extractant analysed using ICPOES. Plant available basic cations (Na, K, Mg, Ca) were analysed using ammonium chloride extraction media and run through Inductively Coupled Plasma Spectroscopy (ICPS). Plant available micronutrients (Cu, Zn, Mn, Fe) were analysed via extract with chelating agent DTPA (diethylene triamine pentaacetic acid) and run through ICPOES.

Incubator Germination Studies

Initial germination trials were undertaken using *T. pungens* seed stock in Petri dishes and incubated in growth cabinets. Seeds were hand sorted into 100 seed batches using the pinch test so that only filled seeds were used. De-husking was carried out using forceps and the seeds were gently squeezed from the husk. Prior to treatment seeds were sterilised using a twostep process. Initially seeds were soaked in 0.5g/L solution of 'Thiabendazole™' fungicide plus one drop Decon™ detergent (Decon Laboratories Limited, Sussex, UK) as a wetting agent for three minutes then washed thoroughly with de-ionised water.

Seeds were then soaked with 2.6% sodium hypochlorite solution for four minutes then washed thoroughly with de-ionised water. All equipment was sterilised using 70% ethanol. Seeds were then treated with selected chemical treatments by imbibitions for 40 hours in treatment solutions.

For each germination treatment four replicates of 25 seeds were germinated in 9 cm diameter plastic Petri dishes containing two 8.4 cm diameter filter papers (Whatman No 1). Petri dishes were incubated at 33°C under dark conditions as optimum germination occurs in the temperature range of 30 to 40°C and under dark conditions (Wells 1999). De-ionised water was added as necessary to keep the filter paper moist and Petri dishes were randomly relocated within the controlled temperature cabinets after each recording event. Germination was said to have occurred when the radicle became visible and was greater than 5 mm in length (Figure 3). Germination was scored every three days for 30 days with all germinated seeds removed once scored. Average percent germination rates after 30 days incubation were calculated. Due to high rates of fungal attack even with trials of filter paper initially soaked with 0.5 g/L 'Thiabendazole™' fungicide, no further Petri dish trials were undertaken.

Figure 3. Photograph of *T. pungens* germinant in petri dish showing radicle development.

Glasshouse Germination Studies

Glasshouse manipulations were also undertaken to investigate the factors affecting successful germination and regeneration of *Triodia* seed. *Triodia* species used in this study were: *T. pungens*, *T. schinzii* and *T. bitextura* from the 'soft' anatomical grouping. All three species form major communities as described by Jacobs (1984) in (Allan *et al.* 2002). *T. pungens* and *T. schinzii* are found over much of Western Australia, Northern Territory, north-western South Australia and Western Queensland. *Triodia bitextura* is found in the monsoonal tropical north (north of Lat. 23° S) of Western Australia, Northern Territory and Queensland. These three species were chosen as all form major spinifex communities as co-dominants or localised dominants often over substrate suitable for harvesting (sandy or gravelly soil plains). Seed stock used was harvested by Greening Australia in 2010 from two locations in Northern Territory (Table 1).

Table 1. Seed harvest locations for three *Triodia* species used in germination trials

Species	Harvest Location
Triodia pungens	Helen Springs Station, Northern Territory
Triodia schinzii	Helen Springs Station, Northern Territory
Triodia bitextura	Manbulloo Station, Katherine, Northern Territory

Germination trials were unable to be performed for *T. longiceps* (species found in Dajarra field sites) as seeding never occurred in Greening Australia harvest locations and seed could not be sourced from Dajarra. Seeds from each species were imbibed with four different treatments plus a control. Treatments included: 5 % smoke water (SW), 10 % SW, 10 mM KNO_3 and 20 mM KNO_3. *Triodia pungens* trials contained an additional treatment of 1 mM giberrellic acid (GA_3) to investigate further treatment effects from Petri dish trials. For each treatment three replicates of 100 seeds were used for each species. Each replicate of 100 seeds was hand sorted using forceps and pinch test (squeezing seed between thumb and fore finger). Each replicate was then imbibed in 50 ml of specified treatment solution for 40 hours. Control treatments were imbibed in 50 ml of deionised water. Seeds were sown in 100 cell seed trays using sandy/peat mix soil, stored and watered everyday to field capacity in temperature controlled glasshouse at 33°C.

Accumulative germination rates were then recorded every three days over a period of four weeks. Germination was determined to have occurred when radicle became visible and was greater than 5 mm in length.

Table 2. Summary of species/treatment combinations used in glasshouse and incubator germination trials. Columns list species and rows list seed treatment. GA_3 = Gibberellic Acid

Glasshouse Studies	Species		
	T. pungens	*T. schinzii*	*T. bitextura*
Control	✓	✓	✓
5% Smoke Water	✓	✓	✓
10 % Smoke Water	✓	✓	✓
10 mM KNO$_3$	✓	✓	✓
20 mM KNO$_3$	✓	✓	✓
1 mM GA$_3$	✓	✗	✗
Incubator Studies			
Control	✓		
5% smoke water	✓		
10% smoke water	✓		
10mM KNO$_3$	✓		
20mM KNO$_3$	✓		
1mM GA$_3$	✓		
De husk	✓		
De husk + 10% smoke water	✓		
De husk + 20mM KNO$_3$	✓		
De husk + 1mM GA$_3$	✓		

Data Visualisation and Statistical Analysis

Floristic data was analysed using computer software package PRIMER (ver. 5.2.8, Plymouth Marine Laboratory, Plymouth, England). Species composition and abundance scores were visualized using Bray-Curtis similarity analysis and non-metric Multi-Dimensional Scaling (MDS) was performed for ordination of samples. After exploratory analysis a three-dimensional solution was suggested, this most accurately represented the data due to lower stress values. The stress value totals the scatter around the regression line (Clarke 1993). A one-way ANOSIM test (equivalent to ANOVA) was performed to determine if significant differences in species composition occurred between treatments and for various pooled treatments. A SIMPER analysis was performed to identify species characteristic of each treatment. This exploratory method calculates the average species similarity between every plot in each treatment. The average similarity is then broken down in to separate contributions from each species to give the average contribution as a percentage for each species within each group. Species used to discriminate significant differences between treatment groups were also extracted from SIMPER analysis by their contribution to average dissimilarity value when comparing between two treatments.

For foliar element concentration, soil nutrient data from Camooweal and germination data, one-way or two-way analysis of variance (ANOVA) and Tukey's HSD post-hoc tests were performed for all measured variables using GraphPad Prism®, Version 3.03 for Windows (GraphPad Software, San Diego, USA). Due to the lack of replication in hand harvested treatments Dajarra foliar element and soil nutrient data was analysed between individual treatments at each site using a student's t test with data grouped into control versus harvest treatment (hand harvest and mechanical harvest).

Results

Floristic Studies - Camooweal

Sites were located in terrain dominated by mature *T. pungens* and hence representative of a suitable site for potential harvesting of *T. pungens*. Control sites were dominated by mature *T. pungens* stands with low diversity of other species. In total, 23 species representing 12 families were recorded across treatment plots (Appendix 4). Control sites differed markedly in species composition from the other treatment (Figure 4). *Triodia pungens* had an average abundance rating of 5 (scale of 1 to 5) and contributed 88.8% of total species similarity between control replicates (Table 5). Annual grass *Enneapogon polyphyllus* had the next highest abundance at control sites contributing 8% to average similarity and had an average abundance score of 2.2.
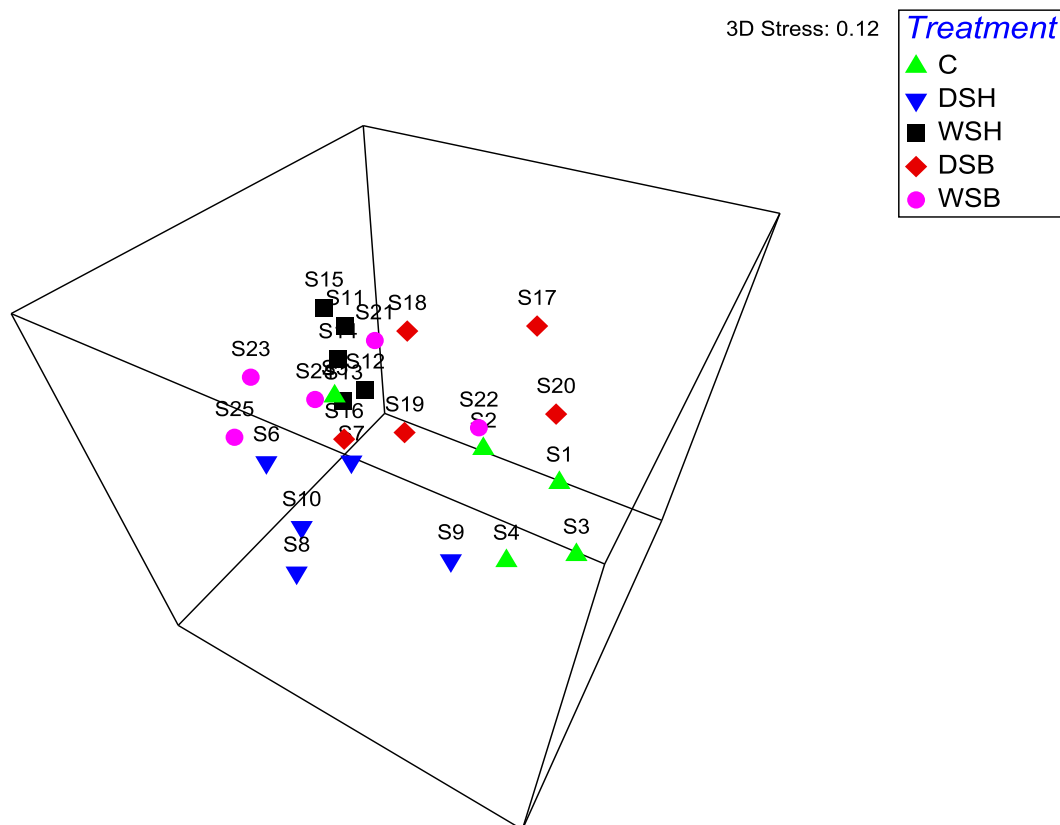

Figure 4. Three-dimensional ordination of floristic data representing species composition and abundance at 25 treatment sites in Camooweal (5 treatments x 5 replicates). Treatments: C = control, DSH = dry season harvest, WSH = wet season harvest, DSB = dry season burn and WSB = wet season burn. The closer sites are to each other the more similar they are in species composition and abundance.

Of all treatments, species assemblages found in wet season harvest (WSH) sites had the highest average similarity index (61.2%) between replicates (Figure 4). Wet season harvest was the only treatment with a species other than *T. pungens* as the most abundant species present. SIMPER analysis showed that annual grass *Sporobolus australasicus* had an equal dominance with *T. pungens* across WSH sites with an average abundance of 5 and 26 % contribution to the similarity score, thus making *S. australasicus* a powerful discriminating species for this treatment (Table 4). *Enneapogon polyphyllus* was the next most abundant in the WSH treatment with an average abundance score of 4.2 and 19 % similarity contribution (Table 3).

Species composition in the DSH treatment excluding *T. pungens* was dominated by the annual grass *E. polyphyllus* and annual herb *Pterocaulon serrulatum* with average abundance scores of 4.4 and 3.8 respectively. Aside from *T. pungens*, DSB treatment sites were characterised by *S. australasicus, Abutilon otocarpum* (perennial herb) and *Chorchorus sidoides* sub sp. *vermicularis* (perennial herb). In contrast, WSB sites were characterised by annual grasses *S. australasicus, E. polyphyllus* and *Eriachne armitti* (Table 3).

To determine if these differences in species composition and abundance were significant ANOSIM was performed. Control sites were significantly different in species composition to DSH, WSH, DSB and WSB treatment (P<0.05). DSH sites were significantly different to WSH, WSB and DSB (Table 5).

Table 3. Cumulative percentage contribution values (Cum. %) of the species ranked by SIMPER analysis as most important in determining similarity within five treatment groups for Camooweal sites. Also shown is the average percentage similarity within each treatment group.

Rank	Control	Cum %	DSH	Cum %	WSH	Cum %	DSB	Cum %	WSB	Cum %
1	*Triodia pungens*	88.8	*Triodia pungens*	34.2	*Sporobolus australasicus*	26.0	*Triodia pungens*	39.67	*Triodia pungens*	28.59
2	*Enneapogon polyphyllus*	97.2	*Enneapogon polyphyllus*	60.4	*Triodia pungens*	52.1	*Sporobolus australasicus*	56.49	*Sporobolus australasicus*	47.60
3			*Pterocaulon serrulatum*	77.7	*Enneapogon polyphyllus*	71.1	*Abutilon otocarpum*	71.16	*Enneapogon polyphyllus*	65.18
4			*Chamaesyce* sp. (Pathungra A. Gunness AG2118)	84.1	*Chamaesyce* sp. (Pathungra A. Gunness AG2118)	80.9	*Corchorus sidoides* sub sp. *vermicularis*	82.80	*Eriachne armittii*	80.98
5			*Tephrosia* sp.	89.1	*Abutilon otocarpum*	90.8	*Enneapogon polyphyllus*	88.03	*Abutilon otocarpum*	87.20
6			*Eulalia aurea*	93.1			*Eucalyptus leucophloia*	91.38	*Tephrosia* sp.	93.15
Average Similarity		56.8		56.1		61.2		48.74		57.95

Table 4. Matrix of average percentage dissimilarity values among all pairs of treatments together with the two species contributing most to that dissimilarity score, from the SIMPER analysis for Camooweal sites.

	C	*Contrib %*	*DSH*	*Contrib %*	*WSH*	*Contrib %*	*DSB*	*Contrib %*
DSH	*Pterocaulon serrulatum*	*16.5*						
	Enneapogon polyphyllus	*13.9*						
WSH	*Sporobolus australasicus*	*18.0*	*Sporobolus australasicus*	*11.6*				
	Enneapogon polyphyllus	*12.6*	*Pterocaulon serrulatum*	*11.5*				
DSB	*Sporobolus australasicus*	*16.1*	*Pterocaulon serrulatum*	*10.2*	*Enneapogon polyphyllus*	*11.1*		
	Corchorus sidoides sub sp. *vermicularis*	*14.84*	*Corchorus sidoides* sub sp. *vermicularis*	*9.9*	*Corchorus sidoides* sub sp. *vermicularis*	*10.5*		
WSB	*Sporobolus australasicus*	*15.9*	*Eriachne armittii*	*12.2*	*Eriachne armittii*	*11.8*	*Corchorus sidoides* sub sp. *vermicularis*	*11.3*
	Eriachne armittii	*15.8*	*Sporobolus australasicus*	*10.7*	*Chamaesyce* sp. (Pathungra A. gunness AG2118)	*10.3*	*Eriachne armittii*	*10.9*

Table 5. Summary of results from Analysis of Similarities (ANOSIM) for un-pooled and pooled species and life form composition and abundance data for Camooweal and Dajarra treatment sites. Significant differences at P<0.05 indicated by different superscript letters.

Camooweal				Dajarra
Un-pooled Species	*Un-pooled Life form*	*Pooled Harvest/Burn Species*	*Pooled Season Species*	*Un-pooled Species*
Control [a]	Control [a]	Control [a]	Control [a]	Control [a]
WSH [b]	WSH [b]	Harvest [b]	Dry [b]	Hand [ab]
DSH [c]	DSH [b]	Burn [c]	Wet [b]	Slashed [b]
WSB [bd]	WSB [b]			
DSB [be]	DSB [b]			

To assess the effect of the disturbance treatments on regeneration of certain life forms, each species was assigned to either annual grass (AG), perennial grass (PG), annual herb (AH), perennial herb (PH) or tree/shrub (TS). As can be expected distinct differences occurred between the life form compositions of control sites when compared to all other treatments (Figure 5). Control sites were characterised by PG which contributed 86 % to average similarity score (Table 6). Wet season harvest sites had the highest average similarity score (71.5) and were characterised by AG followed by PG whereas WSB sites were dominated by AG followed by PH. Dry season harvest and DSB were similar in life form contribution with a cumulative percent contribution to the average similarity score of ~70 % composed of PG and PH (Table 6). The only significant difference (P<0.05) that occurred between life form compositions was between control sites and DSH, DSB, WSH and WSB.
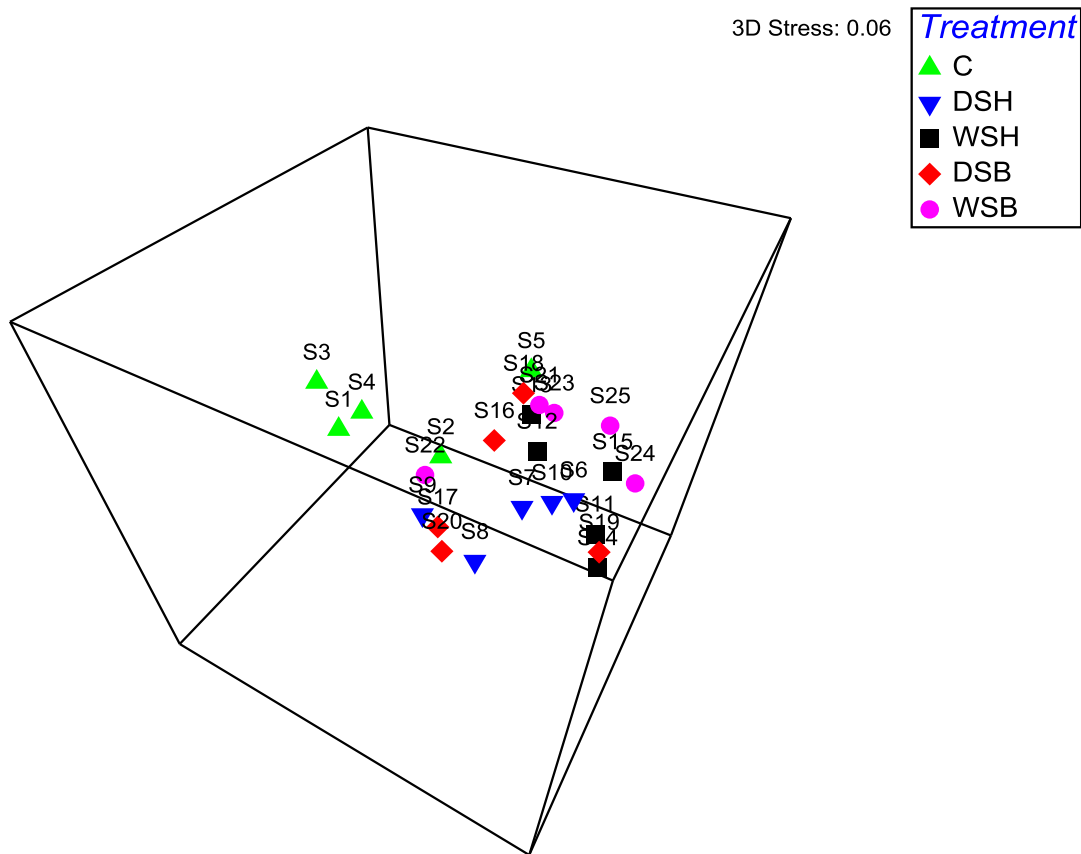
Figure 5. Three-dimensional ordination of floristic data representing life form composition and abundance at 25 treatment sites in Camooweal. Treatments: C = control, DSH = dry season harvest, WSH = wet season harvest, DSB = dry season burn and WSB = wet season burn. Numbers refer to individual sites (see Appendix 1).

Table 6. Cumulative percentage contribution values (Cum %) of the life form groups ranked by SIMPER analysis as most important in determining similarity within 5 treatment groups for Camooweal sites.

Rank	Control	Cum %	DSH	Cum %	WSH	Cum %	DSB	Cum %	WSB	Cum %
1	PG	86.4	PG	38.2	AG	43.1	PH	37.01	AG	45.0
2	AG	94.5	PH	70.7	PG	72.3	PG	70.1	PH	70.9
3			AG	94.9	AH	86.3	AG	94.4	PG	94.3
4					PH	96.2				
Average Similarity		58.4		70.3		71.5		60.4		70.9

To further explore the effect of harvesting on regeneration and subsequent species composition with regeneration observed after fire, treatment sites were pooled into control, harvest (DSH +WSH) and burn (DSB + WSB) (Figure 6). An ANOSIM of this pooled data showed significant species composition differences (P<0.05) between control and harvested, control and burnt and harvest versus burnt (Table 5). The top three discriminating species in ranked order between control and harvest were: *S. australasicus, E. polyphyllus* and *Pterocaulon serrulatum,* between control and burnt: *S. australasicus, E. armitti* and *E. polyphyllus* and between harvest and burn: *E. armitti, P. serrulatum* and *Chamaesyce* sp. *(pathungra A.Gunness AG2118).*
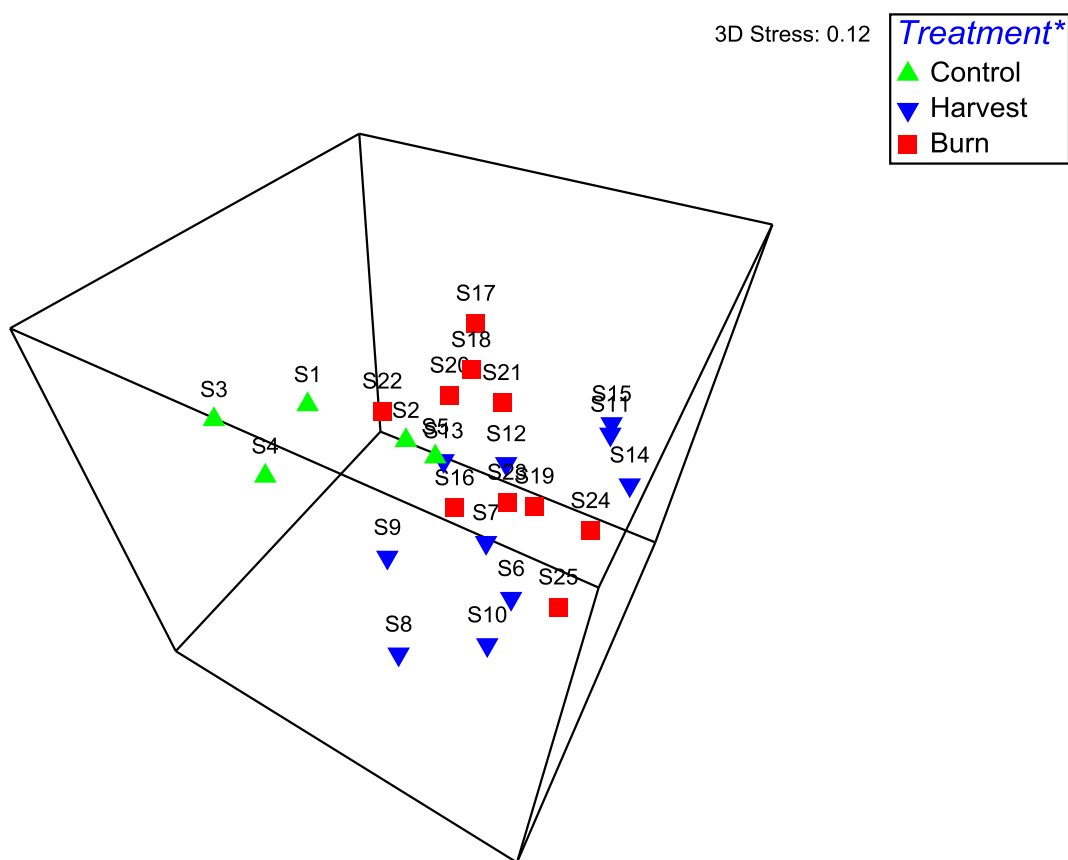

Figure 6. Three-dimensional ordination of floristic data representing species composition and abundance at 25 treatment sites in Camooweal. Treatments grouped into control, harvested (DSH + WSH) and burnt (DSB + WSB).

To explore the effect of season of occurrence of a vegetation disturbance i.e. harvesting or burning on regenerating species composition and abundance samples were pooled into control, dry season disturbance and wet season disturbance (Figure 7). For the purpose of an ANOSIM, the site 5 outlier was removed from the analysis (Figure 7).

The location of the expanding quadrat within control site 5 largely covered an area of exposed ground between mature spinifex hummocks and thus allowed for a higher than usual diversity of plants as than previously observed in other control sites. An ANOSIM of this pooled data showed significant species composition differences (P<0.05) between control and dry season and control and wet season (Table 5).
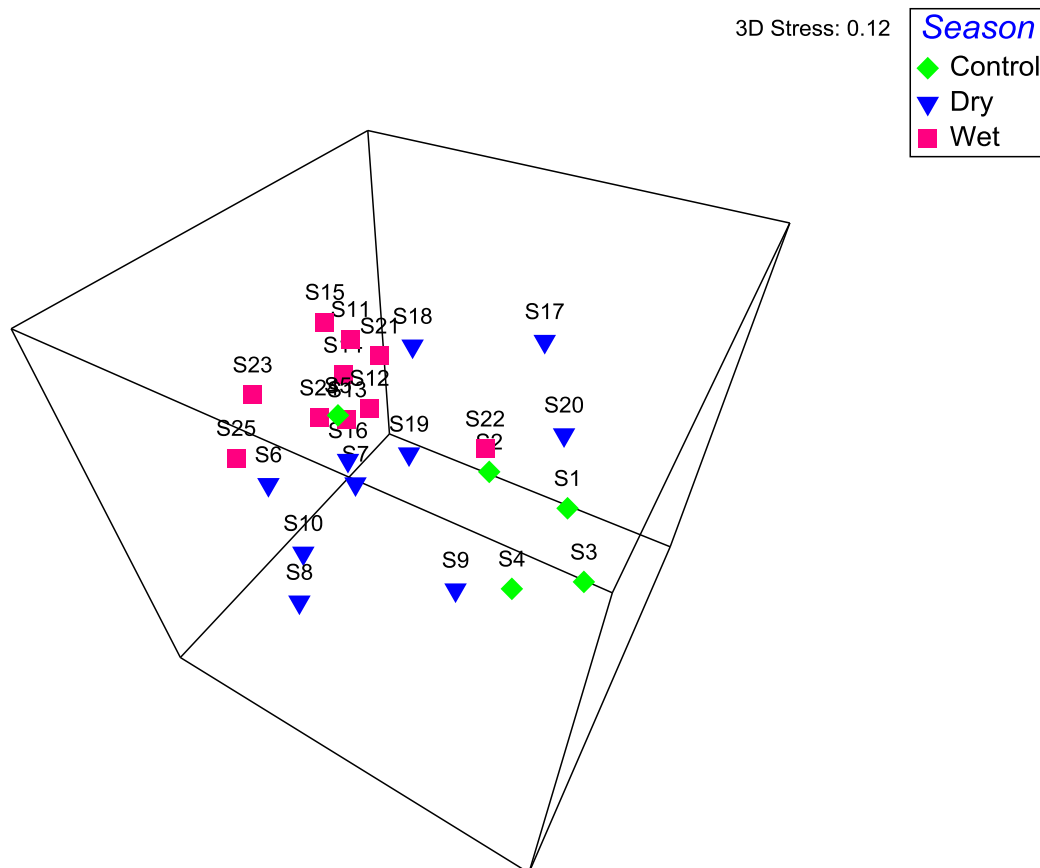

Figure 7. Three-dimensional ordination of floristic data representing species composition and abundance at 25 treatment sites in Camooweal. Treatments grouped into season of treatment application. Treatment grouping = control, dry season (DSH + DSB), wet season (WSH + WSB).

Floristics Studies – Dajarra

In total 25 species representing nine families were recorded across treatment plots located in Dajarra (Appendix 4). Sites were located in terrain dominated by mature *T. longiceps* and hence control sites were therefore dominated by mature *T. longiceps* stands with a low diversity of other species. MDS and SIMPER analyses were performed on this data and a clear clustering of control sites was observed (Figure 8). This further reflected in the high average similarity score (63.01) for species composition between replicates of this treatment

(Table 7). Hand harvested sites were highly variable with an average similarity of 36.4. The most abundant species across these sites excluding juvenile *T. longiceps* were the annual grass *E. polyphyllus* and the perennial herb *Sclerolaena cornishiana,* with average abundance scores of 3.33 (Table 7). Slashed (mechanically harvested) sites had an average similarity score of 45.5 and were dominated by species *S. australasicus* (annual grass)*, Aristida contorta* (annual grass) and *E. polyphyllus* (annual grass). Results of the ANOSIM displayed significant differences in species composition and abundance between control sites and slashed sites (P<0.01) (Table 5). The top three contributing species to the dissimilarity score and hence discriminating species between these two treatments were: *S. australasicus, A. contorta,* and *E. polyphllus* (Table 8). There were no significant differences observed between control and hand harvested sites and between hand harvested and slashed treatments.
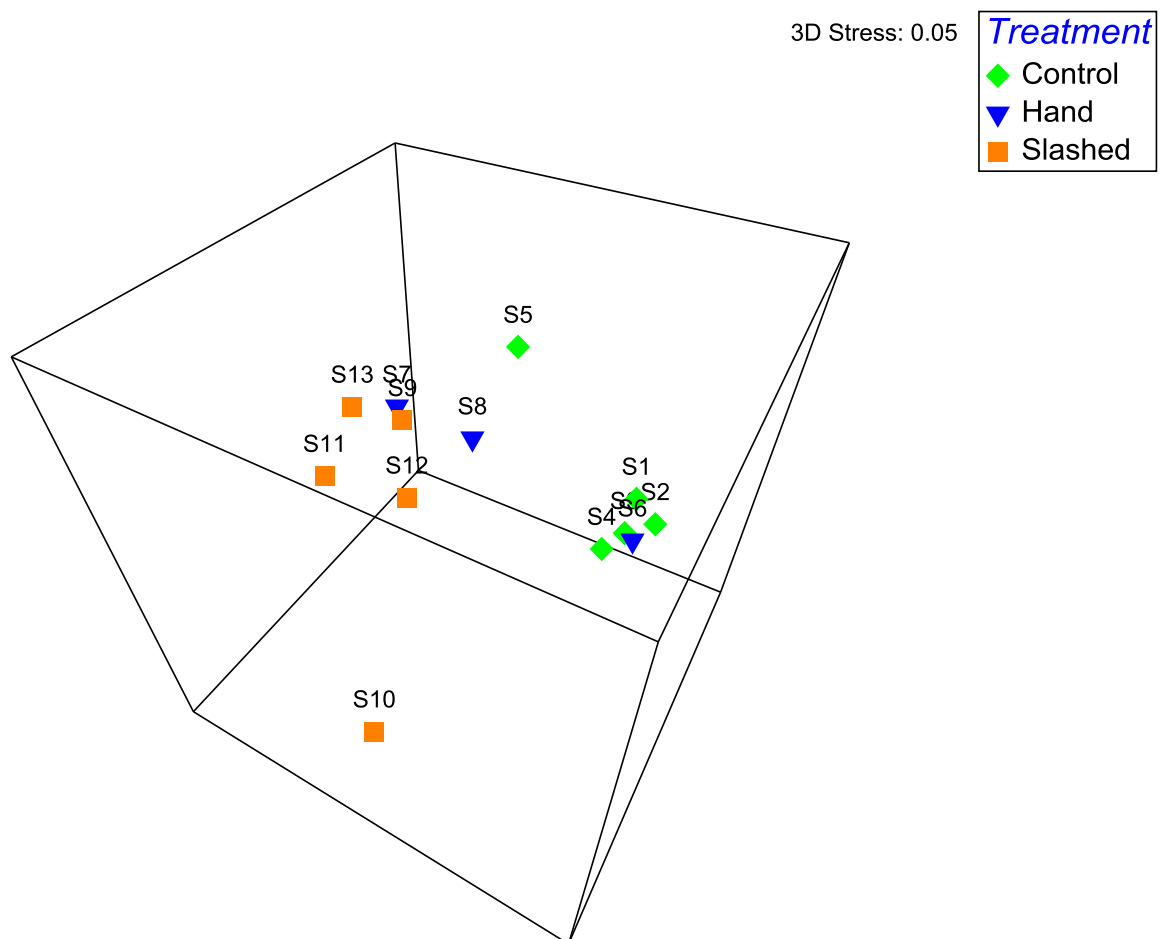

Figure 8. Three-dimensional ordination of floristic data representing species composition and abundance at Dajarra treatment sites. Treatment replicates: 5 x control, 5 x mechanical harvested (slashed), 3 x hand harvested.

Table 7. Cumulative percentage contribution values (Cum. %) of the species ranked by SIMPER analysis as most important in determining similarity within five treatment groups for Dajarra sites. Also shown is the average percentage similarity within each treatment group.

Rank	Control	Cum %	Hand	Cum %	Slashed	Cum %
1	*Triodia longiceps*	98.1	*Triodia longiceps*	62.7	*Triodia longiceps*	36.3
2			*Enneapogon polyphyllus*	79.7	*Sporobolus australasicus*	56.6
3			*Sclerolaena cornishiana*	96.6	*Aristida contorta*	73.8
4					*Enneapogon polyphyllus*	85.1
5			.		*Bulbostylis barbata*	91.8
Average Similarity		63.0		36.4		45.5

Table 8. Matrix of average percentage dissimilarity values among all pairs of treatments together with the two species contributing most to that dissimilarity, from the SIMPER analysis for Dajarra sites.

	Control	Contrib %	Hand	Contrib %
Hand	*Sclerolaena cornishiana*	17.7		
	Enneapogon polyphyllus	17.6		
	Aristida contorta	12.3		
Slashed	*Sporobolus australasicus*	15.6	*Sporobolus australasicus*	13.1
	Aristida contorta	13.2	*Aristida contorta*	10.7
	Enneapogon polyphllus	12.5	*Sclerolaena cornishiana*	10.4

Foliar Elemental Analysis

Elemental analysis of spinifex leaves was carried out to determine and compare concentrations in biomass exposed to different harvest and burning regimes and hence at different maturity stages. Of the total foliar elements analysed (N, C, P, S, Si, Al, Ca, Cu, Fe, K, Mg, Mn, Na) in *T. pungens* at the Camooweal plots, the elements with significant differences between treatments were N, P, Ca, Na, Si, Mg, Al and Fe (Table 10). Nitrogen concentrations were lowest in control (mature) biomass, but were only significantly different ($P<0.01$) to levels observed in WS harvest. Phosphorus concentrations were lowest in DS harvest and burn (second youngest biomass) and significantly different ($P<0.05$) to highest concentrations observed in WS harvest and burn biomass (youngest biomass). For the elements Ca, Na, Si and Mg, the mature biomass had the highest concentrations when compared to younger biomass from harvest and burnt plots, and no differences were observed between harvested and burnt treatments. Foliar concentrations of Fe were approximately equal and highest in DS and WS harvest biomass and were significantly higher ($P<0.05$) than lowest concentrations observed in control biomass. DS and WS burn Fe concentrations were also relatively equal and were not significantly different to control or DS and WS harvest treatments. Al concentrations at control sites were significantly lower (96.6 µg g^{-1}) than WS harvest Al levels (380.8 µg g^{-1}).

Table 9. Macro- and micro- foliar element concentrations for *T. pungens* biomass from Camooweal treatment sites. Only elements with significant differences between treatments are shown with values being averages of five treatment replicates ± one standard deviation. Different superscript letters indicate significant differences at P<0.05 using Tukey's post-hoc test.

Treatment	N %	P %	Na mg g^{-1}	Ca mg g^{-1}	Si mg g^{-1}	Mg mg g^{-1}	Al µg g^{-1}	Fe µg g^{-1}
Control	0.82± 0.04^a	0.051± 0.009^{ab}	0.18± 0.06^a	3.7± 1.0^a	13.7± 4.0^a	1.8± 0.2^a	96.6± 46.6^a	607± 319^a
DSH	0.91± 0.06^{ab}	0.042± 0.003^a	0.06± 0.02^b	2.7± 0.2^{ab}	8.6± 2.8^b	1.4± 0.2^b	201± 71.5^a	1953± 1005^b
DSB	0.87± 0.05^{ab}	0.046± 0.002^a	0.06± 0.02^b	2.6± 0.5^b	8.3± 1.6^b	1.5± 0.2^{ab}	195.6± 75.5^a	1008± 382^{ab}
WSH	0.97± 0.06^b	0.055± 0.007^b	0.06± 0.03^b	2.2± 0.3^b	10.1± 1.6^{ab}	1.4± 0.2^b	380.8± 1412^b	1990± 581^b
WSB	0.90± 0.08^{ab}	0.054± 0.005^b	0.05± 0.01^b	2.5± 0.3^b	8.6± 0.6^b	1.6± 0.2^{ab}	186.8± 76.7^a	1104± 4012^{ab}

For analysis of foliar element concentration in *T. longiceps* biomass from Dajarra plots treatments were grouped in to control and harvested (hand and mechanical harvest treatments) and student's t tests were performed for all measured elements. Of the total foliar elements analysed in *T. longiceps* significant differences (P<0.05) were only observed for percent N concentrations between control (mature) biomass and harvested (juvenile) biomass. These values were 0.61% and 0.74% respectively (data not shown). When comparing foliar concentrations for *T. lonigceps* with *T. pungens* results from this study and put in the context of other *Triodia* and arid zone grassland species (Table 5) *T. longiceps* fits within most of the observed ranges for these elements. However, outliers exist for *T. longiceps* concentrations of Mn and Cu which are significantly lower than values obtained in other studies on different *Triodia* species (Table 11).

Table 10. Macro- and micro- foliar element concentrations for five *Triodia* species and two other Australian grass species. Values indicate average values attained from specified study results. All biomass harvested during dry season. Juvenile age for *T. pungens* and *T. longiceps* is 17 and nine months respectively. Highlighted values for *T. pungens* and *T. longiceps* are values obtained from the author's results.

Species	Age	Location	N %	P %	C %	S mg g⁻¹	K	Si	Ca	Mg	Na	Al µg g⁻¹	Fe	Mn	Cu	Zn
T. pungens	Mature	Camooweal, QLD	0.8	0.05	44.0	1.3	9.2	13.7	3.1	1.8	0.19	96.6	607	322	3.6	13.7
T. pungens	Juvenile	Camooweal, QLD	0.9	0.05	45.0	1.3	8.5	9.4	2.3	1.5	0.05	285	1547	290	3.0	13.0
T. pungens[1]	Mature	Kimberley Region, WA	0.9	0.01			9.4		2.9	2.2						
T. longiceps	Mature	Dajarra, QLD	0.6	0.04	45.6	0.8	6.5	7.2	3.6	3.0	0.04	59.8	314	38	1.5	18.4
T.longiceps	Juvenile	Dajarra, QLD	0.7	0.04	44.9	0.7	5.4	4.9	3.0	2.3	0.04	19.0	258	30	1.6	17.2
T.schinzii [2]	Mature	Great Sandy Desert, WA	0.4	0.03		1.0	5.9	4.0	3.0	0.7	0.31	100	255	120	4.0	29.0
T.basedowii [3]	Mature	Great Sandy Desert, WA	0.3	0.01		0.8	3.4	9.1	2.4	0.5	0.25	180	525	105	5.1	17.0
Themeda triandra Grassland [4]	Mature	Pilbara Region, WA	0.5	0.14												
Eriachne helmsii [5]	Mature	Pilbara Rangeland, WA	0.6	0.08			1.9		7.8	0.5						

[1](Wells 1999), [2&3](Grigg et al. 2008), [4] (Bennett et al. 2003) [5](Islam & Adams 1999)

Soil Nutrients

Of the plant available and total concentrations of nutrients in soil sampled from Camooweal total N, Ca, Na, Al and plant available P and S showed significant differences between treatments (Table 12). For N the highest concentration was observed in DS burn (0.2%) and was significantly different to the lowest concentration in WS burn (0.16%). Harvest and control sites did not differ significantly in N concentration from burnt treatments. Control sites had the highest average concentrations of total Ca with DS harvest and burn and WS burn having significantly lower concentrations. For total Na control sites also had the highest average concentration with significantly lower concentrations observed for DS harvest and burnt and WS harvest plots. Available P was significantly higher in WS harvest when compared to control and DS burn sites. Available S was highest in control sites, however was only significantly different to DS burn.

Soil nutrient analysis at Dajarra sites showed no significance for any nutrient across treatments when sites were pooled into control and harvest (hand harvested and mechanically harvest sites) due to site locations being within a landscape with a nutrient gradient of high nutrient (plains) to sites of lower nutrient status (hillslope). However, when sites were analysed by comparing treatments against each other within one site i.e. control versus average of hand and mechanical values at site A (Appendix 2) trends were observed. Within all sites sampled (Sites A, C, D and E) available P levels were lower in harvested treatments when compared to controls. This trend was also observed for available S, total Ca and total K (data not shown).

Table 11. Soil macro- and micro- nutrient concentrations sample from Camooweal treatment sites. Values are shown only for nutrients with significant differences between treatments. Different superscript letters indicate significant differences at $P<0.05$ using Tukey's post-hoc test. Values equal averages of three treatment replicates ± one standard deviation.

Treatment	Total N %	Total Ca mg kg^{-1}	Total Na mg kg^{-1}	available P mg kg^{-1}	available S mg kg^{-1}	Total Al mg g^{-1}
Control	0.18 ± 0.01^{ab}	293 ± 72.9^{a}	353 ± 50.8^{a}	10.3 ± 2.8^{a}	6.2 ± 1.9^{a}	26.1 ± 1.4^{ab}
DSH	0.19 ± 0.02^{ab}	116 ± 11.7^{b}	245 ± 46.1^{b}	12.9 ± 1.1^{ab}	4.4 ± 0.3^{a}	25.0 ± 2.9^{a}
DSB	0.20 ± 0.01^{a}	164 ± 8.6^{b}	214 ± 23.9^{b}	9.2 ± 1.7^{a}	3.5 ± 0.2^{b}	26.3 ± 1.8^{ab}
WSH	0.18 ± 0.02^{ab}	198 ± 58.9^{a}	197 ± 40.9^{b}	14.8 ± 1.2^{b}	3.6 ± 0.2^{a}	24.1 ± 4.5^{a}
WSB	0.16 ± 0.01^{b}	147 ± 5.6^{b}	$282.\pm 19.7^{a}$	13.0 ± 0.7^{ab}	4.9 ± 0.7^{a}	33.1 ± 1.6^{b}

Germination Experiments

Incubator – Growth Cabinets

The germination response of *T. pungens* to different seed treatments was highly variable. De-husk + 1mM GA_3 and de-husk + 20mM KNO_3 treatments showed a highest positive response with average germination percentiles after 30 days incubation of 32 and 33 percent respectively (Figure 9). These two treatments were highly significant from all other treatments ($P<0.001$). The next highest treatment responses and in descending order of percent germination were: de-husk + 10% SW, 10mM KNO_3, 1mM GA_3, 10% SW, de-husk and control (Figure 9). The low germination responses seen in these treatments and hence possible differences that may have occurred between treatments were inhibited by high rates of fungal infection. The two treatments observed with the fastest germination response (first germinants seen two days after incubation commencement) were in the treatments with the highest overall percent germination; the de-husked treatments (De-husk + 1mM GA_3 and de-husk + 20mM KNO_3).
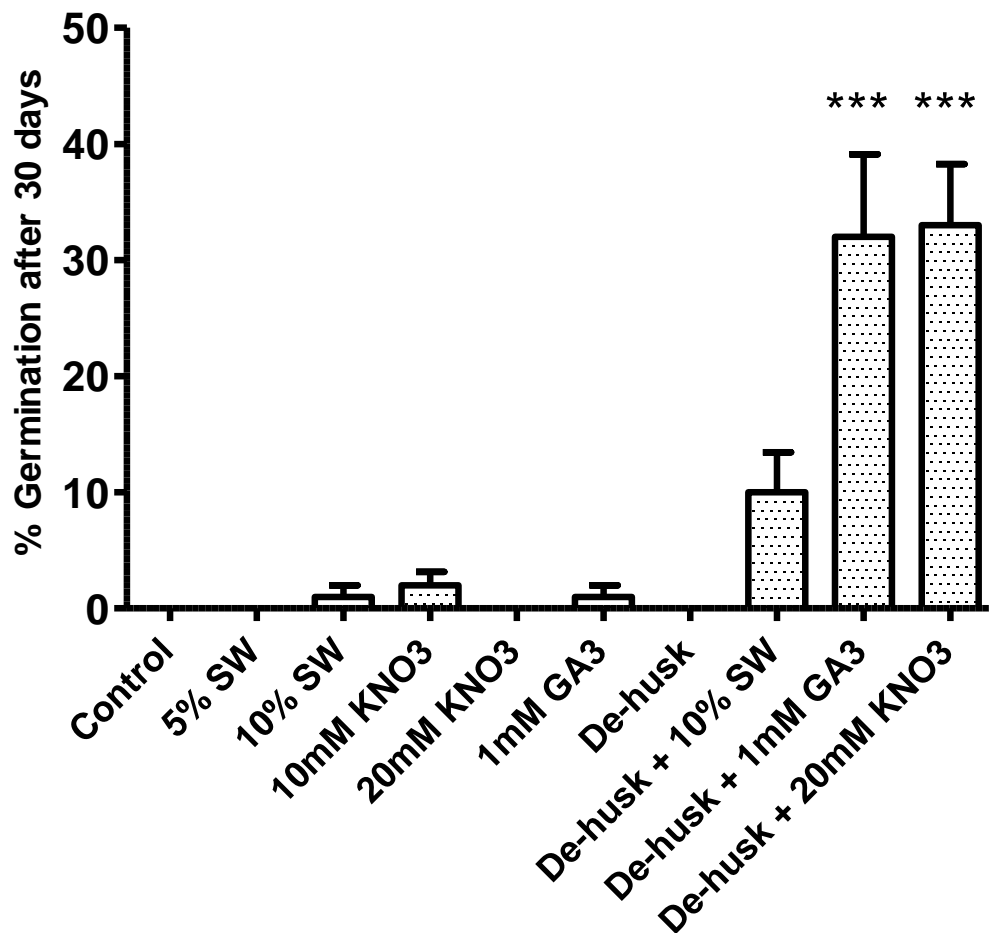
Figure 9. The effects of ten different seed treatments on the percent germination of *T. pungens* after 30 days incubation under 33°C in dark conditions. Each value represents the average of four replicate Petri dish samples each containing 25 seeds. Error bars represent one standard error. A one-way ANOVA was performed followed by a Tukey's post-hoc test. *** (P< 0.0001) denote treatments not significantly different from each other but significant from all other treatments.

Glasshouse

The germination response of three *Triodia* species to a variety of seed treatments employed to mimic conditions from fire regimes was investigated. The control replicates for each species produced expected low germination rates of an average of ~13% which was observed for all three species. The highest percent germination increase was observed for *T. pungens* with a percent increase of 30% from control to 10% SW, 13% to 40% average percent germination respectively.

Results from a one-way ANOVA showed that the average germination rate observed for *T. pungens* in 10% SW treatment was significantly different to germination rates seen for this species in controls, 10mM KNO$_3$ and 1mM GA$_3$ treatments (P<0.05). Overall *T. pungens* outperformed both other species in the SW treatments yet underperformed when compared to other species in KNO$_3$ treatments whereby a marginal percent germination decline from the control was observed (Figure 10).

Between treatments for *T. bitextura* the highest positive response was observed in 20mM KNO$_3$ with a 19 percent germination rate (Figure 10). This rate was only significantly different (P<0.05) to 10% SW treatment (6%) which was lower than the control (12%). For both the SW treatments *T. bitextura* produced the lowest germination percent and a decline in germination when compared to the control (Figure 10) however was not significantly different.

Between treatments for *T. schinzii* the highest positive response was observed in 10mM KNO$_3$ with a 23 percent germination rate however this treatment was not significantly different from the other treatments. Overall *T. schinzii* displayed less variability in germination response to the treatments. Whilst there germination increases were observed for all treatments when compared to the control there were no significant differences according to one-way ANOVA.

To compare if germination responses differed between species within the same treatment a two-way ANOVA was performed. Significant differences between species were only seen within 10% SW and 5% SW treatments. For 10% SW differences were observed between species with *T. pungens* significantly different to both *T. bitextura* (P<0.001) and *T. schinzii* (p<0.05). In 5% SW *T. pungens* was only significant to *T. bitextura* (P<0.01).
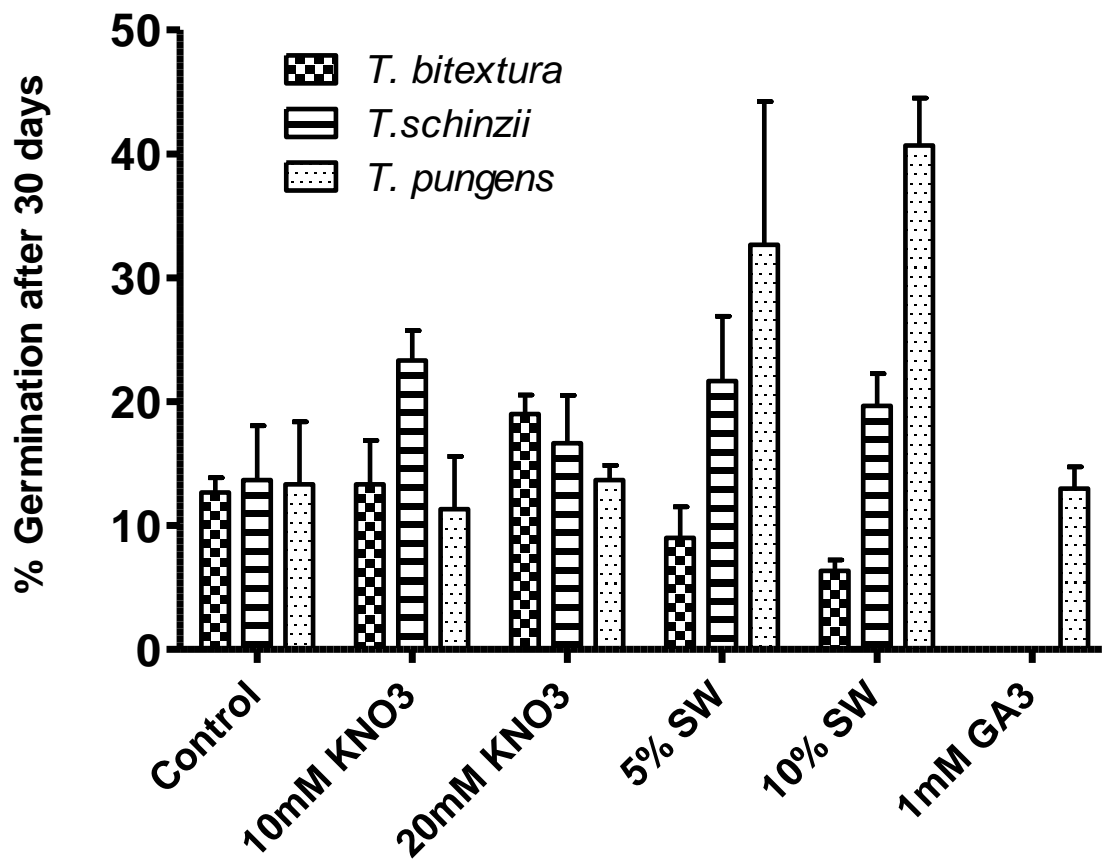
Figure 10. The effect of six different seed treatments on percent germination of three *Triodia* species after 30 days in soil in seedling trays under 33°C glasshouse conditions.

Discussion

This study presents the first evidence that the effects of harvesting spinifex are distinct from the effects of burning spinifex. Differences in species composition and abundance of regenerating vegetation were observed between harvested and burnt sites in *T. pungens* dominated grassland which suggests that both disturbance regimes impact differently on the ecosystem. However, life form composition and abundance of vegetation did not differ between harvested and burnt sites. Interestingly, season of harvest significantly altered species composition in harvested but not burnt sites. Pooling season of burn or harvest, no differences in species assemblages between treatments were observed. Different harvesting methods, hand harvesting or mechanical slashing, resulted in similar species composition in *T. longiceps* dominated grassland.

Fire is considered an important driver of floristic composition and the effect of fire on plant composition and structure is well documented (Burbidge (1944); Suijdendorp (1981); Jacobs (1984) Griffin (1990) Allan *et al*. (2002) Wright & Clarke (2008). Typically, recently burned spinifex grasslands have an increase in species diversity which declines with time since fire. Early states of succession in the studied communities were dominated by a suite of resprouting perennials, short-lived grasses and herbs in genera *Solanum, Eragrostis, Aristida, Tephrosia, Sida* and *Pterocaulon*. According to Allan *et al.* (2002) richness of plant species of recently burnt areas can be two to three fold greater than mature spinifex areas. This increase in diversity after fire was observed in the Camooweal experiment as control plots had an average three species compared to seven species in burnt plots.

Contrary to comparatively well-studied post fire regeneration, no knowledge exists on the effects of harvesting and consequent regeneration of spinifex grasslands. This study has demonstrated that, when compared to mature vegetation, regeneration after harvesting results in 2- 3-fold increase in species diversity. This indicates that removal of spinifex biomass by fire, but also after harvesting facilitates growth of other species. The increase in plant diversity observed after fire has been attributed to the ability of plants to profit from the resource liberation that occurs as a result of fire. Typically ash released from burnt plant material ('ash-bed effect') supplies a flush of particular inorganic nutrients for new plant growth (Vogl 1979). In general, plant communities that regenerate post-fire capitalise on the reduced competition for nutrients, water and light.

It can be argued that the high diversity seen in regeneration at harvested sites could be due to the reduced competition for resources and also the ability of certain species to vegetatively resprout as in the case of *T. pungens* (personal observation). This was also observed in the proportion of species present in regenerating vegetation across all treatment sites that are known to be facultative resprouters, and clearly profited from the removal of spinifex biomass via harvesting (Appendix 4).

Our results showed that composition and abundance of regenerating plant species at harvested sites were significantly different than at burnt sites. This may be attributed to the ability of fire to break down dormancy mechanisms of the existing seedbank via smoke, heat or scarification of the seed coat priming certain species for germination after fire. However the mechanisms which trigger fire stimulated growth are still largely unknown for many species in spinifex grasslands (Wright & Clarke 2007). It is hypothesised that harvested sites would allow germination of species which do not require fire-triggers but which profit from less competition for moisture and nutrient. Since a large number of regenerating species in harvested plots were facultative resprouters, we have early indication that while seed regeneration may be low after harvest, resprouting is facilitated.

No differences were observed between species composition and abundance when pooled between sites from a dry season disturbance or wet season disturbance regime. However differences existed in season of harvest when un-pooled data was analysed. The impact of seasonality of fire occurrence has been little studied though it is known to vary widely (Allan *et al.* 2002). Therefore the impact of fire season on flora at any one location is largely unknown. In the tropical north, fires typically occur in the long dry season from April to November. In central Australia burning occurs in the summer months October to January; whereas in southern regions frequency of fires is greatest in the summer to autumn period (Allan *et al.* 2002).

Latz (1995) reported that the assemblage of plants germinating after fire will differ depending on fire intensity and season. Latz (1995) further noted that the vegetation regenerating following a low intensity winter fire in an area with predominantly summer rainfall favoured establishment of perennial plants at the expense of short-lived fire ephemerals. We made a similar observation in dry season (winter) burnt sites in Camooweal whereby regeneration was dominated more so by perennial herbs and grasses than wet season (summer) burnt sites.

However, these differences were not significant and could be explained by the small treatment plot size which limited the fire intensity, hence not reaching the severe conditions of summer fires. The season of harvest changed the species composition and abundance in harvested sites. Wet season harvest sites (WSH) were dominated by a higher composition of annual grass species than perennials as was the case in dry season harvest (DSH). This could be due to the more mature state of DSH harvest sites which were harvested six months prior to WSH. Casson (1994) found the season of burn in one *Triodia* association was less important for regeneration than annual rains. However, long-term monitoring of harvested sites from an early successional stage through to development of mature grasslands is necessary to gain an understanding of long term effects of season of harvesting on this ecosystem.

We present the first findings on the effect of different harvesting methods. No significant differences were observed between species composition and abundance at slashed and hand harvested sites, despite mechanical harvesting being a more invasive technique. However, hand harvested sites had a higher occurrence of Chenopodiaceae species *Sclerolaena cornishiana* when compared to slashed sites and was a discriminating species between these two treatments. When considering harvesting it would be an important management consideration to assesses prior and current land use, especially if under a pastoral lease as this could play a large role in regeneration potential and diversity of sites after harvesting.

Vegetation regenerating after fire plays a critical role in resource capture and recycling. Ash released from burnt plant material ('ash bed affect') supplies a spike in availability of inorganic nutrients for new plant growth. This liberation of nutrients can be short lived depending on the nutrient (Ford *et al.* 2007). Nutrients such as N and K can easily be leached from sandy soils, hence fire ephemeral species play an important role in retrieving and assimilating these nutrients into plant biomass. Large scale losses of nutrient capital could occur in these typically low nutrient systems if annual and ephemeral vegetation was absent. It is important to assess nutrient economy of soil and the dominant plant layer in this arid zone ecosystem to determine if plants access to certain soil nutrients may be adversely affected by harvesting as opposed to burning. Quantifying foliar elemental concentrations, this study has provided early insight into nutrients which are removed via biomass harvesting in a low nutrient environment where most nutrients are recycled via senescence and fire.

Foliar P and N concentrations of spinifex from burnt sites were consistently higher than in plants at unburnt sites during the first year (Holm and Allen (1988), and we observed similar differences in foliar N content between mature and juvenile *T. pungens* and *T. longiceps*. (Appendix 5). This higher N concentration is due to less structural tissue at juvenile stages and explains the higher palatability of *T. pungens* to cattle.

We used the nutrients levels attained for spinifex biomass and soil from a *T. longiceps* treatment plot in Dajarra to quantify impacts on N and P nutrient relations from harvesting. In the dry season of 2009, 319kg of mature spinifex biomass was removed from 200m^2 slashed site C and average N and P concentrations of the slashed material was 0.59% and 0.064% respectively. Therefore harvesting removed ~9.4g N and 1g P from the system. To investigate the impact of this removal of nutrients, we compared soil analyses between paired control and slashed sites. Total soil % N decreased from 0.17% in control site to 0.15% in slashed site (11.7% decline). Plant available P in soil decreased from 12.46 mg/kg to 12.02 mg/kg (3.6% decline). While N can be renewed in ecosystems via biological N-fixation, P has to be replenished from the total pool of P, and it remains to be established if P losses from the available P-pool in this nutrient poor system could present future problems in harvesting regimes.

Macro-nutrients are stored primarily in leaves as storage capacity of shoots is limited (Wells 1999), and nutrients in above ground biomass are translocated from leaves and stems to roots and storage organs in some tropical perennial grasslands in Australia (Casson 1994). In plants that exhibit this response, resources are usually withdrawn from leaves and stems at the end of the wet summer growth period. This is advantageous during typical dry season fires as resprouting species capitalise on nutrient reserves in storage organs and minimise losses with fire. This strategy does not appear to be universal in *Triodia* species. Holm and Allen (1988) showed that *T. pungens* displayed seasonal translocation of resources in populations in north-west Australia. In contrast, Casson (1994) describes more southerly distributed *T. pungens, T.wiseana* and *T. basedowii* displayed limited reallocation of N and P. It can be argued that translocation of resources is less important for these xeromorphic species as adult hummocks are normally fire killed in the more intense fires in these regions and seedling establishment over resprouting is common (Casson 1994). The overall less reliable and lower amounts of rainfall received in these spinifex communities could also limit ability of translocation of nutrients.

No records exist for nutrient translocation in *T. pungens* communities growing in summer rainfall climate of Camooweal, yet nutrient translocation is likely to occur. However, further analysis of nutrient levels in leaves and roots and storage organs over sequential seasons is needed to confirm this notion.

Harvesting of spinifex has to be sustainable to avoid degradation of some of Australia's last intact grasslands. For harvesting to be sustainable it must not reduce the rate or amount of biomass regeneration and not reduce the diversity of species present. Spinifex grasslands display regional differences in the rate of biomass accumulation after fires. This is also likely to be observed after harvesting. A broad pattern exists for biomass accumulation that follows the north to south rainfall gradient. In the north, higher rates of spinifex regrowth occur due to the reliability of rainfall and fire intervals are dependent on the recovery rate of spinifex (Allan *et al.* 2002). In comparison spinifex grasslands in the southern regions have a slower growth rate and hence fire intervals are typically longer (Allan *et al.* 2002). Generally, spinifex grassland have potential to re-burn 5-7 years after fire depending on rainfall but can take 18-20 years to reach full maturity as fuel (Burrows *et al.* 2009).

Little is known about regeneration biology of hummock grass species in relation to fire. The extent to which regrowth after fire is vegetative (from existing stool/runners), or from seed germination seems to vary both within and between *Triodia* species (Bogusiak *et al.* 1990). The distinction between fire-killed and resprouting species is fundamental for understanding a plant communities' ability to cope with fire regimes and their likely response to changed regimes such as harvesting (Rice & Westoby 1999). We observed that *T. longiceps* and *T. pungens* can resprout and regenerate from seed at field sites. Therefore after harvesting, both species are able to vegetatively regenerate, however the impact on sexual reproduction of *Triodia* and associated species after harvesting remains largely unknown. We aimed to investigate factors influencing such reproduction strategies of spinifex seed so that assessments can be made on the potential impacts of removing fire from such a system.

Studies to date have focussed on the hypothesis that heat produced by fire, or chemicals in smoke or ash disable dormancy mechanisms (Davidson & Adkins 1997) (Appendix 5). These studies have concluded that most spinifex seed is killed by excessive heat (>80°C), ash is not stimulatory and some other mechanism controlling germination must be responsible (Westoby *et al.* 1988; Bogusiak *et al.* 1990) which may include recently identified smoke-derived butanolides (Flematti *et al.* 2004).

Studies have shown that a number of *Triodia* species exhibit higher germination when treated with smoke products (Appendix 5). The post-fire presence of water soluble nitrogenous compounds in the soil has also been linked to stimulation of certain species (Bell *et al.* 1999) assumedly those that have evolved in pyritic environments (Appendix 5).

Our results of examining the effects of pre-sowing treatments on germination have elicited a varied response between the three *Triodia* species. Of significance is the increase in germination rate in *T. pungens* with treatments of 10 % smoke water (SW) and 5% SW. In a study by Farley *et al.*(2002) *T. longiceps* also exhibited a marked increase in germination rate under a 5% smoke water treatment (Appendix 5). These results indicate that if fire was to be removed from these *Triodia* grasslands and replaced with harvesting, significant reductions in *Triodia* seeding establishment would occur. However, other germination studies, using seed collected from different populations over successive seasons have identified polymorphic dormancy mechanisms which differed spatio-temporally (Wells 1999). Thus, we argue that the manner of spinifex regeneration is not a species attribute but rather dependant on a suite of environmental factors. If this is the case, then results observed from this study may not directly apply to the field locations examined as seed used in germination treatments was not harvested from our field locations. Seasonal change in the smoke responsiveness of spinifex from the same population would need to be investigated for a more comprehensive assessment of impact of harvesting specific field sites.

Before harvesting of spinifex is to be considered, a wide range of management considerations need to be addressed. Currently, fire management in spinifex grasslands is of primary concern for landscape health. There is now compelling evidence that fire regimes in much of the spinifex grasslands have changed with the cessation of traditional Aboriginal burning from a fine grain mosaic of burnt patches at different seral states to a coarse grain, simplified mosaic of infrequent, large wildfires (Rice & Westoby 1999). This alteration in fire regimes has consequences for plant diversity particularly colonisation by fire sensitive species. In order to break up the run of major wildfires it has been proposed to re-create the fine grained mosaic of different post-fire seral states (Bowman *et al.* 2008) and for less than 10% of a vegetation type to be burnt in a given year (Tropical Savannas 2010). Prescribed burns should occur when soil moisture is high which is soon after rain in the early wet season, wet season or start of the dry season in northern areas.

Whilst further field research is needed to determine the best method of harvesting it is surmised that the most sustainable regime would be similar to the above mentioned burning regime, whereby a mosaic of harvesting events after good wet seasons are intermixed with wet season burning events. This strategy could aid in reduction of biomass (fuel) available for large intense dry season wildfires with the additional benefit of reducing greenhouse gas emissions. Unlike burning harvesting could be carried out in the dry season after seeding events which typically occur at end of wet season. These harvesting/burning regimes should be on the same interval as natural fire regimes (e.g. >5yrs) thus allowing for intervening wet seasons to allow growth to maturity for seeding events to take place and to replenish soil seedbank. Harvested sites should be surrounded by mature vegetation to lessen erosion affects and supply habitat refugia for fauna. According to study by Burrows *et al.* (1991), fuel accumulation was less than 0.30 t ha^{-1} year $^{-1}$ over 30 years in spinifex grasslands (*T. basedowii*, *T. schinzii*) in the Gibson Desert, Western Australia. Spinifex communities in northern Australia such as *T. pungens* seem to be most suitable for harvesting as they occupy a more favourable climate with reliable wet seasons, a key determinant in rate of biomass accumulation.

Many ecological concerns exist regarding harvesting of spinifex grasslands. Of key concerns are the possible threats from introduced species colonising exposed land due to inadequate regeneration from ill-suited harvesting regimes. Of most concern is *Pennisetum ciliare* (buffel grass) which, when established, reduces the diversity of the ground layer and potentially suppresses regeneration of trees and shrubs. Contaminated mechanical harvesting equipment could easily introduce *P. ciliare* seed which could become established in currently uninvaded spinifex grasslands. The removal of mature perennial spinifex from a system could also increase erosion as the presence of spinifex is known to increase infiltration of soil moisture and reduce wind erosion (Wiedemann 1971). Further disturbance of soil, nutrient and water relations could occur from adverse impacts on beneficial microbiotic crusts from harvesting machinery. According to Letnic (2004) grazing has been observed to disrupt these fragile microbiotic crusts therefore the same effects could be induced by harvesting.

This study has provided the first evidence on the impacts of harvesting versus burning of spinifex grasslands. Whilst initial recommendations have been made on the sustainability of harvesting and harvesting practice the ecological information from this study is based on relatively site-specific locations sampled during one season. There still exists insufficient knowledge on the long term effects of harvesting on spinifex grassland ecology. Long-term monitoring of large scale trial plots would be needed to understand these ecologically important spinifex grasslands.

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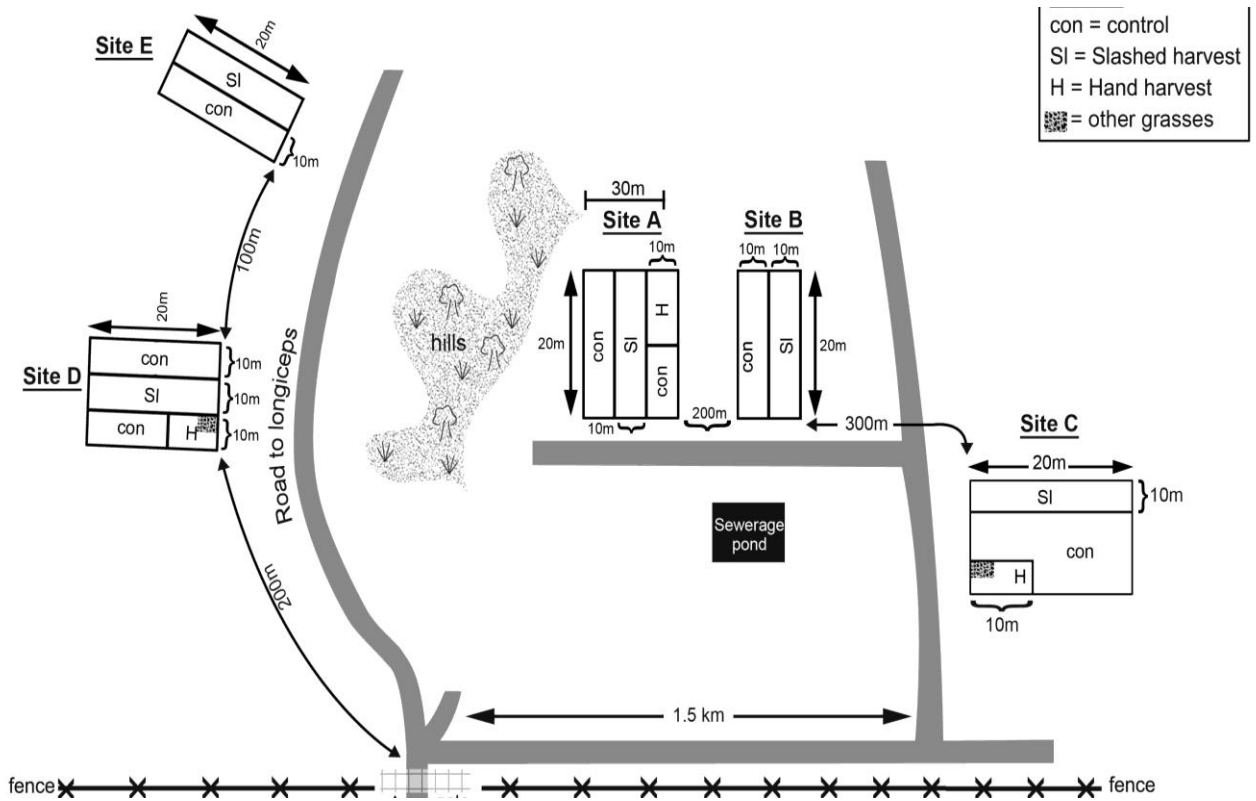
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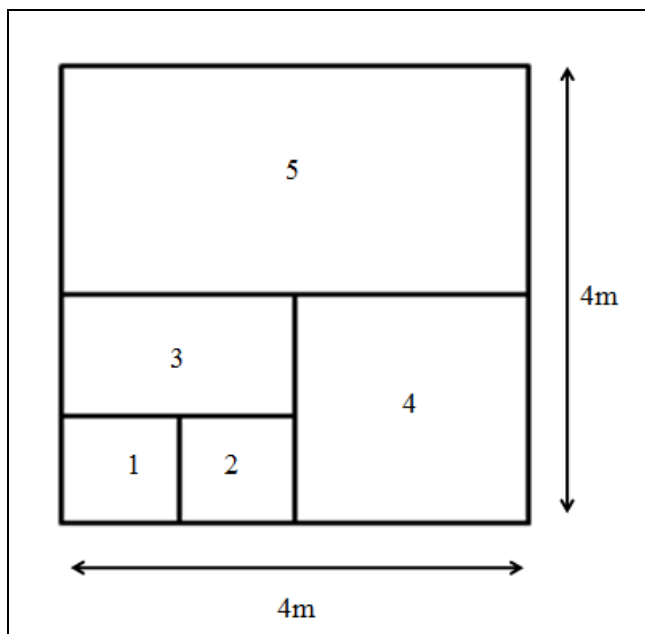
Appendix

1. Control	2. DS Harvest	3. WS Harvest	4. DS Burn	5. DS Burn
6. WS Harvest	7. WS Harvest	8. WS Burn	9. DS Harvest	10. Control
11. WS Burn	12. WS Harvest	13. DS Burn	14. WS Burn	15. DS Burn
16. DS Burn	17. DS Harvest	18. WS Burn	19. Control	20. DS Harvest
21. WS Harvest	22. DS Harvest	23. Control	24. WS Burn	25. Control

Appendix 1. Experimental plot design in Camooweal consisting of 25, 10m x 10m treatment plots (dry season burn (5), dry season harvest (5), wet season burn (5), wet season harvest (5))

Appendix 2. Treatment site layout for Dajarra sites showing 5 x control, 5 x slashed (mechanical) harvest and 3 x hand harvest sites (Figure created by Linda Thomson).

Appendix 3. Expanding quadrat used in floristic assessments of Camooweal and Dajarra sites.

Appendix 4. List of species present in Camooweal and Dajarra treatment plot. Seeder: >70% mortality when subject to 100% leaf scorch Resprouter: <30% mortality when subject to 100% leaf scorch. Facultative resprouter: response variable, depending on conditions e.g. moisture and fire intensity. [1](Crowley *et al.* 2007)

Camooweal			
Species	*Family*	*Life Form*	*Fire Response*
Abutilon otocarpum	Malvaceae	PH	Seeder (fire ephemeral) or facultative resprouter[1]
Acacia elachantha	Mimosaceae	TS	
Aristida latifolia	Poaceae	PG	Resprouter[1]
Aristida pruinosa	Poaceae	PG	Facultative resprouter[1]
Bulbostylis barbata	Cyperaceae	AG	Seeder[1]
Chamaesyce sp. (Pathungra A. Gunness AG2118)	Euphorbiaceae	AH	
Corchorus sidoides sub sp. *vermicularis*	Tiliaceae	PH	Resprouter[1]
Enneapogon polyphyllus	Poaceae	AG	Seeder[1]
Eragrostis leptostachya	Poaceae	AG	
Eriachne armittii	Poaceae	AG	
Eucalyptus leucophloia	Myrtaceae	TS	Facultative resprouter[1]
Eulalia aurea	Poaceae	PG	Facultative resprouter[1]
Gossypium australe	Malvaceae	PH	Facultative resprouter[1]
Polygala sp. (White Mountains M.B. Thomas+ 1738)	Polygalaceae	AH	
Portulacca oleraceae	Portulacaceae	AH	Resprouter[1]
Pterocaulon serrulatum	Asteraceae	AH	Facultative resprouter[1]
Pterocaulon sp.(undescribed species)	Asteraceae	AH	
Senna glutinosa sub sp. glutinosa	Caesalpiniaceae	TS	Facultative resprouter[1]
Sida fibulifera	Malvaceae	PH	Seeder[1]
Sporobolus australasicus	Poaceae	AG	Seeder[1]
Tephrosia sp.	Fabaceae	PH	
Tephrosia stuartii	Fabaceae	PH	
Triodia pungens	Poaceae	PG	Facultative resprouter[1]

Dajarra

Species	Family	Life Form	Fire Response
Abutilon otocarpum	Malvaceae	PH	Seeder (fire ephemeral) and facultative resprouter[1]
Aristida contorta	Poaceae	AG	Facultative resprouter[1]
Aristida latifolia	Poaceae	PG	Resprouter[1]
Bulbostylis barbata	Cyperaceae	AG	Seeder[1]
Enneapogon polyphyllus	Poaceae	AG	Seeder[1]
Evolvulus alsinoides var. *villosicalyx*	Convolvulaceae	AH	Facultative resprouter[1]
Indigofera colutea	Fabaceae	AH	Seeder[1]
Iseilema vaginiflorum	Poaceae	AG	Seeder[1]
Oxychloris scariosa	Poaceae	PG	
Panicum decompositum var. *decompositum*	Poaceae	PG	Resprouter[1]
Perotis rara	Poaceae	AG	Seeder[1]
Pterocaulon serrulatum	Asteraceae	AH	Facultative resprouter[1]
Pterocaulon sp. (undescribed species)	Asteraceae	AH	
Salsola kali	Chenopodiaceae	AH	
Sclerolaena cornishiana	Chenopodiaceae	PH	Seeder[1]
Sclerolaena cuneata	Chenopodiaceae	PH	
Sclerolaena lanicuspus	Chenopodiaceae	PH	
Sida fibulifera	Malvaceae	PH	Seeder[1]
Sida sp. Unknown	Malvaceae	PH	
Solanum quadriloculatum	Solanaceae	PH	Resprouter[1]
Solanum succosum	Solanaceae	PH	Facultative resprouter[1]
Sporobolus actinocladus	Poaceae	AG	Resprouter[1]
Sporobolus australasicus	Poaceae	AG	Seeder[1]
Trianthema triquetra	Aizoaceae	PH	Seeder[1]
Triodia longiceps	Poaceae	PG	Facultative resprouter[1]

Appendix 5. Previously trialled germination enhancing treatments for six *Triodia* spp.

Species	Hormone	Chemical	Smokewater	Physical	Temp (°C)
T. bitextura	Embryo media (MS basal salts including Gibberellic acid) Significantly inc. germination by factor of ~6. [1]	KNO$_3$ 10mM Significantly inc. germination compared to control & NH$_4$NO$_3$ 10mM [1]	Aerosol smoke & smokewater (5% ,10%) no consistent promoting factors between three cohorts [1]	Oven storage 60°C + removal palea & lemma inc. germination [1]	30, 35, 40 ca.80% within 6 days sowing [1]
T. longiceps	1000 ppm Gibberellic Acid Germination response control vs. treated: ~10% to ~35% [2]		5% Smoke water Germination response control vs. Treated: 19.8 to 70.8% [3]	Removal of hull structures + scarification Germination response control vs. Treated: ~10 to ~35% [3]	30-40 optimum[2]
T. basedowii	1000ppm Gibberellic Acid Germination response control vs. treated: 5% - 60%, 25 days [4] 23% - 41% [5]	KNO$_3$ 10mM Germination response control vs. treated: 1 – 7% [1]	No response to aerosol smoke [1]	Loosening pericarp Germination response control vs. treated: 27% - 90% [6]	30, 35, 40 ca.80% within 6 days sowing [1] Inhibited by cold vernalisation [1]
T. pungens		KNO$_3$ 10mM Germination response control vs. Treated: 30 – 48% [1]		Oven storage 60°C with removal palea and Lemma increased germination [1]	30, 35, 40 ca.80% within 6 days sowing [1] Inhibited by cold vernalisation [1]
T. wiseana			No response to aerosol smoke [1]		30, 35, 40 ca.80% within 6 days sowing [1]
T. bynoei	No presowing treatment required as produces readily germinable seed [1]				>25 [1]

[1] (Wells 1999) [2] (Farley *et al.* 2002) [3] (Davidson & Adkins 1997) [4] (Jacobs 1973) [5] (Westoby and Nuthern in review) [6] (Westoby *et al.* 1988)