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Increasing Shrub Use by Livestock in a World with Less Grass

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Abstract

Much of the world's rangeland is dominated by woody species. Competing land uses and continued encroachment of woody species into non–woody-dominated rangelands have reduced grasslands in many parts of the world. Land use conversions to fuel and feed global populations, especially the increasing number of middle class people seeking broader, meat-based diets, will certainly continue. Halting and/or reversing further encroachment of woody species into grasslands is slow, expensive, and in some cases not possible. Yet, global livestock numbers continue to increase to meet the growing demand for red meat and other livestock products. How do we reconcile a world with less grass and the concurrent increased demand for forages to feed livestock? Strategies and mechanisms are needed to safely enhance shrub use by ruminants in order to capitalize on a presently underutilized forage resource. A number of approaches are presently available (e.g., choosing appropriate species and breeds, providing dietary supplements and additives, behavior modification, genetic selection) to increase shrub consumption, and new technologies such as biochemical markers of shrub intake need to continue to be identified and developed. Such strategies could provide important means for rural communities to adapt to changing land cover and climate.

Resumen

La mayor parte de los pastizales del mundo están dominados por especies leñosas. El cambio de uso de suelo y la continua expansión de especies leñosas dentro de pastizales dominados por no-leñosas ha reducido los pastizales en muchas partes del mundo. La conversión de tierras para abastecer y alimentar la población global, especialmente con el aumento en el número de personas de clase media que buscan dietas basadas en carne ciertamente continuara. El vacilante y/o posible re vertimiento de la invasión de especies leñosas en los pastizales es lento, caro y en algunos casos imposible. De hecho, el número global de ganado continuara creciendo para cubrir la demanda de carne roja y otros productos derivados del ganado. ¿Cómo podemos conciliar a un mundo con menos pasto y la creciente demanda de forrajes para alimentar el ganado? Se necesitan estrategias y mecanismos que de manera segura promuevan el uso de arbustos por los rumiantes con el fin de capitalizar los recursos forrajeros subutilizados actualmente. Hay disponibilidad de puntos de vista (ejm. Seleccionar razas y especies apropiadas, proveer suplementos dietéticos y aditivos, modificar el comportamiento, selección genética) para aumentar el consumo de arbustos y nuevas tecnológicas tales como los marcadores bioquímicos en consumo de arbustos que se necesita continuar en la identificación y desarrollo de estos. Estas estratégicas pueden ofrecer importantes medios en las comunidades rurales para adaptar en la cambiante cobertura del suelo y el clima.

Key Words: animal behavior, cattle, genetics, goats, plant secondary metabolites, sheep

INTRODUCTION

Approximately 50% of the world's land surface is grazed by domestic livestock (Holechek et al. 2011) and woody plants are a significant component of many of these areas (Fig. 1) and play an important role in ecosystem function. These rangelands comprise a diverse group of ecosystems ranging from wooded grasslands to desert scrub, but all contain woody plants that are unused or underused by livestock. Grazing-based livestock production occurs mainly on land traditionally viewed as poorly suited to crop production, mostly in arid and semiarid regions (Steinfeld et al. 2006). About a third of the ruminants worldwide in 2003 (approximately 1.5 billion cattle and buffaloes and approximately 1.8 billion sheep and goats; Food and Agriculture Organization of the United Nations [FAO] 2011) were located in grazing-based production systems. These systems support 406 million cattle and buffaloes and 590 million sheep and goats, with 342 and 405 million, respectively, of these animals in developing countries (Steinfeld et al. 2006).

Grasslands are in decline (a trend expected to continue) for a number of reasons (e.g., competing land uses, urban sprawl, invasive species), though two dominant factors are conversion to cropland and woody plant encroachment (FAO 2003). Cereal production is anticipated to increase by approximately a billion tons (approximately 1.3% annually globally; approximately 1.5% in developing countries) by 2030 and oil crop production is projected to increase by approximately 2.5% annually (FAO 2003). Approximately 20% of the increased crop production in developing countries (120 million ha) is projected to occur via increased arable land cover (FAO 2003). Extensive rangelands previously viewed as unsuited to cultivation have been and are continually being converted into intensive agronomic systems for fuel, food, and fiber production to meet increasing demands, especially given escalating

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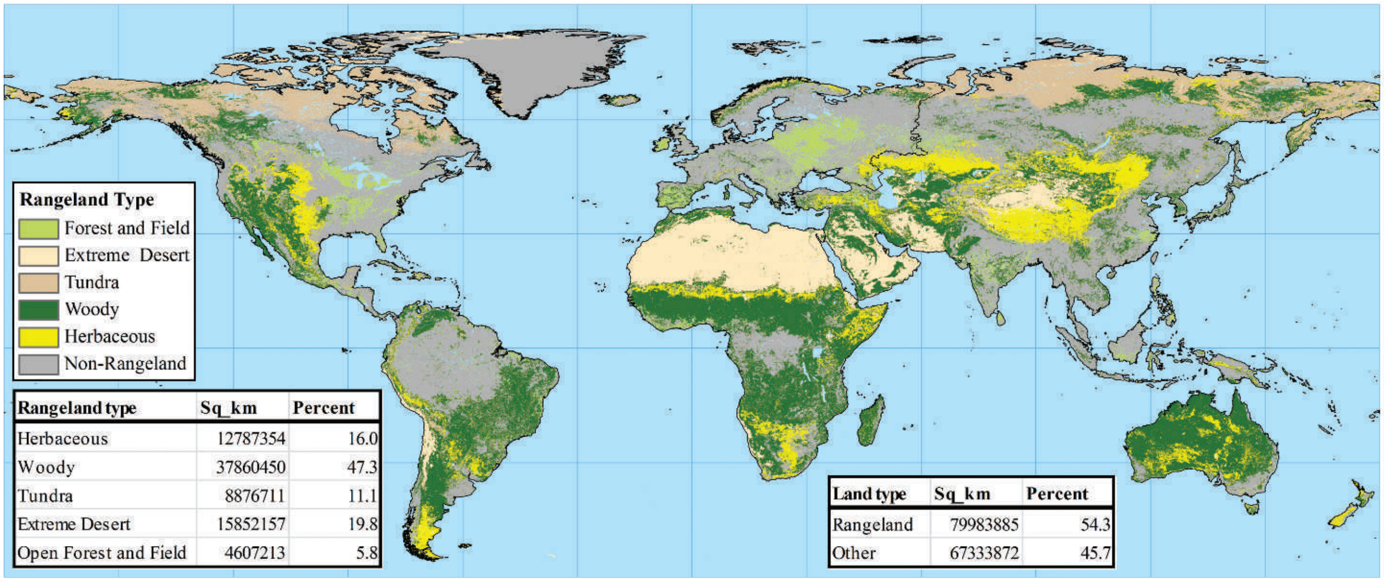

Rangeland type	Sq_km	Percent
Herbaceous	12787354	16.0
Woody	37860450	47.3
Tundra	8876711	11.1
Extreme Desert	15852157	19.8
Open Forest and Field	4607213	5.8

Land type	Sq_km	Percent
Rangeland	79983885	54.3
Other	67333872	45.7

Figure 1. Global rangeland distribution based on an assimilation of 72 land cover classes into one of five rangeland types or "other" (US Geological Survey 2008).

commodity prices around the world (Herrick et al. 2012 [this issue]). Woody plant expansion will also likely continue based on past trends and future projections (Hughes 2003; Van Auken 2009). An increase in woody species dominance is particularly evident in arid and semiarid ecosystems (Asner et al. 2004). A host of factors contribute to shrub encroachment, including their resistance to long-term drought, their resilience with respect to overgrazing (past and present), the reduction or outright elimination of prescribed burning, shrub tolerance of climatic extremes, seed dispersal rates, ability to compete for soil nutrients, changes in herbivory rates by small mammals and insects, changes in natural fire cycles, invasion by introduced species, climate change, and increased atmospheric CO_2 (Archer 1994; Roques et al. 2001; Grice 2006; Morgan et al. 2007; Van Auken 2009). Restoration of degraded rangelands is a worthy goal but it is expensive and in some cases nearly impossible (Van Auken 2009). Given that CO_2 enrichment favors shrub encroachment (Morgan et al. 2007) and assuming global climate change continues along current projections (Hughes 2003), the probability of successful restoration of shrublands will likely decrease in the near future. However, recent evidence that the combined effects of increased temperature and CO_2 may favor C_4 plants (Morgan et al. 2011) could temper these projections.

Concurrent with the reduction in total grassland area, ruminants have experienced large and disproportionate shifts in both numbers and species during the past 30 yr, with increases concentrated in developing countries (Table 1; Fig. 2). Societal demand for animal protein and livestock products has increased in part because of increased population, urbanization, and improved economic status, particularly in developing countries, and this trend is expected to continue through to 2030 (FAO 2003, 2009). Growth of rural and peri-urban small-scale agriculture in areas such as sub-Saharan Africa may also partly explain the increase in small ruminant numbers (Rischkowsky et al. 2006; McDermott et al. 2010). The total number of ruminants in Africa, Asia, and South America has increased by a combined 951 million animals during the past 30 yr (Table 1). In contrast, continents composed mainly of developed countries either changed minimally or experienced a substantial decrease in animal numbers during the same 30-yr span (Table 1). Goat numbers increased on nearly every continent (Table 1), with most of the increase in Africa and Asia. Approximately 423 million goats were added to the planet during the past 30 yr (Fig. 2), which equates to a net

Table 1. Total cattle, sheep, and goat numbers by continent (in thousands), 1979 and 2009.[1]

Continent	Species	1979	2009	Change
Africa	Cattle	171 602	275 385	103 783
Africa	Sheep	176 635	294 473	117 837
Africa	Goats	137 642	298 226	160 585
Asia	Cattle	354 264	431 589	77 325
Asia	Sheep	309 287	451 299	142 013
Asia	Goats	268 238	524 846	256 608
Central America/Caribbean	Cattle	46 680	54 477	7 797
Central America/Caribbean	Sheep	7 759	11 441	3 682
Central America/Caribbean	Goats	11 598	12 963	1 365
Europe	Cattle	248 041	125 210	−122 831
Europe	Sheep	264 645	132 402	−132 243
Europe	Goats	16 791	15 916	−874
North America	Cattle	122 861	107 702	−15 159
North America	Sheep	12 809	6 575	−6 234
North America	Goats	1 380	3 099	1 719
Oceania	Cattle	35 765	38 612	2 847
Oceania	Sheep	197 754	105 139	−92 615
Oceania	Goats	272	3 604	3 333
South America	Cattle	231 857	347 247	115 390
South America	Sheep	100 423	75 938	−24 485
South America	Goats	18 940	21 090	2 150

[1] Source: FAO (2011).

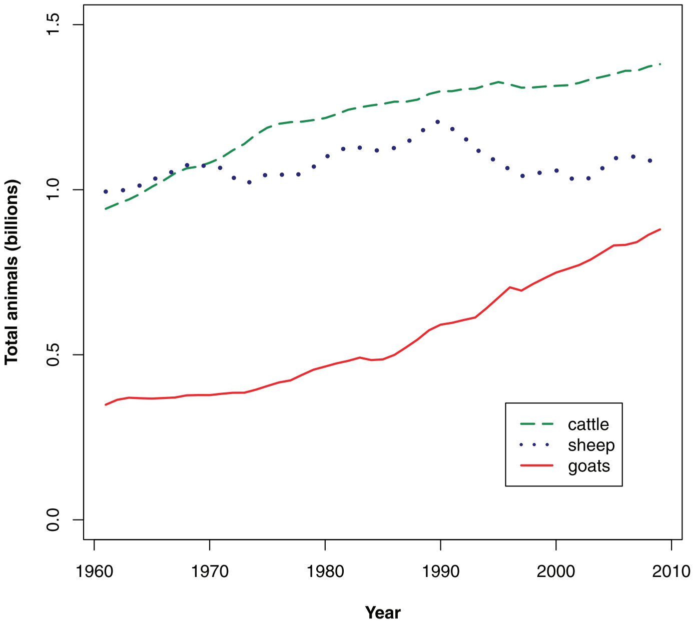

Figure 2. Global cattle, sheep, and goat numbers, 1961 to 2009 (FAO 2011).

increase of nearly 1.2 million goats per month. Cattle production is projected to increase by >1% annually worldwide (>2% in developing countries), while sheep production is projected to increase by approximately 2% annually worldwide and slightly above that in developing countries through 2030 (FAO 2003). By 2030, 1 858 million cattle and buffaloes and 2 309 million sheep and goats are projected globally (1 522 and 1 856 million, respectively, in developing countries; FAO 2003). The projected total numbers for cattle, sheep, and goats in developing countries alone in 2030 will exceed that for the entire globe at the beginning of the 21st century. We estimate that 3.2 billion tons of additional livestock forage per year will be needed to feed these additional animals, though any concomitant change in wildlife populations could attenuate this estimate slightly.

Shifting animal demographics, projected demands for red meat and crop production, and competing land uses all point to a need to increase utilization of less-preferred forages, particularly in the shrub-dominated rangelands of developing countries. Forage requirements to meet current and future animal product demands globally cannot be sustained by grass in many parts of the world and producers will continue to be forced to adapt. Certainly much of this gap will be bridged by other production systems as the trend for ruminants is toward more intensive systems and mixed farming and away from extensive grazing (FAO 2003). Another option is to enhance the use of shrubs on existing rangelands.

Shrubs generally contain ample nutrients but are well defended from herbivory via chemical (i.e., plant secondary metabolites [PSMs]) and/or physical (e.g., spinescence, morphology) traits. Most shrub species are consumed by livestock to some extent, but consumption is often low and inconsistent, depending on shrub and animal species and availability of alternative forages. For example, total intake by sheep was not affected by 5% mesquite (*Prosopis glandulosa*) in the diet but 10% and above depressed intake (Baptista and Launchbaugh 2001), whereas sheep consumed tarbush (*Flourensia cernua*) at up to 30% of the diet without adverse effects on intake or rumen function or short-term toxicity (Fredrickson et al. 1994; King et al. 1996a, 1996b). Goats in a mixed-species treatment spent about three-fold more time consuming one-seed juniper (*Juniperus monosperma*) than did sheep (Utsumi et al. 2010).

The literature is replete with studies of the role of secondary chemistry in herbivory for both domestic livestock and wildlife on every continent. Many PSMs (both individuals and classes) have been shown to affect herbivores (e.g., intake, preference, behavior, site and extent of digestion, digestion kinetics, physiology, metabolism, nitrogen retention, rumen function, fermentation, rumen microflora and microfauna). The outcomes of PSM consumption by ruminants range from negligible (or even positive in low amounts) to acutely toxic, depending on the particular PSM consumed, the amount (dose) consumed, and the other dietary components. Thus, the questions we must address in order to increase shrub utilization in global rangelands and mitigate the anticipated forage shortfall are 1) how to ameliorate metabolic compromise of PSM consumption when shrubs are consumed, and 2) how to encourage shrub consumption when more highly preferred alternative forages are available in order to avoid grassland degradation. The solutions are two-fold: 1) matching animals with landscapes, and 2) increasing individual animal performance.

MECHANISMS TO INCREASE SHRUB USE

Genetics and Selection

Animal genetics have been exploited for centuries to choose animals best adapted to a given environment and to create animals with specific traits. An obvious means to increase shrub consumption is to use existing animals (species and/or breeds) that are anatomically and physiologically suited to thrive in shrubland ecosystems. This approach may partially explain the addition of over 423 million goats worldwide in the past 30 yr (Fig. 2). Goats in general are better browsers than sheep or cattle and more able to cope with chemical and physical challenges presented by shrubs (Rogosic et al. 2006; Salem et al. 2006; Utsumi et al. 2010). For certain shrub species, this advantage has been attributed at least partly to tannin-binding salivary proteins. Alonso-Díaz et al. (2010) found evidence of the presence of inducible salivary tannin-binding proteins in goats experienced with tannin diets; however, Lamy et al. (2011) observed no proline-rich proteins in saliva of sheep or goats fed a high-tannin diet. Differences also exist among breeds in browsing ability. Spanish goats are more adept browsers than Angora goats (Pritz et al. 1997). Cattle breeds better adapted to shrublands may be more suited to browsing than traditional British and European breeds. Winder et al. (1996) reported that Brangus cows consumed more shrubs (primarily *Yucca elata* leaves) than did Angus or Hereford cows during dormant winter months. Criollo evolved in arid and semiarid regions of the Iberian Peninsula and northern Africa and have a 400+ yr history on Southwestern desert rangelands. These small-framed cattle spend less time grazing, travel farther per day and farther from water, and use a wider habitat range than traditional British breeds of cattle, all of which suggest they have less impact on a given location and are less likely to contribute to degradation than traditional British breeds (Roacho-Estrada et al. 2009; Peinetti et al. 2011). However, dietary preferences of these cattle have not been examined and evidence for their increased tendency to consume browse is anecdotal. Other opportunities may exist to identify and utilize animals with specific genetic traits that allow them to exploit shrublands.

Animal-to-animal variability exists within species, breed, and even a given herd or flock in propensity to consume various shrub species. For example, consumption of tarbush by sheep (King et al. 1996a) and Mediterranean browse species by goats (Baraza et al. 2009) varied among individuals. It may be possible to capitalize on this variation through genetic selection of animals with a specific trait for enhanced shrub consumption and PSM metabolism/detoxification (i.e., create a designer animal or herd). Snowder et al. (2001) estimated the heritability of sagebrush (*Artemisia tridentata*) intake to be 0.25–0.28 (moderately heritable) and Waldron et al. (2009) reported juniper (*Juniperus ashei* and *Juniperus pinchotii*) intake by goats to be approximately 13% heritable. Though progress would likely be slow, shrub selection has a genetic basis that might be exploited to alter a subset of a population for more efficient utilization of arid shrublands.

Physiology and Detoxification

As knowledge of processes involved in PSM metabolism continues to expand, physiological markers may be developed to identify and select for animals more willing to consume shrubs and more capable of coping with their detrimental properties. For example, PSM clearance is related to cessation and resumption of feeding in lambs dosed with 1,8-cineole (Dziba et al. 2006). If animals browse alternative plants during the elimination phase in order to decrease blood levels, mechanisms that increase clearance rate might enhance sagebrush intake (Dziba et al. 2006). Campbell et al. (2010) observed pharmacokinetic differences in genetic lines of goats previously selected for high or low juniper consumption; after dosing with terpenes to simulate 30% juniper intake, low consumers exhibited greater maximum plasma camphor concentration (five-fold greater systemic camphor exposure) than high consumers. Because circulating camphor apparently feeds back on physiological mechanisms regulating intake, it should be possible to select for tolerance to juniper terpenes using serum camphor as a screening tool (single dose, noninvasive) to identify outlier high consumers for breeding programs (Campbell et al. 2010). Thus, challenging animals with a particular PSM (or mixture) and measuring clearance might be a tool to identify individuals genetically predisposed to coping with PSMs to match with specific landscapes comprising a specific botanical composition. If clearance rates of various PSMs are reasonably inheritable, sire selection could be used to make fairly rapid progress in breeding programs. Possibly, other endocrine or metabolic markers associated with shrub intake can be identified by challenging animals with PSMs and systematically searching for biochemicals related to clearance.

Liver enzyme assays and gene expression (polymerase chain reaction, microarrays, transcript analysis) can also be used to assess detoxification capacity (Sorensen et al. 2006). If genes related to shrub intake can be identified, it may be possible to develop genetic or bio-markers to assist with selection of browsers in breeding programs. Proline-rich salivary proteins present in many browsing wildlife species allow them to bind and deactivate tannins (Robbins et al. 1987) and efflux transporter permeability proteins that decrease PSM absorption have been reported in woodrats (*Neotoma* spp.; Sorensen and Dearing 2003, 2006). Inserting genetic information into an animal to enhance salivary protein secretion or efflux transporter concentration or manipulating microbial populations or inoculating designer microbes with elevated toxin-degrading activity could improve an animal's ability to consume PSMs. Though some of these approaches are speculative and futuristic, capitalizing on unique traits of outliers of a population or alternative species may be an avenue to increase browse utilization in shrubby environments.

Supplements and Additives

A variety of management practices to enhance shrub use have been examined, many involving some form of supplementation. Nutrients are depleted (e.g., protein, minerals, and glucose) by ruminants as they process and eliminate PSMs, and supplements and additives can minimize the negative effects of PSMs and increase shrub intake (Villalba et al. 2002a; Dziba et al. 2007; Rogosic et al. 2009). Not only do PSMs dilute food energy concentration and increase cost of PSM metabolism and excretion, they also have been shown to decrease basal metabolic rate in some small mammals (Lamb et al. 2004; Mangione et al. 2004; Sorensen et al. 2005) and cause diuresis (Dearing et al. 2001, 2002). Though not studied in ruminants, it is conceivable that supplementation is needed to accommodate increased energy needs for maintenance and travel to water (Estell 2010). A high plane of nutrition (especially protein, but also energy and other nutrients) can help an animal cope with and potentially consume more PSMs because of the role of these nutrients in tannin-binding, acid/base balance, and provision of precursors for conjugation and enzyme formation for detoxification (Illius and Jessop 1996; Villalba et al. 2002b; Utsumi et al. 2009). Charcoal, alkaline treatments, and polyethylene glycol (PEG) have all been shown to decrease PSM absorption and/or increase shrub intake in ruminants (Murdiati et al. 1990; Villalba and Provenza 2001; Rogosic et al. 2008). Charcoal has been reported to adsorb terpenes and increase shrub intake (Banner et al. 2000; Rogosic et al. 2009) though results have been inconsistent (Bisson et al. 2001; Villalba et al. 2002a). The most widely studied additive for enhancing shrub use is PEG with high-tannin shrubs. In both pen and field studies, PEG has been shown to increase intake of diets or shrubs containing condensed tannins by sheep (Titus et al. 2000; Villalba et al. 2002b), goats (Decandia et al. 2000; Titus et al. 2001; Salem et al. 2006), and cattle (Landau et al. 2000; Henkin et al. 2009). Researchers in Tunisia developed PEG-containing supplement blocks that increased voluntary intake of tannin-rich browse (*Acacia cyanophylla*) and growth rate of sheep (Ben Salem et al. 2000). PEG also improved growth of kids browsing high-tannin shrubs (Gasmi-Boubaker et al. 2006) and in vitro digestion and fermentation characteristics of high-tannin shrubs (counteracting negative effects on microbes) (Gasmi-Boubaker et al. 2006; Salem et al. 2007). Utsumi et al. (in press) recently demonstrated that one-seed juniper with or without quebracho tannin reduced several plasma amino acids in sheep and goats, some of which were restored with PEG supplementation. When given PEG free-choice, sheep regulated PEG intake in relation to tannin intake (Provenza et al. 2000) and spent more time in areas with PEG present when eating high-tannin diets (Villalba and Provenza 2002).

Consumption of PSM-laden woody plants can be affected by body condition (BC). Pfister et al. (2008) reported that cattle in low BC generally ate more pine (*Pinus ponderosa*) needles and Frost et al. (2008) observed goats in low BC consumed more redberry juniper (*J. pinchotii*) than those in high BC. Though PSMs have a greater negative effect on intake and preference with a low vs. high quality diet (both energy and protein; Villalba and Provenza 2005), animals on higher plane of nutrition may not eat any more PSMs than those receiving lower nutrient intake in real situations unless forced to do so (Villalba and Provenza 2005). The paradox is that animals in low BC are most likely to consume PSMs but animals on a low plane of nutrition are least capable of handling them.

Behavior and Conditioning

Opportunities may exist to capitalize on innate behaviors to enhance shrub consumption. Under some circumstances, animals can maintain PSM intake below a critical threshold (Pfister et al. 1997; Dziba and Provenza 2008) by regulating intake rate and/or pattern (number of feeding bouts, meal size, length between bouts) or timing (modify spatially or temporally) in response to blood metabolite concentrations (Perevolotsky et al. 2006; Marsh et al. 2007; Dziba and Provenza 2008). For example, cattle spread eating bouts over a longer timeframe with lower intake at one time when consuming high-tannin diets (Landau et al. 2000). Diet mixing, diet switching, changing location (from plant/patch/landscape), and selecting complementary diets are strategies used to consume chemically diverse diets (Wiggins et al. 2006; Rogosic et al. 2008; Villalba et al. 2011). Villalba et al. (2004) demonstrated that sheep were able to mix feeds with different types of PSM to maintain intake near control levels, but not when only one PSM was offered. Training animals to mix and match diets could increase diet breadth and allow them to consume different classes of toxins (Villalba and Provenza 2009), thereby minimizing negative effects on metabolism and maintaining exposure below critical thresholds, and theoretically could improve nutrient status (assuming plants not normally consumed are greater in one or more nutrients than in the diet otherwise). Conditioning ruminants to PSMs by restricting the amount of familiar diet offered may increase subsequent intake of diets containing those PSMs simply because they are not forced to learn about complementary interactions when alternatives are high quality and familiar (Shaw et al. 2006a). The timing, sequence of encounter, and quality of familiar/preferred diets offered also affect conditioning success and subsequent use of shrubs containing PSMs (Villalba et al. 2004; Shaw et al. 2006a; Papachristou et al. 2007; Mote et al. 2008). Animals can be conditioned to consume PSMs even when alternatives are available (Papachristou et al. 2007), but behavior modification to increase intake has met with mixed success. Pen studies have shown promise when choices were few and alternatives were restricted, but extending conditioning and training to field situations with complex botanical mixtures has been less successful because of the difficulty integrating multiple signals from complex and constantly changing environments (Duncan and Young 2002; Ginane et al. 2005; Favreau et al. 2010). Applying learning theory to browsing herbivores is challenging because meals are not discrete and contain more than one food, microbial digestion delays postingestive consequences, and foods contain both toxins and nutrients (Duncan et al. 2006). Effectiveness of diet training is influenced by exposure, familiarity, and social influences of peers and dam (Provenza et al. 1992, 2003a), with intrauterine and early life exposure to stimuli improving learning in some studies (Distel and Provenza 1991; Simitzis et al. 2008) but not others (Pritz et al. 1997; Fredrickson et al. 2000; Frost et al. 2003). More efficient use of conditioning periods and considering factors such as amount/type/order of diets (both preferred and nonpreferred) and amount of PSM and number of classes of PSM offered together as well as encouraging temporal association of synergystic feeds may provide management opportunities to change subsequent behavior and shrub use on rangelands (Papachristou et al. 2007; Villalba and Provenza 2009; Lyman et al. 2011). In pastoral or intensive systems where animals can be moved into paddocks at night or when improved pastures are available, the sequence of consuming high-quality vs. unpreferred and/or high-PSM plants could potentially be manipulated within or among days or seasons. Even in more extensive systems, strategic location of small, highly productive irrigated and/or seeded paddocks (or arid-adapted species) could be used to optimize mixing and matching of species and sequence of use. Except for highly specialized operations, these approaches require inputs that may not be applicable to most arid rangelands. These techniques might have utility for small farm-holders in developing countries that integrate various crops and crop residues with more extensive browsing systems.

Management

Provenza et al. (2003b) suggested grazing systems with short-duration, high-density stocking might encourage animals to learn to “mix the best with the rest” (i.e., learn benefits of complementary foraging). Increasing animal density reduced the time goats spent grazing herbaceous vegetation and increased time spent browsing one-seed juniper (Utsumi et al. 2010), while sheep browsing time was influenced very little by animal density in that study. Both higher stocking density and longer exposure time (fewer alternatives) increased sagebrush use by sheep, which carried over to subsequent preference tests with the same animals (Shaw et al. 2006b). Animal density affects selectivity and temporal disassociation of intake of different species may hinder the ability of an animal to learn about complementary foods (Provenza et al. 2007). In the study by Utsumi et al. (2010), goats appeared to adjust feeding behavior in response to increased animal density by increasing both number and length of feeding bouts on juniper. Because goats on the high-density treatment began consuming juniper earlier, it may have allowed them to temporally associate the benefits of diet mixing. At issue is whether increased density and mixed stocking can be employed to increase shrub use without harming the herbaceous component. Effects of animal density will be influenced by initial pasture conditions, animal species, grass species and resilience, etc.

Exposure to PSMs can increase tolerance through metabolic changes such as enzyme induction (McLean et al. 2008), and gradual adaptation to PSMs can allow rumen microbes to adjust and overcome negative effects on digestion and microbial populations in some situations (Duncan et al. 2000; Malecky et al. 2009). Adaptation to PSMs could be important during the first few weeks in which naive animals are introduced to a pasture or when plant chemistry changes radically due to seasonal and environmental fluctuations. Grazing strategies that minimize PSM intake and maximize shrub damage by capitalizing on variable shrub chemistry in time and space are theoretically possible, as PSM content can vary within and among plant species, and is affected by plant age, season, leaf age, and a host of other biotic and abiotic factors (Meyer and Karasov 1991; Bryant et al. 1991; Swihart and Bryant 2001). However, plant assemblages contain multiple species that undoubtedly react differently to seasonal and environmental conditions, and practical opportunities to alter factors such as plant phenology on large landscapes are limited beyond standard management decisions based on forage quality and quantity and avoiding use of areas or plants during periods of high toxicity. Yet, this chemical variation among and within species and within plants affords an individual animal the opportunity to select a diet that meets its needs and is the basis for selecting outlier animals.

Efforts to utilize woody forages more effectively may require new management paradigms that promote tighter control of ruminant feeding decisions to enhance diet mixing and PSM dilution. Local knowledge accrued over centuries by herder and smallholder cultures of the developing world may prove to be valuable for developing paradigms for adapting to this new reality. Practices such as hand-harvesting, mowing, piling, ensiling, cutting fodder, or otherwise preserving shrubs are potential alternatives of harvesting that allow PSMs to volatilize or degrade (similar to caching by rodents). Mixing (diluting) harvested shrubs as a dietary component may be a means of feeding shrubs. Whitney and Muir (2010) reported that air-dried redberry juniper (lower in monoterpenes than freshly harvested) could replace cotton seed hulls in feedlot diets of lambs without decreasing long-term intake or gain. Whether harvesting practices are cost-effective is likely site-specific; they are labor intensive but otherwise inexpensive, and while they may be cost-prohibitive in the United States, they could have applicability in other areas. Most ruminants in developing countries are in mixed farming systems, with crop residues and other nontraditional harvested roughages contributing to feed sources (FAO 2003; McDermott et al. 2010).

Benefits of PSM Consumption

Though PSMs are generally considered detrimental, certain compounds have been shown to confer health benefits at low concentrations (antifungal, antibacterial, antiamoebic, antitumor, antiparasitic, antibloat; Mueller-Harvey 2006; Forbey et al. 2009; Villalba et al. 2010). Whether animals use PSMs to self-medicate and capitalize on “nature’s pharmacy” is currently being debated (Provenza et al. 2007; Forbey et al. 2009); however, Villalba et al. (2010) observed greater consumption of an alfalfa–tannin mixture by lambs with internal parasites compared to dewormed controls, suggesting that they modified their preference for tannins after learning the benefits of tannin consumption.

Various PSMs (e.g., tannins, terpenes, saponins) can alter microbial populations (including protozoa), protein degradation, and fermentation in potentially beneficial ways. For example, low levels of tannins can increase protein bypass and decrease rumen ammonia (Barry and Blaney 1987; Ben Salem et al. 2005; Min et al. 2006). Essential oils have been shown to reduce rumen deamination, positively affect fermentation (both volatile fatty acid concentration and ratios), and reduce methanogenesis (Cardoza et al. 2006; Alexander et al. 2008; Benchaar and Greathead 2011). Not only are these effects beneficial to the individual, but may also translate to positive environmental benefits (i.e., decreased methane production and ammonia excretion; Ben Salem et al. 2005; Min et al. 2006; Macheboeuf et al. 2008). Thus, efforts to incorporate woody plants into ruminant diets could have a side benefit of positive environmental effects. The extent to which PSM consumption could reduce impacts of rising animal numbers on the global environment is unknown, but the potential for reducing greenhouse gas emissions and implications for climate change mitigation could stimulate research in this arena.

PROGRESS AND CHALLENGES

Efficient use of a world with less grass and more woody species poses many challenges. It is a simple reality that animals generally do not prefer high-PSM shrubs, especially if reinforced by negative feedback, and will not eat much shrub biomass for very long under most circumstances. Progress in the development of applications for increasing shrub use has been slow for a number of reasons, in part because enhanced shrub use has only recently become a focus. Traditionally, animal scientists working in rangeland environments measured what an animal ate, and controlled experiments focused on forage intake and resulting animal production (Sayre et al. 2012 [this issue]). It was of little concern that (or why) livestock avoided certain shrub species. Capitalizing on this underused forage resource became of interest as the cover and use of shrublands (encroached or otherwise) and animal numbers increased. A few research programs explored the relationship of secondary compounds and mammalian herbivory (particularly wildlife) in the 1970s and 1980s (e.g., Schwartz et al. 1980; Welch et al. 1983; Elliott and Loudon 1987), but scientific literature on the subject was scarce before the 1990s. The classic study by Provenza and Malechek (1984) describing the role of condensed tannins in regulating intake of blackbrush (*Coleogyne ramossissima*) by goats was the springboard for a great deal of research that produced a wealth of information about the relationship of shrub use by livestock and PSM concentrations. Most of this research by necessity has been related to basic mechanisms of physiology and behavior.

Additionally, the problem of low shrub use is site specific. The causes of low acceptability can vary greatly among woody plant species. Shrubs, shrublands, and PSMs can be uniquely different and diverse, and generalizing about them results in oversimplification of a complex situation. Different species contain different arrays of compounds in different concentrations in infinite and constantly changing permutations. We are still defining the chemical profiles of most shrub species. However, discovery speed is advancing rapidly with improved instrumentation and the integration of disciplines. The fields of ecology, pharmacology, natural-product chemistry, and many others using animal models as diverse as woodrats and marsupials have contributed greatly to our understanding of the role of shrub PSMs in animal behavior, distribution, and metabolism (e.g., Foley and Moore 2005; Sorensen et al. 2006; Wiggins et al. 2006).

MANAGEMENT IMPLICATIONS

Practical solutions to increasing shrub use are being developed, though progress has not been rapid. Opportunities exist to capitalize on animal genetics, behavior, and physiology to identify and develop animals capable of utilizing shrubs and detoxifying PSMs. Supplements and additives can be used to increase intake and ameliorate detrimental effects of PSMs in some cases. However, additives and supplements are expensive. Genetic progress is limited by a long generation interval and low heritability traits, and physiological markers need much further study. A decade ago, Launchbaugh et al. (2001) reviewed antiquality compounds and made management recommendations to deal with them (provide early experience; select adapted species, breeds, and individuals; use diet additives; practice genetic selection). Few truly new approaches have been developed since then, but a great deal of new knowledge and concept refinement has occurred.

Much of the world's rangeland contains substantial woody vegetation, and though it is not realistic to expect many shrub-dominated rangelands to support sustainable livestock production given our current state of knowledge, it is inevitable that they will continue to be grazed. There are over three billion cattle, sheep, and goats today, and we are headed towards four billion in the next 20 yr. Over half of these animals will be small ruminants capable of utilizing a wide diversity of plants as forage, but still requiring use of known proper management practices. Yet, nearly two billion of these animals will be cattle with more restricted dietary tendencies, and we will need to exploit every possible mechanism to increase their shrub intake. Over the past 30 yr we have identified elements of these management practices and mechanisms, and this knowledge needs to be expanded and used. Progress will likely be most rapid through a combination of immediate (e.g., supplements and additives, behavior modification) and long-term (e.g., genetic selection for shrub consumers) approaches in conjunction with undeveloped technologies such as biochemical markers of shrub intake and other as yet unidentified methods.

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