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Phosphorus Availability and the Nutrient and Carbon Content of Mulga Understorey Species: Comparisons with Other Vegetation Types in Sub-tropical, Semi-arid Rangelands in the Pilbara, Western Australia

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Abstract: Phosphorus addition increased mineral concentrations and improved the nutrient status of the perennial shrub *Ptilotus obovatus* (Cotton bush) and the ephemeral only after summer rain. In the ephemeral and the perennial species, most nutrients (N, K, Ca, Mg) were present at concentrations sufficient for herbivores except P. Concentrations of total nitrogen provide misleading estimates of the availability of crude protein for herbivores if traditional conversion factors (e.g. protein = 6.25 x N) are applied because of the presence of substantial concentrations of non-protein N in the foliage of most species. *In vitro* dry organic matter digestibility (IVDOMD) of *Ptilotus obovatus* varied seasonally from 24.71 to 51.8 % and was negatively related to concentrations of total phenolics and of condensed tannins.
In unfertilised plots outside the thicket, there was no evidence that the area within the thicket was more fertile than that outside. When fertiliser P was added, the relative (to unfertilised plots) response within and outside the thicket was identical, again suggesting that fertility was not different. Further comparison with nearby grassland also suggested there were few differences in fertility.

Key words: Ecosystems, thickets, herbivores, anti-nutritional, water use efficiency, life-form

Introduction

The areas within or adjacent to shrub or tree canopies or other physical/biological barriers (e.g. logs) have been regarded as 'islands of fertility' (Tongway et al. 1989) in many rangeland ecosystems. Recently, Ludwig et al. (1997) drew on such observations in developing their 'landscape' scale hypotheses that might be used to explain the patchy distribution of plants in arid ecosystems, especially in 'non-functional' or degraded ecosystems. It has long been argued that resource-rich 'islands' retain nutrients effectively, thereby providing the major and associated species with greater nutrient availability. In the long term, growth and net primary productivity is commonly not increased by addition of nutrients in arid and semi-arid ecosystems. Chapin et al. (1986) summarised that under these conditions, increases in nutrient availability should be translated into increased nutrient concentrations and quality of foliage for herbivores.

Ptilotus obovates (cotton bush), a compact branching perennial, dominates the understorey of considerable areas of Mulga woodlands and thickets ('run-on' areas) in the Pilbara region as well as being one of the most common components of open shrublands (Mitchell & Wilcox 1994). Other *Ptilotus* spp., including *Ptilotus exaltatus* (Purple mulla mulla), *Ptilotus macrocephalus* (Pussytail mulla mulla) and *Ptilotus aerovoides* (Mat mulla mulla) grow in areas adjacent to Mulga thickets where there is little overstorey cover and which are commonly bare of perennial vegetation.

The aims of this study were to:

a) evaluate the seasonal variation in foliar concentrations of nutrients, carbon fractions and anti-nutritional components in species in the understorey of an *Acacia aneura* thicket, including estimates of their nutritive value for herbivores

b) test the response of nutrient concentrations and nutritive value in these species to added P. P was chosen on the basis of long-standing suggestions that Australian ecosystems are limited by P (e.g. Westoby 1988).

c) compare nutrient concentrations and response to added P among species within and outside thickets of *Acacia aneura*.

Materials and Methods

We compared the nutrient and carbon characteristics and the response to added P of the understorey species in a Mulga thicket, with those of species growing outside thickets either a) in a 'bare soil' community, immediately adjacent to the thicket where perennial species were largely absent and b) in a perennial grassland on a single large alluvial plain of Hamersley station (22 ° 20 'S, 117 ° 37 'E), some 45 km north-west of the town of Tom Price, Western Australia.

Mean annual rainfall (over 80 years) at Hamersley homestead is 354 mm with 243 mm falling between December and March inclusive. Long term maximum and minimum daily temperatures range from 6 °C in July to 34 °C in December. During 1996-97, the total rainfall was 535 mm and some 400 mm fell between December 1996 and February 1997.

The experimental layout was a Randomised Block Design with three replicates of each of two (+P / -P) treatments in a homogenous thicket of Mulga (*Acacia aneura*) with a Cotton bush (*Ptilotus obovatus*) as understorey, outside thicket and in open grassland. Fertiliser was added as a single broadcast application of 200 kg P ha^{-1} in August 1996. In the same month, the everlasting daisy *Brachycome ciliocarpa* as well as several *Abutiloton* spp. were abundant in the understorey and in March 1997, Black Jack (*Bidens bipinnata*) was a common species. At other sampling times *Ptilotus obovatus* was the sole species present in the understorey. Outside thicket, in winter the vegetation was dominated by Amaranthaceae - *Ptilotus exaltatus* (Purple mulla mulla), *Ptilotus macrocephalus* (Pussytail mulla mulla), *Ptilotus aerovoides* (Mat mulla mulla); Chenopodiaceae - *Dysphania kalpari* (Green crumbweed) and Malvaceae - *Abutilon otocarpum* (Desert chinese lantern), while in summer the Poaceae were dominant including *Dactyloctenium radulans* (Button grass), *Urochloa gilessi* (Hairy-edged armgrass), *Enneapogon polyphyllus* (Limestone grass). Biennial and perennial species present throughout 1996-97 and belonging to the Chenopodiaceae were *Salsola kali* (Buck bush) and *Maireana tomentosa* (Felty bluebush).

In open grassland, the dominant vegetation at the site was

Table 1: Chemical characteristics of soils for Experiments 1, 2 and 3. Values are means of three determinations from a bulk sample of the surface soil (0 – 10 cm). Standard errors given in parentheses

Experiment	Soil property				
	pH	Conductivity (mS cm^{-1})	Organic C (%)	Total N (mg g^{-1})	Available P (μg g^{-1})
1 Acacia thicket	6.45 (0.02)	30.4 (2.1)	1.44 (0.03)	1.01 (0.10)	2.1 (0.1)
2 Outside thicket	6.50 (0.14)	43.0 (0.4)	0.56 (0.04)	0.72 (0.25)	4.2 (0.1)
3 Grassland	7.10 (0.50)	55.4 (3.4)	1.21 (1.04)	0.99 (0.40)	4.7 (0.1)

Table 2: Summary of analysis of variance of nutrient concentrations in Experiment 1 comparing (a) sampling dates and phosphorus treatments for *Ptilotus obovatus* , (b) phosphorus treatments and life forms in August 1996 (perennial shrub vs ephemeral forbs), and (c) phosphorus treatments and life forms in March 1997

Effect	df	MS	P	df	MS	P
	Nitrogen			Phosphorus		
(a) *Ptilotus obovatus*						
Sampling (Sa)	3	182.727	<0.001	3	0.37616	<0.001
Treatment (T)	1	11.816	0.023	1	0.1350	0.083
Sa x T	3	5.545	0.062	3	0.08126	0.147
Error	14	1.804		14	0.03887	
(b) August 1996						
Life form (Lf)	1	117.0625	<0.001	1	0.065408	<0.001
Treatment	1	0.3072	0.592	1	0.001408	0.483
Lf x T	1	0.0176	0.896	1	0.000675	0.623
Error	6	5.7422		6	0.002522	
(c) March 1997						
Life form	1	4.465	0.269	1	0.02803	0.269
Treatment	1	0.682	0.651	1	0.10083	0.060
Lf x T	1	6.395	0.195	1	0.00333	0.689
Error	6	3.010		6	0.01886	
	Nitrate-N			Potassium		
(a) *Ptilotus obovatus*						
Sampling	3	0.456283	<0.001	3	60.00356	<0.001
Treatment	1	0.009600	0.187	1	0.34800	0.009
Sa x T	3	0.001378	0.841	3	0.22300	0.009
Error	14	0.004983		14	0.03835	
(b) August 1996						
Life form	1	0.630208	<0.001	1	10.84901	<0.001
Treatment	1	0.000675	0.553	1	0.02901	0.211
Lf x T	1	0.000008	0.947	1	0.05201	0.110
Error	6	0.001714		6	0.01479	
(c) March 1997						
Life form	1	0.725208	<0.001	1	14.67441	<0.001
Treatment	1	0.012675	0.119	1	1.15941	<0.001
Lf x T	1	0.000675	0.689	1	0.00607	0.542
Error	6	0.0003836		6	0.01455	
	Calcium			Magnesium		
(a) *Ptilotus obovatus*						
Sampling	3	3.15116	<0.001	3	4.42453	<0.001
Treatment	1	0.00282	0.623	1	0.03604	0.093
Sa x T	3	0.01156	0.407	3	0.01846	0.221
Error	14	0.01115		14	0.01112	
(b) August 1996						
Life form	1	3.466875	<0.001	1	3.12120	<0.001
Treatment	1	0.001408	0.622	1	0.00750	0.497
Lf x T	1	0.003008	0.476	1	0.00083	0.818
Error	6	0.031283		6	0.01437	
(c) March 1997						
Life form	1	0.097200	<0.001	1	0.00367	0.778
Treatment	1	0.000033	0.916	1	0.03521	0.396
Lf x T	1	0.012033	0.083	1	0.00041	0.925
Error	6	0.002781		6	0.04208	
	NPN			Dry Organic Matter Digestibility		
(a) *Ptilotus obovatus*						
Sampling	3	4.2422	<0.001	3	1129.074	<0.001
Treatment	1	0.4817	0.276	1	1.131	0.617
Sa x T	3	1.1766	0.059	3	1.135	0.852
Error	14	0.3745		14	4.336	

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Table 2: Continued

Effect	df	MS	P	df	MS	P
	NPN			Dry Organic Matter Digestibility		
(b) August 1996						
Life form	1	19.35480	<0.001	1	52.878	0.018
Treatment	1	0.02430	0.420	1	3.360	0.445
Lf x T	1	0.00480	0.714	1	0.550	0.752
Error	6	0.03242		6	5.025	
(c) March 1997						
Life form	1	0.7400	0.124	1	1198.401	<0.001
Treatment	1	0.3816	0.247	1	2.359	0.572
Lf x T	1	0.0040	0.899	1	0.853	0.731
Error	6	0.0322		6	6.595	
	Soluble Sugar			Starch		
(a) *Ptilotus obovatus*						
Sampling	3	80.024	<0.001	3	0.201471	<0.001
Treatment	1	1.175	0.340	1	0.000337	0.840
Sa x T	3	0.038	0.992	3	0.001849	0.872
Error	14	1.202		14	0.007946	
(b) August 1996						
Life form	1	0.097	0.803	1	1.128533	<0.001
Treatment	1	0.720	0.504	1	0.000133	0.869
Lf x T	1	0.021	0.908	1	0.000033	0.934
Error	6	1.427		6	0.004492	
(c) March 1997						
Life form	1	1.703	0.566	1	0.005208	0.144
Treatment	1	1.080	0.646	1	0.001008	0.487
Lf x T	1	0.006	0.973	1	0.003008	0.248
Error	6	4.611		6	0.001842	
	Total Phenolics			Condensed Tannins		
(a) *Ptilotus obovatus*						
Sampling	3	2.9053	<0.001	3	0.07038	0.201
Treatment	1	0.0876	0.519	1	0.02010	0.400
Sa x T	3	0.0046	0.995	3	0.04642	0.360
Error	14	0.1997		14	0.04001	
(b) August 1996						
Life form	1	0.01687	<0.001	1	0.0030083	0.015
Treatment	1	0.00141	0.842	1	0.0002083	0.411
Lf x T	1	0.00141	0.842	1	0.0002083	0.411
Error	6	0.03258		6	0.0002667	
(c) March 1997						
Life form	1	0.66741	0.007	1	0.0002083	0.418
Treatment	1	0.00101	0.894	1	0.0010083	0.104
Lf x T	1	0.04441	0.386	1	0.0000083	0.868
Error	6	0.05281		6	0.0002750	

Table 3: Concentrations of N, NPN (non protein nitrogen), NO_3, P (mg g^{-1} oven dry weight), K, Ca, Mg and *in vitro* dry organic matter digestibility (% oven dry weight) in the leaves and stem of *P. obovatus*. Where fertiliser treatment was not significant, values are means of both +fertilizer and −fertilizer treatments. When the effect of fertilizer was significant, means for both treatments and the Least Significant Difference (LSD, $p < 0.05$) between means are shown. Where the effect of P was not significant, combined means are presented

Species	N	NPN	NO_3	P	K	Ca	Mg	IVDOMD
August 1996.								
Leaves +P/-P	17.13	4.99	0.64	0.91	5.44	1.81	1.31	44.9
Stem +P/-P	6.34	-	0.39	0.41	1.74	0.53	0.08	28.2
November 1996								
Leaves +P/-P	11.97	5.65	0.49	0.74	3.86	1.95	0.71	25.0
Stem +P/-P	4.60	-	0.30	0.43	1.60	0.64	0.07	15.0
March 1997								
Leaves +P	15.68	6.9	1.01	1.13	10.01	0.41	2.66	57.3
-P	13.89	6.5	0.93	0.98	9.35	0.47	2.57	57.0
LSD	n.s.	n.s.	0.05	0.14	0.47	n.s.	n.s.	n.s.
Stem +P/-P	7.53	-	0.35	0.70	5.32	0.25	0.72	21.1
June 1997								
Leaves +P	26.78	5.79	0.33	1.57	2.58	1.81	0.95	48.0
-P	22.74	6.39	0.31	1.09	2.02	1.94	0.72	47.1
LSD	1.61	-	n.s.	0.40	0.39	0.06	0.05	n.s.
Stem +P/-P	12.11	-	0.39	0.96	0.86	0.53	0.15	36.0

Table 4: Concentrations of N, NO$_3$, P (mg g^{-1} oven dry weight), K, Ca, Mg and *in vitro* dry organic matter digestibility (% oven dry weight) in the leaves and stem of ephemeral forbs. Where treatment was significant, the Least Significant Differences ($p < 0.05$) between foliage means is shown. Where the effect of P was not significant, combined means are presented.

Species	N	NPN	NO$_3$	P	K	Ca	Mg	IVDOMD
August, 1996								
B. ciliocarpa								
Leaves +P/-P	17.14	7.05	0.12	2.64	4.18	0.47	0.23	53.4
Stem +P/-P	4.75	-	0.15	1.55	2.58	1.54	0.13	48.8
***Abutiloton* spp**								
Leaves +P/-P	29.62	7.8	0.25	2.59	2.85	1.00	0.35	44.6
Stem +P/-P	10.99	-	0.13	1.48	2.65	0.81	0.25	33.4
March 1997								
B. bipinnata								
Leaves +P	16.57	7.4	0.50	1.07	7.75	0.65	2.71	37.9
-P	15.94	6.5	0.45	0.85	7.17	0.59	2.59	36.5
LSD	n.s.	n.s.	0.05	0.14	0.47	n.s.	n.s.	n.s.
Stem +P/-P	5.19	-	0.24	0.73	6.29	0.28	0.82	16.6

Table 5: Summary of the effects of added P (+, added P; -, no added P; +/-, ratio of + to -) on nutrient concentrations (nitrogen, N; phosphorus, P; calcium, Ca), in vitro dry organic matter digestibility (IVDOMD) and δ^{13} C of plant species (C$_3$ unless indicated) in three plant communities in the Pilbara. The number of replicates from which the bulk means were calculated varies depending on the life form of the species, some species were only vegetative for short periods. The communities are a) a 'run-on' thicket of Mulga (*Acacia aneura*), b) an adjacent 'run-off' area, and c) a nearby grassland. The total number of replicates (n) throughout the year is shown.

Species Name	n	δ^{13} C	N			P			Ca			IVDOMD		
			+	-	+/-	+	-	+/-	+	-	+/-	+	-	+/-
a) Mulga thicket														
Perennial shrubs (s) and ephemeral forbs (f)														
P. obovatus (s)	24	-28.48	17.9	16.5	1.1	1.1	0.9	1.2	1.5	1.5	1.0	43.6	43.5	1.0
B.ciliocarpa (f)	6	-27.98	17.3	17.1	1.0	2.7	2.6	1.0	0.5	0.5	1.0	53.4	54.4	0.9
Abutilon spp. (f)	6	-26.14	29.7	29.6	1.0	2.6	2.7	0.9	0.9	1.0	1.0	44.5	44.4	1.0
B. bipnnata (f)	6	-27.22	16.6	15.9	1.0	1.1	0.8	1.3	0.7	0.6	1.1	37.9	36.5	1.0
Mean		-27.72	20.4	19.8	1.0	1.8	1.8	1.1	0.9	0.9	1.0	44.9	44.7	1.0
b) 'Outside thicket'														
Perennial shrubs and ephemeral forbs														
M.tomentosa (s)	24	-26.95	19.1	18.3	1.0	1.1	0.9	1.2	0.5	0.5	1.0	43.8	42.7	1.0
A. otacarpum (f)	18	-25.57	18.4	17.3	1.1	1.4	1.3	1.1	1.2	1.2	1.0	40.2	40.0	1.0
P.exaltotus(f)	18	-25.36	21.2	21.0	1.0	1.2	1.0	1.2	1.3	1.4	0.9	62.6	62.6	1.0
P.macrocephalus(f)	6	-24.20	22.2	22.5	1.0	1.3	1.3	0.9	1.2	1.2	1.0	68.9	69.1	1.0
P.aerovides(f)	6	-24.37	22.7	23.1	1.0	1.9	1.8	1.0	0.9	0.9	0.9	44.1	45.8	1.0
D.kapari (s)	6	-24.90	17.1	16.5	1.0	1.9	1.8	1.1	0.9	1.0	0.9	44.1	45.8	1.0
Mean		-23.45	20.2	19.8	1.0	1.3	1.2	1.1	1.0	1.3	0.8	52.1	52.2	1.0
S.kali (f,C$_4$)	24	-12.83	20.1	19.6	1.1	1.1	0.9	1.2	1.1	1.3	0.9	48.5	47.6	1.0
Ephemeral grasses (C$_4$)														
D.radulans	6	-13.12	5.8	4.6	1.3	0.9	0.6	1.5	0.3	0.4	0.9	28.8	32.1	0.9
U.gilessi	6	-12.02	10.5	6.0	1.7	0.8	0.6	1.3	0.2	0.2	0.8	27.8	32.7	0.9
E.caerulescens	6	-12.11	7.6	5.5	1.4	0.5	0.5	1.1	0.4	0.3	1.2	31.3	28.5	1.1
Mean		-12.62	7.9	5.4	1.4	0.8	0.6	1.3	0.3	0.3	1.0	29.4	31.1	1.0
c) Grassland														
Ephemeral forbs														
A. otacarpum	12	-25.59	14.4	13.6	1.1	1.2	1.5	1.1	0.9	0.9	1.0	45.1	45.0	1.0
C.cinerum	12	-26.61	19.2	18.7	1.0	2.0	1.9	1.0	0.8	0.9	1.0	51.5	53.0	1.0
S.fibulifera	12	-27.00	16.2	15.5	1.1	2.0	1.8	1.1	0.9	1.0	0.9	43.5	43.6	1.0
Mean		-26.39	16.6	15.9	1.0	1.7	1.7	1.0	0.9	0.9	1.0	46.7	47.1	1.0
Perennial grasses (C$_4$)														
E.helmsii	24	-13.00	7.6	7.1	1.0	0.9	0.7	1.3	0.8	0.7	1.1	35.3	33.3	1.1
T. basedowii	24	-14.00	6.6	6.2	1.1	0.8	0.6	1.3	0.8	0.7	1.1	31.6	29.7	1.1
Mean		-13.50	7.1	6.6	1.1	0.9	0.7	1.3	0.8	0.8	1.1	33.5	31.5	1.1

Eriachne helmsii (Buck wanderrie grass) and *Triodia basedowii* (Hard spinifix). At different times of the year, other species of forbs and grasses comprised the remaining vegetation. The most abundant other species were: grasses - *Paspalidium clementi* (Clements paspalidium), *Iseilema membranaceu* (Small Flinders grass), and forbs - *Abutilon otocarpum* (Desert chinese lantern), *Cullen cinerum* (Marshmallow), *Sida fibulifera* (Silver sida).

A chemical description of the surface soils (0-10 cm) at each Experimental site is given in Table 1.

Samples of the aboveground biomass (minimum n = 6) were taken from each replicate just after P application in August 1996 and then in November 1996 and March and June 1997. Shoot samples were plunged immediately into liquid nitrogen and stored in liquid N until returned to the laboratory in Perth. In the laboratory, plant samples were freeze-dried and separated into stems and leaves. Total N, P and cation concentrations were determined by acid digestion of 100 – 200 mg of plant sample at 320 °C with H$_2$SO$_4$ and H$_2$O$_2$. Diluted digests were analysed colorometrically for N and P by the procedure described by Keeney & Nelson (1982) and Murphy & Riley (1962) respectively. Cations were analysed using the Atomic Absorption Spectrophotometer. The samples were analysed for nonprotein nitrogen, NPN, (Licitra *et al.,*

1996), nitrate (Cataldo *et al.*, 1975), *in vitro* dry organic matter digestibility (IVDOMD) using the acid-pepsin procedure (Catling *et al.*, 1994), carbohydrate content (Dubois *et al.* 1956), total phenolics TP, (Makkar *et al.*, 1993), and condensed tannins CT, (Porter *et al.*, 1986).

Dried plant material from all experiments was further ground for $\delta^{13}C$ analysis in a ball mill to ensure thorough homogenisation. A 2-mg subsample of the tissue was analysed on Tracer Mass Stable Isotope Analyser (Europa Scientific, UK) as described by Macfarlane & Adams (1998) and $\delta^{13}C$ values are expressed in parts per thousand (‰) and were calculated with respect to a Pee Dee Belemite standard $\{ = [(^{13}C/^{12}C_{sample})/(^{13}C/^{12}C_{standard})-1] \times 1000\}$.

All samples were analysed in duplicate and mean values were used for statistical analysis. Data were analysed as a completely randomised design by using GENSTAT 5. Fixed effects were season of sampling and P-treatment and all treatment means were compared using the Least Significant Difference test, when the overall treatment F was significant at $p < 0.05$.

Results

Concentrations of all measured nutrients varied significantly among sampling dates in *P. obovatus* (Table 2) whereas the effect of P-treatment was significant only for N and K. When data were aggregated, life-form had a significant effect on concentrations of N, P, nitrate-N, K, Ca, Mg, non-protein N (NPN) and on the *in vitro* dry organic matter digestibility (IVDOMD) in August but only on nitrate-N, K, Ca and IVDOMD in March. For aggregated species and only in March, the concentration of K varied significantly with application of P; concentrations of all other nutrients and the IVDOMD did not vary significantly.

Concentrations of P in *P. obovatus* were significantly increased by the addition of P fertiliser only after rain (March and June 1997, Table 3). Nitrogen concentrations were also significantly increased after rain, as were those of potassium and magnesium and nitrate-N, while that of calcium decreased significantly. Nitrate-N contributed a small fraction of total nitrogen in dry months compared with wet months. Foliar concentrations of NPN were almost half of those of total N in samples collected in November 1996 and March 97 compared with other months, when it was only between 29-33 %. The digestibility (IVDOMD) of the foliage was greatest immediately after rain and least before rain. Foliar concentrations of all nutrients were always greater than stem concentrations – the differences were greatest for Mg, N, nitrate-N and K. Concentrations of phosphorus were greater in the ephemeral forbs *Abutiloton* spp. and *Brachycome ciliocarpa* than in the perennial *P. obovatus* (Tables 3, 4) when sampled in August but concentrations of NO_3-N, K, Ca and Mg were generally least in the ephemeral species. Black jack (*B. bipinnata*) was poorly digestible (low IVDOMD) compared with other species. Concentrations of condensed tannins did not exceed 0.4 % (dry weight basis) while those of total phenolics reached as much as 3.3 % in the perennial *P. obovatus* (Fig. 1b). Starch concentrations were, on average, less than 5 % of the total non-structural carbohydrates with soluble sugars contributing the remainder (Fig. 1a). Maximum concentrations of starch in leaves were found after rain.

When results of mulga thicket compared with outside thicket and grassland, several observations are immediately obvious (Table 5). First, there was, overall, a general lack of a response to added P in the concentrations of most measured nutrients or foliage fractions. Ratios of the concentration of an element or compound in foliage of a species in fertilised plots to those in foliage of the same species in unfertilised plots were close to unity for K, Mg (results not presented), Ca and the IVDOMD for all species in all three communities. Ratios for N were between 1.3 and 1.4 for annual grasses but unity or close to unity for all other life-forms in all experiments. The

response of P concentrations in foliage to additions of P were more variable but again strongest in the annual (and perennial)
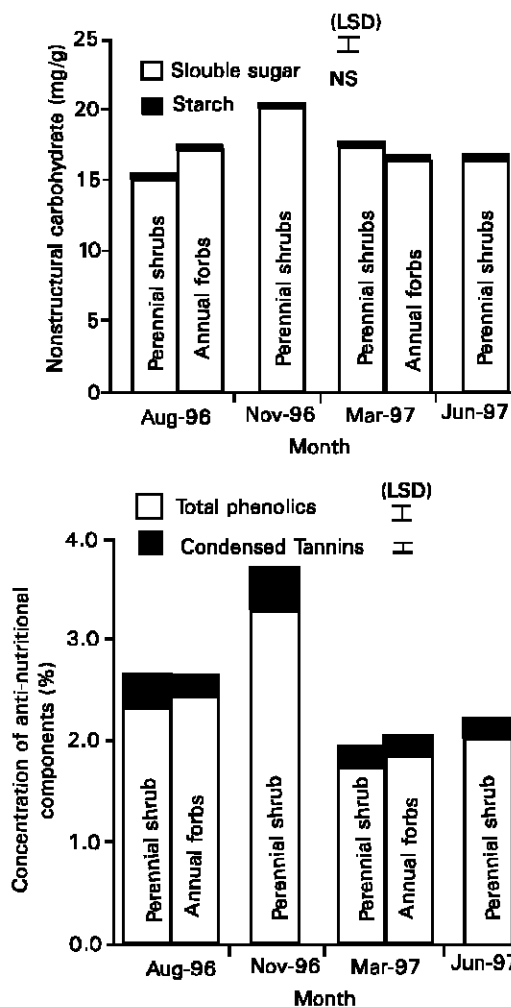

Fig. 1: Carbon fractions in foliage.
  a) Concentrations of starch and soluble sugars as a proportion of plant dry weight in foliage of different life forms throughout the sampling period. All species values were means of 3 replicates.
  b) Concentrations of total phenolics (TP) and condensed tannins (CT) (% oven dry weight) in foliage of different life forms throughout the sampling period. Total phenolics (TP) and condensed tannins varied significantly ($p < 0.05$) with season and least significant differences ($p < 0.05$) between season are shown.

grasses (Table 5). $\delta^{13}C$ of species from all three communities did not vary significantly with phosphorus additions and mean values are presented in Table 5. $\delta^{13}C$ of C_4 annual and perennial grasses were all between -12 and -14 and of C_3

shrubs and forbs between -24.2 and -28.5. The mean $\delta^{13}C$ for species growing in the area adjacent to the Mulga thicket, where perennials were largely absent, was significantly different (less negative) to that of the species within the thicket. The range of $\delta^{13}C$ values for the two areas did not overlap. Mean $\delta^{13}C$ for species from the nearby perennial grassland were between these two values and not significantly different from either.

Discussion

In understorey perennial and ephemeral species in a Mulga thicket, the patterns of seasonal variation and response to added phosphorus in the nutrient and carbon concentrations and nutritional and anti-nutritional factors have been measured. The concentrations of N and P are generally greatest after rainfall and least at the end of long dry spells. Nitrogen concentrations also decline quickly when growth is rapid, so much so, that in grasses in particular, N: P ratios are usually low by standards of other vegetation types (e.g. Koerselman & Mueleman, 1996). Phenology also plays a major role in determining nutrient concentrations. For example, flowering of ephemeral forbs reduces concentrations of N and P in foliage and foliage may even senesce completely at this stage (Mitchell & Wilcox, 1994).

In *P. obovatus*, concentrations of non-protein nitrogen were always greater than 30% of total leaf N but ranged up to almost 50% at the end of long dry spells. Hence while many species have concentrations of N in foliage greater than the basic requirements for cattle or other ruminants (NRC 1996), for much of any year, a large proportion of that N will not be present as easily digestible protein or simple nutritional amino acids. Further research is needed to better quantify the amount of N available to herbivores.

In all three plant communities, few of the shrub species responded strongly to addition of P (Table 5). Grasses, both perennial and ephemeral, responded most and generally had the lowest concentrations of P and N compared with annual forbs and perennial species. Ephemeral forbs also responded to added P, albeit only slightly. Poor responses to P have been attributed to high temperatures (Wilson *et al.*, 1986) but other reasons seem more likely. Most importantly, while some native species may have a capacity to sequester available phosphorus beyond immediate metabolic requirements (or 'luxury uptake'), that capacity may never be realised because P will only be available when the demand for P is greatest (i.e. during periods of rapid growth). Because of the generally poor mobility of P in soils, P-availability will be always be strongly linked to the availability of water, especially in highly weathered, strongly P-fixing soils. Hence, responses to P were only seen after significant summer rain and it will remain difficult to separate the effects of improved root growth on phosphorus availability from the effects of added P, *per se*. Growth is determined by water availability in these environments and P-availability, P-uptake, water availability and growth are all tightly coupled.

Taken together, our observations on the processes determining N and P concentrations in the plant and those responsible for P availability in the soil, probably preclude the use of N: P ratios as useful diagnostic tests of nutrient deficiency in arid systems. When water is not limiting, N: P ratios above about 16 suggest a P deficiency and those below 16 suggest an N deficiency (Koerselman & Muelemans, 1996). We have measured ratios above 30 and below 10, which better reflect the interaction of phenology and climate than N or P limitations. Similarly, Ca:P ratios have also been used as

indices of forage suitability or quality for ruminants (Ricketts *et al.*, 1970) and will be subject to the same problems of interpretation in arid environments.

Overall the digestibility (IVDOMD) of most forbs was greater (40-45 %) than recommended by Holechek & Herbal (1986) for the maintenance of cattle. Winter forbs were more digestible than the summer forb. The perennial shrub, *P. obovatus* under Mulga thicket, was less digestible than the forbs and the preponderance of perennial shrubs for long periods probably contributes to the limitation of animal production on dry rangelands (Karue, 1975).

In nutrient poor environments where growth is nitrogen- rather than carbon-limited, ecological dogma suggests that species may accumulate considerable concentrations of carbon-rich anti-nutritional compounds as defences against herbivores (Coley *et al.*, 1985). In the Pilbara, both annual and perennial species accumulated carbon-based secondary metabolites and the faster growing annuals accumulated less than the perennials. Concentrations of phenolics and tannins varied seasonally and were greatest when water availability was least and coincided with high temperatures (Lees *et al.*, 1994). Addition of fertiliser had little or no effect on carbon-based anti-nutritional compounds, probably due to the strong water-P coupling described above (Bryant *et al.*, 1987).

In arid and semi-arid ecosystems, the species composition and form and function of the overstorey or perennial vegetation may dictate or at least modify the edaphic factors for ephemeral or understorey vegetation. Equally importantly in these exacting environments, plants have generally well-developed mechanisms and phenologies to cope with and compete for short supplies of water or nutrients. For example, 'annuals' grow rapidly to maturity after rain while perennials have an extensive root system that helps them use a larger proportion of the water available in the profile. Other, less obvious features may also come into play. Joffre & Rambal (1993) suggested that the growth of understorey species might be facilitated by a greater availability of water under the tree canopy. Our $\delta^{13}C$ results suggest strongly that either more water is available in the Mulga thickets than outside or that the improved 'evaporative climate' under the canopy is more conducive to stomatal opening. There also seems reasonable evidence that less water is available to plants within in the nearby grasslands than within the thicket. We are presently further examining the distribution of Mulga and associated trees in relation to water availability as well as their capacity to 'lift' water and make it available to other species in order to help distinguish between the possible causes of the apparent reduction in WUE of the Mulga understorey.

The greater productivity of trees and shrubs with access to water will also increase organic matter turnover and nutrient availability within the thicket. Our results neither confirm or deny suggestions (Ludwig *et al.*, 1997) that patches of perennial vegetation or those which might trap mobile resources are in fact more fertile than other patches and more work is needed. However, we would point out that any increase in productivity brought about by a greater capacity of a vegetation patch to access water, will increase nutrient availability. This is the essence of nutrient cycling and a hypothesis that is deserving of greater attention in the arid zone, as is the role of temporal climatic variation in determining supposed nutrient limitation in many rangelands (Chaneton *et al.*, 1996). We suspect that much of that nutrient limitation will be a water limitation in disguise.

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