Goats and deer do not use terpenoids to select or avoid browsing on *Juniperus pinchotii* Sudw. trees

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ABSTRACT

A comparison between heavily browsed and non-browsed *Juniperus pinchotii* trees revealed that, in contrast to the recent *J. ashei* study (Adams et al., 2013), the percentage of total volatile leaf oil yields were not significantly different ($P > 0.05$) between non-browsed trees (1.08%, DM-basis) and browsed trees (0.94%, DM basis). Only one terpene in the mg/g data, α-pinene, was significantly different ($P \leq 0.05$) between browsed and non-browsed trees. Only citronellol was significantly different ($P \leq 0.05$) in the percent total oil data. Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were highly significantly different ($P \leq 0.05$) between browsed and non-browsed samples. In contrast, no significant differences ($P > 0.05$) were found for crude protein (CP), extractable condensed tannins (ECT), protein-bound tannins (PCT), total % condensed tannins (TCT), and *in vitro* dry matter digestibility (IVDMD). A comprehensive analysis of the leaf oil of *J. pinchotii* is reported. Published on-line www.phytologia.org *Phytologia 95(3): 238-245 (August 1, 2013).*

KEY WORDS: *Juniperus pinchotii*, goats, deer, browsing, terpenes, fiber, condensed tannins, digestibility, diet selection.

Recently, we reported on differences between browsed and non-browsed trees of *Juniperus ashei* Buch. (Adams et. al., 2013). In that study, we found that the yields of volatile leaf oil to be the major factor associated with browsed and non-browsed samples, with browsed trees being much lower (2.18% DM) than non-browsed trees (3.47% DM). Associated with oil yields were 12 terpenoids, all with larger mg/g in the non-browsed trees. However, the profile of terpene composition was not very effected, as only 3 terpenoids were significantly different ($P \leq 0.05$); as a percent of total oil, two of these declined in the non-browsed trees (p-cymene, 2.66, 2.18%, and sempervirol, 1.66, 1.03%). Limonene increased in the non-browsed trees from 8.31 to 10.41%. It appears that selection was based mostly on the total oil yield rather than individual oil components. Of the other variables investigated: extractable condensed tannins (ECT); protein bound CT (PCT); fiber bound CT; percent total condensed tannin (TCT); percent crude protein (CP); % neutral detergent fiber (NDF); acid detergent fiber (ADF); *in vitro* dry matter digestibility (IVDMD), only PCT and IVDMD showed significant differences.

The genus *Juniperus* contains species with a large array of terpenoids and other secondary compounds (Adams, 2011). It is common to find trees that have been browsed by deer (as well as domestic goats and sheep). Schwartz et al. (1980a) observed browsing by deer and then tested confined deer in feeding trials using foliage of *J. deppeana*, *J. monosperma* and *J. scopulorum*. They found that

the consumption of juniper foliage varied inversely with the total oil yields among these three species. Schwartz et al. (1980a) also found that the levels of oxygenated terpenoids were a greater feeding deterrent than the amount of hydrocarbon terpenoids. Recently, Marko et al. (2008) reported that leaf essential oil concentrations were lowest in *J. communis* when heavily browsed by sheep and rabbits, and highest in non-browsed plants.

Juniper foliage intake by goats is limited by the presence of monoterpenes (Riddle et al., 1996; Pritz et al., 1997). Monoterpenes have a clearly defined ecological defensive role as feeding deterrents in a variety of mammals and insects (Gershenzon et al., 1992). Negative post-ingestive consequences experienced by large ungulates following consumption of high levels of monoterpenes include rumen microbial inhibition (Oh et al., 1967; Schwartz et al. 1980b), hepatic pathogenesis (Straka, 1993; Bisson et al., 2001;Pritz et al., 1997), and feeding cessation (Dziba et al., 2006). Furthermore, the presence of condensed tannins (CT) in plant leaves has been associated with protection against herbivory (Feeny, 1976) by inducing post-ingestive feedback (Provenza, 1995). The strength or direction of this feedback depends on individual plant-herbivore characteristics and, therefore, requires individual situation-testing (Stamp, 2003). The objective of the present study was to correlate plant chemical and nutritive values in *J. pinchotii* leaves with the incidence of browsing by goats (and to a much lesser extent, deer).

MATERIALS AND METHODS

Study Site - The study was conducted at the Texas AgriLife Research Station, Sonora, located on the southwestern edge of the Edwards Plateau (30º 15.747' N, 100º 34.164' W, 707 m). Annual precipitation averages approximately 600 mm; it is bimodal, with largest amounts occurring in spring and fall. Soils in the study pasture are Tarrant silty clays; soil depth overlaying a fractured limestone substrate ranges from about 10 to 450 mm. Dominant herbaceous species include *Hilaria belangeri* (Steud.) Nash and *Bouteloua curtipendula* (Michx.) Torr. Dominant woody species include *Quercus fusiformis* Mill., *Q. pungens* Liebm. var. *vaseyana*, *J. ashei* and *J. pinchotii*. Fires within the area have not occurred for at least 100 years before data collection. From 1983 to 1993, stocking rates in the study pasture were maintained at a moderate level (i.e., 11.3 ha/animal). From 1994, stocking rates in the study pasture have varied from 18 to 10.4 ha/animal. A combination of cattle, sheep, and goats were grazed on the pasture until 2003 when all cattle were removed from the study area. The area is currently grazed by goats and deer.

Plant material - Ten browsed *J. pinchotii* trees were randomly selected along a serpentine transect line of approximately 200 m. Trees showing severe browsing (e.g., all lower branches up to approximately 1 m were essentially defoliated) and having new, immature growth on the browsed branches were sampled as "browsed trees". This corresponds to the 'heavily browsed' category of Marko et al. (2008, Fig. 2, right). Ten trees with no evidence of browsing were sampled along the transect as 'non-browsed' trees, corresponding to the 'non-browsed' category of Marko et al. (2008, Fig. 2, left). Trees with other levels of browsing were excluded from sampling. *Juniperus pinchotii* has two kinds of leaves: whip- (decurrent) and scale-like leaves that remain functional for 4-6 years. The whip leaves are only found on the new growth (leaders). At the study site, due to drought, very few whip-leaves were observed and the occasional branch with whip-leaves was excluded from sampling, as Adams and Hagerman (1976) found significant differences in the oils from whip- and scale-like leaves of *Juniperus*. No samples were taken from the branches with new, immature whip-leaves. Careful attention was given to sample at least 1 m above the browse line. As the browse line was up to 1 m above the ground, samples were taken at 2 to 2.5 m heights from both non-browsed and browsed trees from the south side. All trees were similar in size and height (3 to 6 m). Foliage was collected on Nov. 5, 2012. Specimens collected: *Juniperus pinchotii,* browsed trees (*Adams 13613-13622*) and non-browsed trees: (*Adams 13623-13632*); herbarium vouchers are deposited in the herbarium, Baylor University (BAYLU).

Essential oils analysis - A portion (200 g FW) of the fresh foliage was kept cool (20ºC) and in the dark, then, within 24 hr, exhaustively steam-distilled for 24 h using a modified circulatory Clevenger-type apparatus (Adams, 1991). Oil samples were concentrated (diethyl ether trap-removed) with nitrogen and stored at -20ºC until analyzed. Steam distilled leaves were oven dried to a constant weight (48 hr, 100ºC) for the determination of oil yield as [oil wt./(oil wt. + oven dried extracted foliage wt.)]. The extracted oils were analyzed on a HP5971 MSD mass spectrometer: 0.2 ul of a 10% solution (in diethyl ether) oil injected, split, 1:10, temperature programmed, linear, 60º - 246ºC at 3ºC/min. (62 mins.), carrier gas He, flow 34.96 cm/sec or 1.02 ml/min, injector 220ºC, detector 240ºC, scan time 1/sec, directly coupled to a HP 5890 gas chromatograph, using a J & W DB-5, 0.26 mm x 30 m, 0.25-micron coating thickness, fused silica capillary column (see Adams, 2007, p. 4, for detailed operating conditions). Identifications were made by searches of our volatile oil library (Adams, 2007) using HP Chemstation library search routines, coupled with retention time data of authentic reference compounds. Quantification was by flame ionization detector on an HP 5890 gas chromatograph operated under the same conditions as the GCMS (above) using the HP Chemstation software.

Condensed tannin analysis - Condensed tannins in air dried (48 hr, 42ºC) leaves were assayed for ECT, PCT, and FCT fractions by methods described by Terrill et al. (1992). Samples were oven-dried and standards prepared from Ashe juniper as recommended by Wolfe et al. (2008).

Crude protein, fiber and in vitro dry matter digestibility analyses - A portion of each foliage sample was air dried (48 hr, 55ºC), ground in a Wiley Mill (Arthur H. Thomas Co., Philadelphia, PA) to pass a 1-mm screen, and analyzed for N (AOAC, 2006); CP was calculated as 6.25 × N. An additional 0.35 g of the ground sample material was placed into separate F57 digestion bags and analyzed for 48-hr true IVDMD using an Ankom Daisy II incubator (Ankom Technol. Corp., Fairport, NY). Bags were placed into an incubation jar containing 400 mL of goat rumen fluid (donors fed Tifton 85 hay) and 1,600 mL of McDougal's buffer solution (1.064 g urea L^{-1}). After anaerobic incubation at 39ºC, all bags were gently rinsed under cold water and washed by hand until water was clear. Bags were subjected to the neutral detergent fiber procedure according to Van Soest et al. (1991), modified for an Ankom 2000 Fiber Analyzer (Ankom Technol. Corp., Fairport, NY) without correcting for residual ash and using α-amylase and Na sulfite. Bags were then rinsed in acetone and dried at 55ºC in a forced-air oven for 48 hr and weighed.

Statistical analyses - Terpenoids (as percentage of total oil and as mg per g dry foliage weight) compared among the samples by ANOVA and SNK (Student-Newman-Keuls) analyses as described by Steele and Torrie (1960). Gower or Manhattan metric (Gower, 1971; Adams, 1975) were computed among all populations using character weighting of F-1 (F from ANOVA). Principal Coordinate Ordination (PCO) was performed to examine the patterns of association among browsed and non-browsed trees (formulation of Gower, 1966 and Veldman, 1967). Differences were considered significant at $P \leq 0.05$, unless otherwise stated.

RESULTS AND DISCUSSION

A comprehensive analysis of the leaf oil of *J. pinchotii* is shown in Table 1. In contrast to a recent *J. ashei* study (Adams et al., 2013), the percentages of total volatile leaf oil yields were not significantly different between non-browsed trees (1.08%, DM-basis) and browsed trees (0.94%, DM-basis; Table 1). This result is also in contrast to the findings of Marko et al. (2008) who found that sheep and rabbit-browsed *J. communis* trees in Hungary had lower total volatile leaf oils than non-browsed trees. Only one terpene in the mg/g data, α-pinene, was significantly different between browsed and non-browsed (Table 1). Likewise, only citronellol was significantly different in the percent total oil data (Table 1). Although no difference in total oils was observed, physiological stress factors due to prolonged drought period may have influenced grazing preference at the tree sites sampled. Also, it is possible that

the time when the trees were browsed, versus when samples were collected, may have limited the ability to accurately detect differences in total oil and terpene composition.

Neutral detergent fiber (NDF) was highly significantly different between browsed and non-browsed samples (Table 1). Acid detergent fiber (ADF) was also significantly likewise different between samples (Table 1). In contrast, no significant differences were found (Table 1) for CP, ECT, PCT, TCT, and IVDMD.

These data, on contrasting browsed and non-browsed *J. pinchotii*, present a different picture of juniper browsing than found in *J. ashei*. However, these two junipers present quite different challenges to goats (and deer). *Juniperus ashei* was shown (Adams et al., 2013) to have two kinds of leaf oil levels in the population: trees with low amounts of oil (2.15%) and trees with 62% greater oil (3.47%). In contrast, oil levels in *J. pinchotii* were not significantly different. Thus, selection by goats or deer for low-oil trees was not possible. In addition, the oil compositions were uniform in this *J. pinchotii* population, so browsers did not select for trees particularly low (or high) in some terpene.

The differences found in fiber concentration (NDF, ADF) may not indicate that goats are selecting for greater fiber. They may be selecting for some mineral or chemical with a strong taste or odor. This unknown factor may be correlated with fiber concentration. Of course, it is possible that goats were selecting from more tender foliage and that was correlated with increased yields of fiber.

To examine the pattern of browsed and non-browsed trees, Principle Coordinate Ordination (PCO) was performed on several sets of data. The PCO using all 36 characters (Fig. 1) shows a random intermixing of browsed and non-browsed trees. Utilizing only the 25 terpenoids (including oil yield) reveals a somewhat different pattern (Fig. 2), with two trees having rather distinct terpenes, but the browsed and non-browsed are still intermingled. A tendency for more of the browsed trees to register to the left of the ordination, based on 25 terpenoids (Fig. 2), is apparent.

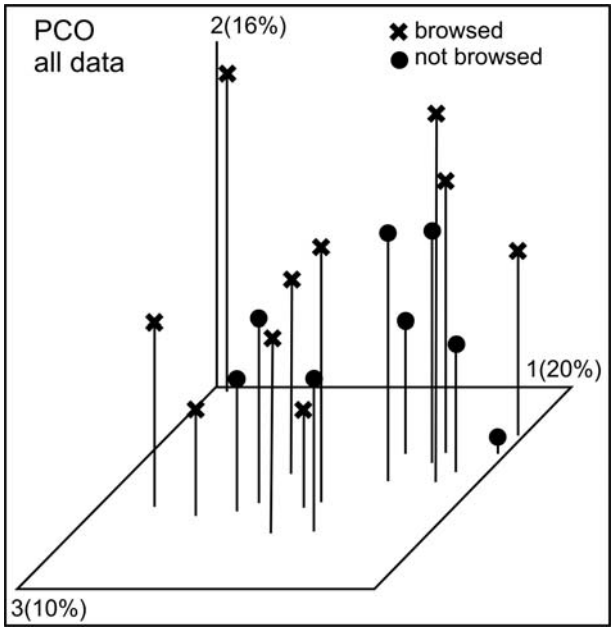

Figure 1. Principle Coordinate Ordination (PCO) based on all data.

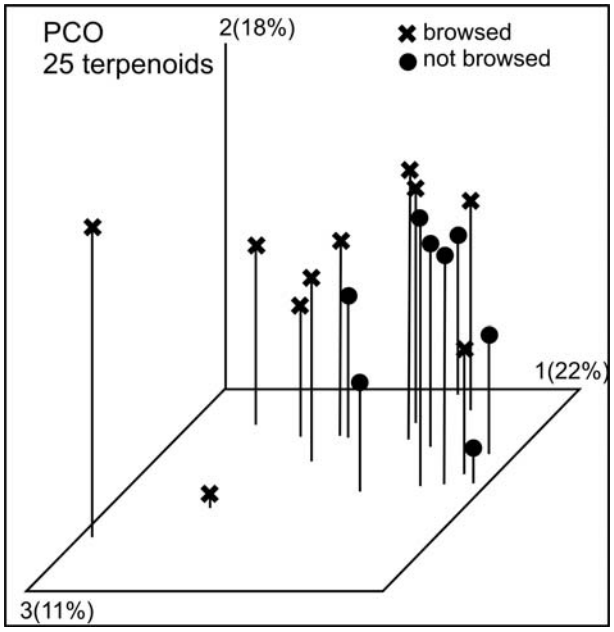

Figure 2. PCO based on only the terpenoids (25).

PCO based on only the 7 fiber, tannin, protein and digestibility characters (Fig. 3) fails to show any pattern of clustering by browsed/ non-browsed groups.

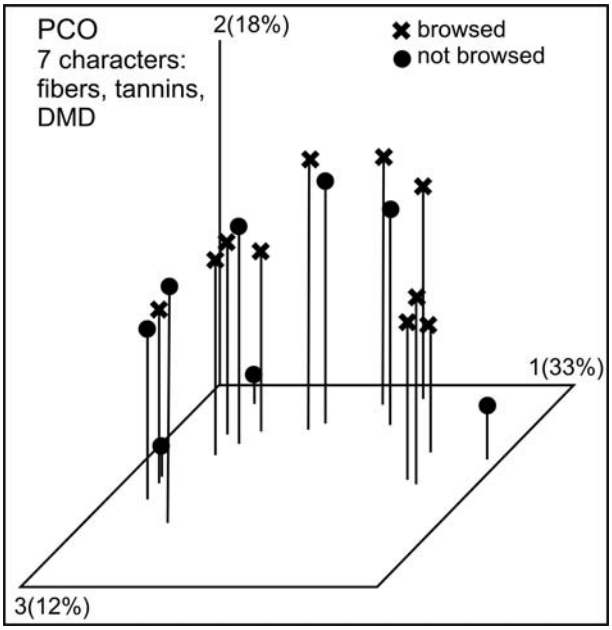

Figure 3. Principle Coordinate Ordination (PCO) based on neutral detergent fiber, acid detergent fiber, crude protein, extractible condensed tannins, protein-bound condensed tannins, total condensed tannins and in vitro dry matter disappearance.

Finally, it should be noted that goats do not browse *J. pinchotii* as readily as *J. ashei* and since goats are sociable animals that congregate under trees that may be marked by odors (urine, etc.) it may be that initial browsing is nothing more than taking a bite from the tree and this is followed by other goats until a browsing pattern is established; thence a particular the tree gets occasional heavy browsing by chance rather than design.

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Table 1. Comparison of leaf oils obtained from browsed and not browsed trees of *Juniperus pinchotii.* brow% = browsed, % total oil data; nbrow% = not browsed, % total oil data; brow mg/g = browsed, mg/g DW data; nbrow mg= not browsed, mg/g DW data; F sig = F ratio and significance, $P \leq 0.05$ = *; $P \leq 0.01$ = **, ns = non significant, nt = not tested. Factors with significant differences are in boldface.

	Factor tested	browsed %	nbrowsed %	F sig	brow mg/g	nbrow mg/g	F sig
	oil yields (% ODW; mg/g ODW)	0.941	1.083	3.71 ns	9.41	10.08	3.68 ns
	neutral detergent fiber(NDF)	**40.05**	**36.86**	**8.61 ****			
	acid detergent fiber(ADF)	**28.17**	**26.37**	**5.66 ***			
	crude protein	7.44	7.31	0.35 ns			
	extractable condensed tannins	6.84	6.30	0.79 ns			
	protein bound tannins	3.40	3.06	1.06 ns			
	total % condensed tannins	10.24	9.35	1.11 ns			
	in vitro dry matter digestibility	64.92	64.33	0.25 ns			
KI	Compound	brow%	nbrow%	F sig	brow mg/g	nbrow mg/g	F sig
921	tricyclene	0.30	0.33	nt	0.03	0.04	nt
924	α-thujene	0.84	0.96	0.23 ns	0.08	0.10	ns
932	**α-pinene**	**1.22**	**1.31**	**0.01 ns**	**0.11**	**0.14**	**4.76 ***
946	camphene	0.45	0.46	nt	0.05	0.05	nt
969	sabinene	24.18	25.42	0.36 ns	2.27	2.75	2.50 ns
974	β-pinene	0.12	0.11	nt	0.01	0.01	nt
988	myrcene	3.07	2.99	0.15 ns	0.29	0.32	2.45 ns
1002	α-phellandrene	0.10	0.10	nt	0.01	0.01	nt
1008	δ-3-carene	0.11	0.18	nt	0.01	0.02	nt
1014	α-terpinene	1.92	1.99	0.01 ns	0.18	0.22	2.52 ns
1020	p-cymene	0.16	0.21	nt	0.02	0.02	nt
1024	limonene	3.21	3.10	0.17 ns	0.30	0.33	1.01 ns
1025	β-phellandrene	2.20	2.11	0.12 ns	0.21	0.23	0.71 ns
1054	γ-terpinene	3.21	3.24	0.67 ns	0.30	0.35	2.36 ns
1065	cis-sabinene hydrate	1.45	1.49	0.17 ns	0.14	0.16	3.76 ns
1086	terpinolene	1.44	1.38	0.78 ns	0.14	0.15	2.59 ns
1098	trans-sabinene hydrate	1.03	1.15	0.97 ns	0.09	0.12	3.79 ns
1099	linalool	0.61	0.67	0.01 ns	0.06	0.07	1.37 ns
1118	cis-p-menth-2-en-1-ol	0.56	0.49	0.39 ns	0.06	0.05	3.05 ns
1141	camphor	24.49	25.36	0.07 ns	2.30	2.74	1.53 ns
1145	camphene hydrate	0.69	0.73	0.21 ns	0.07	0.07	1.36 ns
1148	citronellal	0.92	0.77	0.54 ns	0.09	0.08	0.94 ns
1165	borneol	0.66	0.74	0.14 ns	0.06	0.08	0.96 ns
1174	terpinen-4-ol	7.38	7.66	0.29 ns	0.70	0.82	4.14 ns
1186	α-terpineol	0.36	0.41	nt	0.04	0.04	nt
1195	cis-piperitol	0.16	0.11	nt	0.02	0.01	nt
1207	trans-piperitol	0.21	0.22	nt	0.02	0.02	nt
1219	coahuilensol, me-ether	0.10	0.10	nt	0.01	0.01	nt
1223	**citronellol**	**4.78**	**3.14**	**5.22 ***	**0.45**	**0.34**	**3.20 ns**
1274	pregeijerene B	0.14	0.13	nt	0.01	0.01	nt
1284	bornyl acetate	1.68	1.69	0.01 ns	0.16	0.18	0.26 ns
1289	thymol	0.11	0.10	nt	0.01	0.01	nt
1389	β-elemene	t	t	nt	<.01	<.01	nt
1451	trans-muurola-3,5-diene	0.10	0.17	nt	0.01	0.02	nt
1475	trans-cadina-1(6),4-diene	0.08	0.11	nt	0.01	0.01	nt
1493	trans-muurola-4,5-diene	0.23	0.40	nt	0.02	0.04	nt
1500	α-muurolene	t	t	nt	<.01	<.01	nt
1514	cubebol	0.27	0.42	nt	0.03	0.04	nt
1522	δ-cadinene	0.11	0.21	nt	0.01	0.02	nt
1528	zonarene	t	t	nt	<.01	<.01	nt
1548	elemol	5.81	3.97	ns	0.55	0.43	1.17 ns
1627	1-epi-cubenol	0.26	0.37	nt	0.03	0.04	nt
1630	γ-eudesmol	0.53	0.37	3.02 ns	0.05	0.04	2.36 ns

KI	Compound	brow%	nbrow%	F sig	brow mg/g	nbrow mg/g	F sig
1649	β-eudesmol	0.80	0.60	2.01 ns	0.08	0.06	0.89 ns
1652	α-eudesmol + α-cadinol	0.80	0.59	2.24 ns	0.08	0.06	0.86 ns
1670	bulnesol	0.32	0.23	nt	0.03	0.02	nt
1792	8-α-acetoxyelemol	t	t	nt	<.01	<.01	nt
1987	manoyl oxide	0.16	0.23	nt	0.01	0.02	nt
2055	abietatriene	t	t	nt	<.01	<.01	nt
2087	abietadiene	t	t	nt	<.01	<.01	nt
2298	4-epi-abietal	0.13	0.20	nt	0.01	0.02	nt