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Chemical composition of *Flourensia cernua* at four growth stages

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Abstract

Tarbush (*Flourensia cernua* DC) is an abundant Chihuahuan Desert shrub but is used sparingly by livestock. Leaves were removed from forty tarbush plants harvested in each of 3 years during four growth stages: (1) early, (2) mid-point, (3) late and (4) curtailed growth (ten plants per growth stage each year). Plants were air dried and all leaves were removed. *In vitro* dry-matter (DM) disappearance was greater for the early growth stage than other stages ($P<0.05$). The fibrous fraction increased with maturity, with neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) contents all less for the early growth stage ($P<0.05$) than other stages. The latter three growth stages did not differ in NDF or ADF content, but ADL content was lower for the mid-point growth stage than for the two later stages ($P<0.05$). Calcium content increased with advancing season ($P<0.05$), whereas phosphorus concentration exhibited an inverse pattern ($P<0.05$). Nitrogen (N) content of tarbush was greatest in the early growth stage ($P<0.05$) and declined substantially thereafter. Soluble N content was greater and acid detergent insoluble N (ADIN) content was lower for early growth ($P<0.05$) than other stages. Insoluble N concentration followed a pattern similar to N, declining with advancing season ($P<0.05$). When expressed as a fraction of total N, insoluble N decreased and soluble N increased with maturity ($P<0.05$). Condensed tannin concentration tended ($P<0.10$) to increase with advancing season. Total phenolic content was lowest for early growth ($P<0.05$), and did not differ among the other stages. Chemical analysis revealed tarbush to be relatively high in N concentration. Fibre fractions, ADIN, ADL and condensed tannins were all generally low whereas total phenolic content of tarbush was quite high. Early use by livestock would be most advantageous in terms of nutrient availability (N, P and *in vitro* digestibility) and lowest total phenolic concentration. Year-to-year variability in chemical composition of tarbush appears to be substantial. It remains to be seen whether overriding intake deterrents would be beneficial to livestock, given the high phenolic concentration in tarbush. Tarbush has several characteristics that make it a suitable model for studying plant–animal interactions of desert shrubs.

Introduction

A transition towards a shrub-dominated state is occurring on arid grasslands throughout the world. Attempts to mitigate this situation (halting and/or remediating desertification) must integrate an array of ecologically viable and socially responsible approaches. Manipulation of herbivore behaviour (e.g. altering dietary preferences) may provide an approach to deal with this problem. Knowledge of plant–animal interactions in this ecosystem may aid in developing technologies that use herbivores to manipulate vegetation. These tools should also extend the forage base for livestock by exploiting presently unused plant species. Tarbush (*Flourensia cernua*) has several characteristics that make it a suitable plant model to explore relationships between shrub chemistry and diet selection. Tarbush is increasing in the Chihuahuan Desert (Buffington and Herbel, 1965) and is nutrient dense (based on cursory examination: Nelson *et al.*, 1970). Also, tarbush is differentially browsed by livestock (Estell *et al.*, 1994), but use is generally low (Nelson *et al.*, 1970; Anderson and Holechek, 1983). Tarbush contains a variety of secondary compounds (Kingston *et al.*, 1975; Dillon *et al.*, 1976; Bohlmann and Grenz, 1977; Aregullin-Gallardo, 1985) that apparently

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affect browsing patterns, and certain growth stages may be toxic to some species of herbivores (i.e. flowering stage; Mathews, 1944; Hailey *et al.*, 1966; Dollahite and Allen, 1975). As we explore possibilities to override threshold mechanisms that limit intake of tarbush, we must examine the spatial and temporal variabilities of its nutrient content and anti-nutritional components. From a management standpoint, there may be an optimal growth stage (high nutrient/low anti-nutritional constituents) in which to use (or force) livestock to consume tarbush. The objective of this study was to examine tarbush leaf production and nutrient concentration during four stages of growth over 3 years. We hypothesized that nutrient concentrations and total phenolic concentrations would decrease and other anti-nutritional factors would increase with advancing plant maturity, and that their concentrations would vary among years.

Materials and methods

A 7·5-ha paddock was constructed on the Jornada Experimental Range (JER, located in south-central New Mexico, USA) in 1988 within an area heavily infested with tarbush. Before 1988, the area was exposed to light or moderate stocking rates for the previous 75 years. Precipitation data were averaged from two rain gauges located within 1 km of the study site. Monthly precipitation for the duration of the study is presented in Figure 1. Total annual precipitation for 1990, 1991 and 1992 was 259, 395 and 288 mm respectively. Total growing season (July, August and September) precipitation for 1990, 1991 and 1992 was 175, 238 and 112 mm respectively. Long-term (1915–93) annual and growing season rainfall for the area is 245 and 131 mm respectively.

Each year (1990, 1991 and 1992), forty points were randomly selected on a randomly located transect spanning the width of the paddock. The tarbush nearest each point was identified, excluding plants greater than 2 m from the transect and small plants (<60 cm height). Ten plants were randomly assigned to and harvested during one of the following growth stages: (1) early growth, (2) mid-point growth, (3) late growth and (4) curtailed growth. Growth stages were defined to represent initiation of leader elongation following summer rains (early growth), mid-point of active leader elongation (mid-point growth), slow leader elongation (late growth) and curtailed leader elongation (curtailed growth). Actual collection dates were: 20 July, 31 August, 12 October and 26 October, 1990: 26 July, 23 August, 11 October and 25 October, 1991: and 8 May, 26 June, 9 October and 23 October, 1992. Two plants completely defoliated by insects during 1991 were removed from the study (one each for late growth and curtailed growth stages).

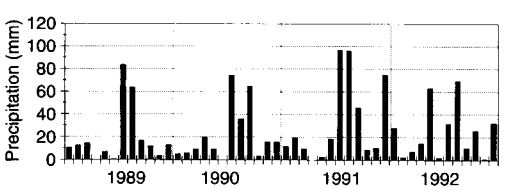

Figure 1. Monthly precipitation of the study site from 1989 to 1992.

When harvested, plants were severed at the base, placed in large plastic bags, immediately transported to the laboratory and spread on tables to air-dry (4–6 d at approximately 22°C). Leaves were then manually removed, freeze dried for 24 h, air equilibrated and weighed and ground through a 1-mm screen (Cyclotec sample mill, Model 1093, Tecator, Herndon, VA, USA) and stored for later analyses. Because tarbush leaves are extremely resinous, air-drying before leaf removal was the only practical way to process whole plants and recover the quantities necessary for subsequent analyses.

Analyses were conducted according to AOAC (1990) procedures for dry matter (DM), ash, ether extract (EE), phosphorus (molybdovanadate method), gross energy (GE, adiabatic bomb calorimetry), total phenolics (Folin–Denis method, tannic acid as standard) and N (Kjeldahl) estimates. Soluble N (0·15 M NaCl method) was measured in accordance with Waldo and Goering (1979). Acid detergent insoluble N (ADIN), neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were analysed using non-sequential procedures as described by Goering and Van Soest (1970). *In vitro* DM disappearance (IVDMD) was in accordance with the method of Tilley and Terry (1963), with ruminal fluid inoculum combined from a minimum of three steers maintained on alfalfa hay. Calcium, sodium and potassium were measured with atomic absorption/emission spectrophotometry (air/acetylene flame). Condensed tannin concentration (vanillin– HCl procedure, catechin as standard) was analysed using the method of Burns (1971) as modified by Price *et al.* (1978). Insoluble available N was calculated as the difference between insoluble N and ADIN; and soluble N, insoluble N, insoluble available N and ADIN were also calculated on a total N basis.

Data were analysed using GLM procedures of SAS (1988) with year, growth stage and their interaction in the model. In the case of a significant F-test ($P<0.05$) for the overall model, means were separated by predicted difference (SAS, 1988). Year by growth stage interactions existed ($P<0.05$) for most variables but, owing to the nature of the interactions, they did not preclude interpretation of main effects. Two exceptions are discussed later.

Results and discussion

Insect (*Zygograma tortuosa*) herbivory during 1990 was extensive, with significant damage by the mid-point growth stage. Conditions were generally dry (Figure 1) during the first several weeks of the 1990 growing season. The third growth stage was originally designed to coincide with flowering, but tarbush did not bloom in 1990; consequently, the late growth stage was harvested in mid-October.

During 1991, conditions before summer growth were very dry (Figure 1) and insect damage was prevalent. Several shrubs exhibited major damage and some shrubs were completely defoliated. Summer rains were too late to stimulate much late summer growth. Again, tarbush did not flower. In 1992, the growing season began much earlier (early May) due to heavy winter and spring precipitation (Figure 1); thus, plant sampling occurred over a longer interval than in the first 2 years. Plants were lush and green for most of 1992, and *Zygograma tortuosa* infestation was extremely light compared with previous years. Tarbush flowered sporadically on the site in 1992, but no study plants bloomed.

Chemical analyses for tarbush leaves are presented in Table 1. Nitrogen content was relatively high, ranging from 39·5 g kg^{-1} DM for the early growth stage to 26·2 g kg^{-1} DM for the curtailed growth stage. Nelson *et al.* (1970) analysed tarbush samples collected using oesophageally fistulated steers in November and December during a single year (samples contained dormant stems and seedheads), and reported 23·7 and 18·4 g N kg^{-1} DM. These data agree with our samples collected in October. *In vitro* DM disappearance was reasonably high for most sampling times and fibre content was typically low. Nelson *et al.* (1970) reported 257 and 280 g ADF kg^{-1} DM and 105 and 111 g ADL kg^{-1} DM for tarbush in November and December respectively – somewhat greater than our values for October collections, probably due to the presence of stems in their samples. Ether extract ranged from 118 to 147 g kg^{-1} DM, which would be expected for plants with a resinous exudate on the leaf surface. Epicuticular wax in tarbush averaged 80–100 g kg^{-1} DM in a companion study (Estell *et al.*, 1994); also, Nelson *et al.* (1970) reported 168 and 78 g EE kg^{-1} DM in samples collected from November and December. Ash content ranged from 118 to 137 g kg^{-1} DM, compared with 86 and 87 g kg^{-1} DM reported by Nelson *et al.* (1970). Mineral concentrations reported by Nelson *et al.* (1970) for Ca (11 and 15 g kg^{-1} DM), P (2·0 and 1·1 g kg^{-1} DM), K (20 and 19·5 g kg^{-1} DM) and Na (0·1 and 0·2 g kg^{-1} DM) agree very closely with our estimates. Our data indicated that ADIN, ADL and condensed tannin concentrations were generally low, whereas total phenolic content was quite high. Thus, anti-nutritional effects due to fibre-bound N, lignification and tannins would not be expected, but consumption of high-phenolic browse might be a cause for concern if consumption exceeds metabolic clearance capabilities. Pronghorn consuming tarbush as the primary source of winter/spring forage during a poor year exhibited malnutrition, intestinal lesions and often death (Hailey *et al.*, 1966). High phenolic/ tannin shrubs have been shown to decrease intake, digestion and N retention in goats and sheep (Holechek *et al.*, 1990; Degen *et al.*, 1995). The main chemical defence compounds in desert shrubs are usually terpenoids and phenolic compounds (Meyer and Karasov, 1991), so it is not surprising that total phenolic levels were high. We are not aware of other data on tannins and phenolics in tarbush for comparison. Whereas flavonoids (Dillon *et al.*, 1976) and derivatives of 4-hydroxyacetophenone (Bohlmann and Grenz, 1977; Aregullin-Gallardo, 1985) are present in tarbush, their contribution to the total phenolic fraction has not been quantified.

Total dry leaf weight per plant was greater ($P<0.05$) both for leaves in the mid-point growth stage and in 1992. Leaf production for plants harvested in the mid-point growth stage in 1992 was approximately twice that of any other collection in any year. Elevated winter precipitation before the 1992 growing season vs. the same interval during the previous 2 years (Figure 1) may account for this difference. These values suggest a substantial biomass production from tarbush-dominated rangeland. The only data we are aware of for comparison are from an assessment of twenty tarbush plants in the late growth stage (R.P. Gibbens, personal communication) in which the mean dry leaf weight was 131 g per plant. Although slightly greater than our values, plants were obtained from another site that may have differed in soil moisture.

Table 1. Leaf production and chemical composition of tarbush leaves at four stages of growth over three years†

	LP (g DM)	IVDMD	Ash	N	SN	ISN	ADIN	NDF	ADF (g kg^{-1} DM)	ADL	EE	Ca	P	Na‡	K‡	CT	TP	GE (kJ g^{-1} DM)
Growth stage																		
E	73·9^{a}	668^{a}	119^{a}	39·5^{a}	14·3^{a}	25·3^{a}	0·8^{a}	186^{a}	142^{a}	53^{a}	143^{a}	9·6^{a}	2·5^{a}	0·1	22·8a	3·0	65·5^{a}	20·5
M	109·6^{b}	610^{b}	130^{b}	28·2^{b}	11·8^{b}	16·4^{b}	1·1^{b}	216^{b}	177^{b}	66^{b}	132^{b}	14·8^{b}	1·2^{b}	0·1	30·9^{b}	3·5	81·1^{b}	20·2
L	82·8^{a}	605^{b}	123^{a,c}	27·7^{b}	12·6^{b}	15·1^{c}	1·1^{b}	221^{b}	183^{b}	71^{c}	131^{b}	16·8^{c}	1·1^{c}	0·1	25·8^{a,b}	3·7	78·6^{b}	20·1
C	66·1^{a}	604^{b}	128^{b,c}	26·2^{c}	12·6^{b}	13·6^{d}	1·2^{b}	214^{b}	182^{b}	73^{c}	133^{b}	19·5^{c}	1·0^{c}	0·1	24·4^{a}	3·7	76·4^{b}	20·0
s.e.m.	8·7	5·4	2·1	0·43	0·49	0·44	0·10	4·2	3·3	1·7	3·4	0·59	0·03	0·01	1·93	0·22	2·27	0·20
Year																		
1990	62·7^{a}	690^{a}	121^{a}	32·7^{a}	13·1	19·6^{a}	1·4^{a}	208^{a}	169^{a}	71^{a}	139^{a}	7·5^{a}	1·6^{a}	0·1	27·3	2·6^{a}	69·8^{a}	20·5^{a}
1991	78·6^{a}	616^{b}	118^{a}	31·9^{a}	13·3	18·7^{a}	1·1^{b}	232^{b}	198^{b}	72^{a}	118^{b}	15·9^{b}	1·4^{b}	–	24·7	3·3^{b}	60·3^{b}	20·4^{a}
1992	107·9^{b}	559^{c}	137^{b}	26·5^{b}	12·1	14·5^{b}	0·7^{c}	188^{c}	146^{c}	55^{b}	147^{a}	22·1^{c}	1·4^{b}	–	–	4·5^{c}	96·1^{c}	19·7^{b}
s.e.m.	7·6	4·7	1·9	0·37	0·43	0·38	0·09	3·7	2·9	1·5	2·9	0·52	0·03	0·001	1·36	0·20	1·98	0·17

†Least square means, $n = 40$, 38 and 40 for 1990, 1991 and 1992 respectively; $n = 40$, 40, 39 and 39 for growth stages E, M, L, and C respectively; the four growth stages were early (E), mid-point (M), late (L) and curtailed (C). LP, total leaf production; DM, dry matter; IVDMD, *in vitro* DM disappearance; SN, soluble N; ISN, insoluble N; ADIN, acid-detergent insoluble N; NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin; EE, ether extract; GE, gross energy; CT, condensed tannins; TP, total phenolics. A growth stage × year interaction ($P<0·05$) was detected for all variables except ADL, K and CT.

‡Data are incomplete due to equipment failure.

Column least square means with different superscripts differ ($P<0·05$).

Ash concentration differed for stage of maturity and year ($P<0.05$), with a greater ash content for 1992 than the other 2 years. *In vitro* DM disappearance was greater for the early growth stage than for other stages ($P<0.05$). Greater digestibility estimates earlier in the growing season are typical of relationships exhibited by numerous other plant species (Van Soest, 1982). A corresponding increase in NDF, ADF, ADL and ADIN between the early and mid-point growth stages (discussed below) was noted. Differences across year (1990 > 1991 > 1992) for IVDMD ($P<0.05$) may be partly explained by increased condensed tannin content. Also, greater total phenolic concentration observed in 1992 could be involved in digestibility reduction. Differences in fibrous components did not correspond to differences in IVDMD from year to year. In particular, ADL and ADIN did not follow anticipated patterns with respect to year-to-year differences in IVDMD.

Nitrogen content of tarbush was greatest during the early growth stage ($P<0.05$) and declined substantially thereafter. Nitrogen content is typically greatest during early, active growth and decreases with forage maturity (Church, 1977; Holechek *et al.*, 1989). Nitrogen content was less in 1992 than the other 2 years ($P<0.05$). Soluble N content was greater for the early-growth stage ($P<0.05$) than other stages. However, a growth stage × year interaction existed for this variable ($P<0.05$). When examined by growth stage within year, soluble N content decreased numerically with plant maturity in 1992, but increased slightly with plant maturity in 1990 and 1991. Lower ADIN concentration was observed for the early growth as well ($P<0.05$), which would be expected if ADIN is associated with plant maturity. Also, ADIN concentration was greatest for 1990, intermediate for 1991 and least for 1992 ($P<0.05$). Insoluble N concentration exhibited a similar pattern to N, declining with maturity ($P<0.05$) and less in 1992 than other years ($P<0.05$). Insoluble available N concentration (insoluble N minus ADIN) decreased ($P<0.05$) with advancing maturity (24·6, 15·3, 14·0 and 12·3 g kg^{-1} DM). Insoluble available N concentration was less for 1992 than for the other years ($P<0.05$). All nitrogenous component concentrations (g kg^{-1} DM) were lower during 1992, and spring precipitation was greatest in 1992 (Figure 1). In contrast, Gonzalez-Coloma *et al.* (1994) reported higher soluble protein content in *Larrea tridentata* when supplemented with water.

Total N, soluble N and insoluble N concentration per unit of DM all decreased with maturity, probably due to dilution by structural components. When expressed on a total N basis, patterns were generally the same as on a DM basis: ADIN concentration increased and insoluble N and insoluble available N concentrations decreased with plant maturity and were lower for 1992. However, soluble N per unit of total N increased ($P<0.05$) with advancing season (361, 416, 459 and 482 g kg^{-1} N) and was greater ($P<0.05$) in 1992 (460 g kg^{-1} N) than 1990 (406 g kg^{-1} N) or 1991 (423 g kg^{-1} N). Thus, a greater proportion of the insoluble N in tarbush was present in the early growth stage and in the driest years. Silva Colomer and Passera (1990) evaluated six *Atriplex* species and observed soluble protein concentrations in these shrubs to be greatest during winter.

The fibrous fraction increased with maturity, as expected (Van Soest, 1982), with NDF, ADF and ADL concentrations all less for the early growth stage ($P<0.05$). The other growth stages did not differ in NDF or ADF content ($P>0.05$), but ADL concentration was less for the mid-point growth stage than for late or curtailed growth stages ($P<0.05$). As plants mature, they generally decrease in nutritive value, and changes in chemical composition are partly attributed to lignification (Van Soest, 1982). All three fibre components (NDF, ADF and ADL) were least for 1992 ($P<0.05$), and NDF and ADF contents were greater for 1991 than 1990, whereas ADL concentration did not differ ($P>0.05$) for these 2 years. Gross energy content was not affected by maturity, but was lower for 1992 than the other 2 years ($P<0.05$). It is not clear why energy content would differ, particularly as EE content was numerically greatest in 1992, with 1991 being lower in EE than the other 2 years ($P<0.05$). Ether extract concentration was greater for the early growth stage ($P<0.05$). However, a growth stage × year interaction was observed; the EE content of tarbush decreased numerically with maturity in 1990 and 1991, but increased with maturity in 1992.

Calcium concentration increased with maturity ($P<0.05$), whereas phosphorus concentration exhibited an inverse pattern ($P<0.05$). Calcium concentration was greatest for 1990, with 1991 greater than 1992 ($P<0.05$). Total mineral concentration generally declines with maturity, as do Ca, P and K concentrations (Church, 1977). Phosphorus is generally associated with active growth and P content declines as forages approach dormancy (Holechek *et al.*, 1989). Phosphorus concentration was greatest in 1990 ($P<0.05$), with no difference for 1991 and 1992. Sodium concentration was measured only in 1990, and was quite low in tarbush. Potassium

content was measured only in 1990 and 1991, and concentrations were not different ($P > 0.05$) between years.

Although condensed tannin concentration was not different among growth stages, a tendency ($P < 0.10$) for differences was detected. Condensed tannin concentration increased with advancing season. Condensed tannin levels were greatest in 1992, intermediate for 1991 and least during 1990 ($P < 0.05$). Condensed tannin concentration was quite low compared with total phenolic concentration; thus, hydrolysable tannins or other phenolic compounds (such as flavonoids or 4-hydroxyacetophenone derivatives) probably contributed to this substantial fraction of tarbush (60–100 g kg^{-1} DM). In contrast to our hypothesis, total phenolic concentration was least for the early growth stage ($P < 0.05$), and not different among the other growth stages. Total phenolic concentration was least for 1991, intermediate for 1990 and greatest for 1992 ($P < 0.05$). Anti-nutritional factors were generally more concentrated in the wet year. Decreased nutritive value with advancing maturity is typical of most forages (Van Soest, 1982) and anti-nutritional factors often increase with season. Many phenolic monomers and compounds are associated with lignin accumulation, and certain phenolics are involved in formation of lignin–carbohydrate complexes (Cornu *et al.*, 1994), possibly explaining the increase in total phenolic concentration as tarbush matured.

Low molecular weight, mobile and bioactive secondary compounds are often associated with immature leaves, especially during the first few weeks when defence is critical (Meyer and Karasov, 1991; Halls *et al.*, 1994; Takabayashi *et al.*, 1994), whereas condensed tannins often accumulate with maturity (Bryant *et al.*, 1991; Shure and Wilson, 1993). These factors are counter to our observations that total phenolic concentration increased with maturity. Possibly, other non-phenolic (e.g. terpenoid, alkaloid) compounds defend tarbush from herbivory during early growth stages.

Forced use of tarbush with high-density multi-species grazing (cattle, sheep and goats) for short time periods resulted in a high percentage of tarbush in ruminant diets (D.M. Anderson, personal communication); thus, tarbush does have a potential as a forage under certain conditions. From a management standpoint, early use by livestock would be preferred in terms of nutrient availability (N, P and IVDMD), and would eliminate possible encounters with flowering tarbush and associated toxicities. Also, concentrations of many low-quality components (ADIN, NDF, ADF, ADL and total phenolics) are greater later in the season. However, earlier in the year, elevated EE content (not true for 1992) may indicate more resin and volatile compounds that might deter intake. Companion studies at this location have shown that tarbush leaves can be consumed by lambs for up to 28 d at 300 g kg^{-1} diet DM (King *et al.*, 1996) and 90 d at 150 g kg^{-1} diet DM (Fredrickson *et al.*, 1994) without reducing DM intake or causing apparent toxicity (certain serum enzymes were elevated on tarbush diets). However, feeding tarbush for 120 d resulted in liver damage (diffuse apoptosis) and possibly muscle damage in some lambs. Furthermore, tarbush flowering is sporadic with respect to timing, location, year and proportion of plants flowering, which also contributes to the variability in optimal time of use. Casual observations indicate that sheep frequently browse tarbush during the winter. Tarbush chemistry fluctuations among years appear to be substantial and could affect management decisions. Whether rainfall patterns or other abiotic or biotic factors (particularly insect herbivory) affect these fluctuations is not clear.

In general, tarbush compares favourably with alfalfa in nearly every nutrient category measured (NRC, 1984) and is of higher quality (more N, less fibre) than two shrubs considered to be forage supplements on rangelands during periods of low forage quality: sagebrush (*Artemisia* species) and saltbush (*Atriplex nuttallii*; NRC 1984). Tarbush has greater nutritional value and substantially lower condensed tannin concentration than mountain mahogany (*Cercocarpus montanus*; Nuñez-Hernandez *et al.*, 1991). Tarbush also compares favourably in terms of N and fibre content with six *Atriplex* species (Silva Colomer and Passera, 1990), as well as mesquite (*Prosopis glandulosa*), four-wing saltbush (*Atriplex canescens*), creosotebush (*Larrea tridentatas*), oak (*Quercus grisea*) and juniper (*Juniperus monosperma*; Holechek *et al.*, 1990). Mesquite, creosotebush and juniper contain substantially more condensed tannins than tarbush, whereas oak and four-wing saltbush are similar (Holechek *et al.*, 1990). Mesquite and creosotebush are similar to tarbush in total phenolic content, and oak and juniper contain only slightly fewer total phenolics than tarbush. It remains to be seen whether over-riding intake deterrents in tarbush would be beneficial to livestock, as indications are that phenolics are fairly abundant in tarbush. Optimum percentage of diet and frequency and length of time of consumption could hinge on tolerance to anti-nutritional factors.

Companion digestion and grazing studies at this location have shown extensive variation in animal preference for tarbush and palatability of individual tarbush plants (Estell *et al.*, 1994; King *et al.*, 1996). We hope to capitalize on this variability to gain insight into diet selection as it relates to secondary chemistry. Practical advantages, in addition to a forage high in N, would be the potential for biological control of an invasive shrub species.

Tarbush appears to be reasonably high in quality and generally low in anti-nutritional factors (except total phenolics), supporting its use as a model for studying plant–animal interactions in desert shrubs. However, tarbush contains more N than most desert shrubs. The abundance of total phenolics may be involved in the low acceptance of tarbush by livestock, and these phenolics need to be further characterized. If the nature of these phenolics is such that a non-reversible disturbance is encountered, animals could be compromised if detoxification and clearance capabilities are exceeded.

Conclusions

The N content of tarbush was relatively high. Fibrous components, ADL, ADIN and condensed tannin concentrations were all generally low, whereas total phenolic content was quite high. Calcium concentration increased whereas P content decreased with maturity. Nutrients, IVDMD and anti-nutritional variables typically followed patterns normally associated with changes in maturity; i.e. N, IVDMD and P values were greater for early growth-stage tarbush leaves, and ADIN, NDF, ADF, ADL and total phenolics were greater later in the season. Because condensed tannin concentration was low compared with total phenolics, hydrolysable tannins or other phenolic compounds constitute much of this substantial fraction. Soluble N and insoluble N concentration in the DM both decreased with maturity, whereas insoluble N decreased and soluble N increased with advancing season when expressed on a total N basis. The interval for optimal use of tarbush is fairly large and somewhat variable, both across growth stage and from year to year. Tarbush has several characteristics of a suitable plant model for studying plant–animal interactions in desert shrubs.

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