

Pasture chemoscapes and their ecological services

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ABSTRACT: Ruminant livestock-production systems are between a rock and a hard place; they are experiencing increasing societal pressure to reduce environmental impacts in a world that demands increased food supply. Recent improvements in the understanding of the nutritional ecology of livestock by scientists may help livestock producers respond to these seemingly contradictory demands. Forages are nutrition and pharmacy centers with primary (nutrients) and plant secondary compounds (PSC; pharmaceuticals, nutraceuticals), which can provide multiple services for the proper functioning of agroecosystems. Legumes with lower contents of fiber and higher contents of nonstructural carbohydrates, coupled with different types and concentrations of PSC (e.g., condensed tannins, terpenes), create a diverse array of chemicals in the landscape (i.e., the “chemoscape”) with the potential to enhance livestock nutrition, health and welfare relative to foodscapes dominated by grasses and other

conventional feeds. These PSC-containing plants may reduce methane emissions and nitrogen (N) excretion from animals while increasing animal growth rate compared with swards dominated by grasses, and provide meat quality that appeals to consumers. Condensed tannins from sainfoin and saponins from alfalfa and manure of cattle consuming these forages also reduce N mobilization in soils, reduce nutrient leaching, and increase plant-available N stores for future use. The challenge for future pastoral production systems is to design multifunctional spatiotemporal arrangements of forages with “ideal” chemical diversity for specific ecoregions, aiming to achieve sustainability while increasing production goals and improving ecosystem services. Thus, the objective of this review is to stimulate the quest for chemically and taxonomically diverse pastoral feeding systems that optimize overall productivity; reduce environmental impacts; and enhance livestock, soil, and human health.

Key words: beef cattle, condensed tannins, intake, legumes, meat quality, soils

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INTRODUCTION

Ruminant livestock production systems are experiencing increasing societal pressures to

reduce environmental impacts, such as land use and greenhouse gas (GHG) emissions, while continuing to meet increased production demands profitably. Livestock producers need to manage for greater environmental sustainability (Sanderson et al., 2007; DeLonge et al., 2016), but rising incomes and urbanization are driving

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human diets to agricultural products that substantially increase environmental impacts (Tilman and Clark, 2014) and to a process of intensification that further shifts the energy resource base of agriculture from solar to fossil energy (Rodríguez-Ortega et al., 2017). Nevertheless, producers and their communities also benefit from reducing costly inputs such as synthetic fertilizers and agricultural equipment, while improving ecosystem functions such as increasing carbon (C) and nitrogen (N) sequestration (White, 2011; Crews and Rumsey, 2017; Wiesmeier et al., 2019), and improving the health (i.e., reductions in parasitism) and welfare (i.e., reductions in stress) of their animals (Broom et al., 2013). Recent advances in the nutritional ecology of livestock and the services provided by the diverse chemistries of certain forage legumes (e.g., bird's-foot trefoil [BFT]—*Lotus corniculatus*; sainfoin [SF]—*Onobrychis viciifolia* Scop) may help attain several of these seemingly contradictory goals.

Cattle evolved grazing diverse plant communities, ingesting different nutrients (e.g., carbohydrates, proteins, minerals) and plant secondary compounds (PSC; e.g., condensed tannins, terpenes) across the landscape (i.e., the “chemoscape”; Provenza et al., 2007) that provide multiple benefits to the proper functioning of agroecosystems (Duke, 1997; Cozier et al., 2006; Forbey et al., 2009; Halvorson et al., 2016). For instance, by managing doses and interactions among nutrients and PSC, livestock enhance their nutrition and ingest appropriate doses of phytochemicals with the potential to improve their health (Waghorn, 2008; Gessner et al., 2017). In addition, some PSC play key roles in the quality of milk and meat from cattle, sheep, and goats (Vasta et al., 2008; Francisco et al., 2015; Chail et al., 2016) by improving the organoleptic properties and fatty acid composition of the product. PSC also influence soil dynamics by slowing mineralization rates due to their antibiotic and N-binding properties (Bradley et al., 2000; Smolander et al., 2012). Such interactions and processes may be optimized if we consider the animal as an integral part of the grazing system interacting with chemicals in the landscape, instead of an individual subjected to prescriptions and formulations. This review was developed with the aim of stimulating the quest for novel pastoral feeding systems that consider the provision of types and concentrations of chemicals in pasturelands (i.e., the chemoscape) that optimize overall productivity and enhance livestock, soil, and human health, thus contributing to the sustainable intensification of agriculture. Such intensification involves increasing food production

from existing farmland while reducing pressure on the environment and maintaining the capacity to produce food in the future.

We begin this review by describing the involvement of PSC and chemical diversity on the productivity and sustainability of pastoral feeding systems, supporting the idea with recent findings on the effects of PSC-containing legumes at increasing animal performance and reducing environmental impacts. We then describe the potential benefits of PSC-containing legumes on meat and soil quality and finally propose the design of chemically and taxonomically diverse pastoral feeding systems aimed at enhancing the ecosystem services of pasturelands.

PLANT SECONDARY COMPOUNDS IN FORAGES

The existence of plant secondary metabolism was recognized in the second half of the 19th century, when it was acknowledged that such compounds were not used in the formation of new cells and thus their function for the plant was unknown (Sachs, 1873). We now know that PSC are significant for plants and herbivores with functions as diverse as attracting pollinators and seed dispersers (Rosenthal and Janzen, 1979), serving as energy escape valves (Hernández and Van Breusegem, 2010), protecting plants from ultraviolet radiation (Mierziak et al., 2014), and defending plants and herbivores against oxidative stress (Gessner et al., 2017) and pathogens (Hoste et al., 2015; Piasecka et al., 2015). PSC are partitioned into three broad classes: phenolics, terpenes, and alkaloids, each with thousands of compounds, making it difficult to make broad generalizations about their post-ingestive actions. In general, PSC promote a variety of deleterious effects on livestock—from antinutritional to toxic—due to their key role as defensive compounds (Palo and Robbins, 1991). On the other hand, some PSC at certain doses may provide herbivores with some health and nutritional benefits. For instance, research in livestock has focused on the potential beneficial actions that certain doses of condensed tannins—a vastly diverse group of soluble phenolics—exert in the metabolism of mammalian herbivores. This was likely a consequence of the pioneering work of Niezen et al. (1995) in New Zealand where they found that a condensed tannin-containing forage (*Hedysarum coronarium*-sulla) had anthelmintic properties. In addition to this health benefit (see Hoste et al., 2015), condensed tannins alleviate bloat (Waghorn, 2008),

reduce enteric methane (Woodward et al., 2001) and ammonia emissions (Koenig et al., 2018), improve nutrient utilization (Barry et al., 2001), and negatively impact pathogenic bacteria (Wu et al. 2009). These actions are mediated by the ability of condensed tannins to form complexes with a variety of chemicals, from proteins and carbohydrates to minerals and other PSC such as alkaloids (Mueller-Harvey, 2006). In addition, there is tremendous variability in the chemical structure of condensed tannins, such as variation in the degree of polymerization, orientation, and proportion of functional groups within the molecule, which has substantial impact on the aforementioned functions, as well as on the likelihood of exerting even negative actions on livestock (Mueller-Harvey, 2006; Hatew et al., 2016). In addition to condensed tannins, other phenolic compounds in plants such as polyphenols have significant antioxidant, immunomodulatory, and anti-inflammatory properties with potential to improve ruminant health and productivity (Winkler et al., 2015; Gessner et al., 2017). Polyphenols are involved in the enhancement of the health condition of the intestinal mucosa, reducing oxidative stress and improving the innate immune function, which reduces the incidence of intestinal pathogens and promotes animal growth (Gisbert et al., 2017; Lipiński et al., 2017). A recent study shows that parasitized sheep increased their preference for a ration containing an array of polyphenols and triterpenic acids with anti-inflammatory and antioxidant effects relative to their uninfected counterparts (Poli et al., 2018). This change in behavior led to an improvement in feed conversion efficiency without effects on parasitic burdens, antioxidative capacity of plasma, or indicators of immunity against gastrointestinal parasites (Poli et al., 2018). Nevertheless, more studies are needed to understand the influence of polyphenols on oxidative stress and inflammation in ruminants (Gisbert et al., 2017).

Beyond phenolics, PSC are partitioned into terpenes and alkaloids. Alkaloids are toxic to mammals (Wink, 2012), but some terpenes may exert antiparasitic, antimicrobial, and antioxidant properties on livestock (Hocquemiller et al., 1991; Lozano-Mena, 2014). Terpenes may also inhibit methane and ammonia production in the rumen, which is beneficial for improving nutrient utilization and animal growth and for reducing GHG emissions (Hu et al., 2005). More research is needed to explore the beneficial and negative effects of novel forage species in grazing systems with these classes of PSC. More studies are also needed to explore

the influence of polyphenols and other PSC in forages on gut health. In addition, innovative research should focus on the potential interactions among PSC and with other chemicals that may lead to synergies that enhance the beneficial effects attained by single compounds (Spelman et al., 2006). Such efforts should complement traditional research that has emphasized just one class of PSC (e.g., condensed tannins) within a particular forage.

CHEMICAL DIVERSITY AND ECOSYSTEM SERVICES

The diverse types and concentrations of chemicals herbivores ingest during grazing may enhance animal nutrition, health, and welfare, and reduce environmental impact. For instance, interactions among chemicals in forages may lead to associative effects that improve the nutrition of herbivores while reducing GHG emissions. Consistent with this idea, beef cattle grazing a combination of tannin-containing legumes (BFT and SF) and a non-tannin-containing legume (alfalfa [ALF]—*Medicago sativa*) showed a 17% to 25% greater dry matter intake (DMI) and average daily gain (ADG) than animals grazing monocultures, suggesting a synergism among pasture species. In addition, methane emissions per unit of gain decreased from 14% to 24% for animals offered combinations compared with control animals grazing monocultures of the same species (Lagrange et al., 2018). Yearlings preferred tannin-containing legumes (60%) over ALF, and animals consuming tannin-containing legumes showed a significant reduction in urinary N excretion relative to those grazing ALF, diverting more of the N to feces, which lessens the loss of N as ammonia into the atmosphere (Lagrange et al., 2017). This effect was also observed when cattle were fed condensed tannin extracts in rations (Koenig et al., 2018), as the high affinity of condensed tannins for binding protein reduces ruminal protein degradation and urinary N excretion. The same pattern of reduced urinary N excretion was observed in cows and heifers consuming tannin-containing hays (SF and BFT; Stewart, 2018), suggesting that condensed tannins remained active in the hay to bind with proteins in the rumen. Previous studies reported that condensed tannins are labile molecules, inactivated in response to the environmental conditions of the haying process (Makkar and Singh, 1991). Nevertheless, more recent research reported that conserved tanniferous forages (i.e., SF hay) had significant bioactive properties against gastrointestinal nematodes, similar to

those observed in the fresh forage, implying that the biological properties of tannins remain in the hay despite changes that occur during the drying process (Heckendorn et al., 2006).

In addition to the aforementioned beneficial effects of single tannin-containing legumes on N excretion, yearlings grazing a choice of SF and BFT (both tannin-containing legumes) showed a greater reduction in the excretion of urinary N (with a concomitant reduction in blood-urea N) than to those grazing monocultures of the same species (Lagrange et al., 2017). The associative effects between tannin-containing legumes may be due to the highly diverse chemical composition of various sources of tannins. For instance, condensed tannins in BFT (procyanidin-rich tannin type) differ from those present in SF (hetero- and homopolymers containing both procyanidin and prodelphinidin units) (Marais et al., 2000; Hatew et al., 2016). This finding suggests a novel case for synergism (i.e., reduced urinary N excretion) among condensed tannins occurring in different forage species. Another recent example of synergism among tannin- and non-tannin-containing forages was observed when sheep were offered combinations of ALF, BFT, and SF; animals consuming the combination had greater DMI and dry matter (DM) digestibility (>10%) than control animals offered the individual forages (Lagrange and Villalba, 2016).

Chemical diversity also allows for complexation of PSC, which can potentially reduce PSC toxicity. For instance, condensed tannins are known to complex with alkaloids (Okuda et al., 1982; Villalba et al., 2016) forming stable complexes that make alkaloids less available in the gastrointestinal tract, thus reducing their toxic effects (Catanese et al., 2014). Endophyte-infected (E+) tall fescue (*Schedonorus arundinaceus* Schreb. Dumort) contains ergot alkaloids that produce negative consequences in livestock such as elevated body temperature and tissue necrosis (Strickland et al., 1993). When lambs and calves consumed tannin-containing legumes such as BFT or SF and then rotated to graze E+ tall fescue, they were able to consume more E+ and nutrients than control animals that did not receive these legumes (Lyman et al., 2011; 2012; Owens et al., 2012). Supplementing E+ with tannin-containing legumes also led to improvements in some physiological parameters indicative of fescue toxicosis, such as reduced rectal temperatures, increased numbers of leukocytes and lymphocytes, and increased plasma concentrations of globulin and prolactin (Catanese et al., 2014). This effect appears to be mediated by a tannin-alkaloid complexation as

condensed tannins isolated from SF bind to ergot alkaloids in *in vitro* tests (Villalba et al., 2016) and polyethylene glycol, a polymer that selectively binds to condensed tannins, reduced the aforementioned benefits of tannin-containing legumes in animals consuming E+ tall fescue (Catanese et al., 2014). In summary, chemical and species diversity may enhance ecosystem services by supporting greater body weight (BW) gains and improving health (provisioning services), while reducing methane and N losses to the environment relative to pasture monocultures (regulating service). These effects have the potential to improve profitability of beef production for ranchers (cultural service).

IS THE GRASS ALWAYS GREENER?

Pastoral livestock systems convert perennial forages into animal products for human consumption. Perennial forages can be grown on agricultural soils that are unsuitable for intensive cropping, thus ruminants that graze perennial forages rather than being fed grain in drylots do not compete with humans for food (Muir et al., 2017). Reducing the unnecessary diversion of grain to ruminants is particularly relevant at a time of increasing global demand for human foods (Wilkinson, 2011, Rodriguez-Ortega et al., 2017). Moreover, ruminant production on grazing lands takes advantage of the high efficiency of the rumen to convert low-quality forage into high-protein human foods (Van Soest, 2018). Only about 20% of U.S. agricultural land can be used for intensive cropping but nearly half of U.S. agricultural land is classified as grazing land and readily supports the production of forages and ruminants (Lal et al., 2003; USDA, 2013), so competition between ruminants and humans for agricultural land or grain crops is an economic and cultural choice, not a necessity.

The seasonal translocation of C from photosynthesis into the soil through root growth and turnover contributes approximately 1,500 kg C/ha/yr from annual cereal crops (Kuzyakov and Domanski, 2000), but cultivation increases microbial breakdown of organic matter, so soil C decreases over time in annual cropping systems. Perennial pasture forages have longer seasonal growing periods than annual cereal crops and can contribute 2,000 to 2,200 kg soil C/ha/yr (Kuzyakov and Domanski, 2000; Bolinder et al., 2007). Converting annual cropping land to perennial pasture increases the rate of C sequestration by approximately 20% (Guo and Gifford, 2002). C sequestration is approximately 25% greater under intensively managed perennial

forage grazing systems than under forages cut for hay or extensive grazing because of the return of organic matter and N to the soil through urine and dung (Conant et al., 2003). Therefore, complementing annual grain-based finishing systems with forage-based systems that use land unsuitable for cropping would continue to support food security while enhancing chemical diversity and mitigating climate change through C sequestration and nutrient cycling (Teague et al., 2016).

Life-cycle assessments of beef finishing systems usually conclude that concentrate-based drylot finishing systems are more efficient than grazing-based finishing systems because they require less land and result in more rapid increases in BW (Pelletier et al., 2010; Clark and Tilman, 2017). Consistent with this scenario, Capper (2012) calculated the cattle population, water use, land area, GHG emissions, and fossil fuel energy associated with the production of 1 billion kg of hot carcass weight beef under three systems: conventional (CON; finished in feedlots with growth-enhancing technology), conventional minus growth-enhancing technology (NAT; natural), and grass-finished (GRASS). She concluded that the CON system required fewer animals and less water, land, and fossil fuel than a grass-finishing system. Like other life-cycle assessments, this one did not consider a perennial legume forage-based beef finishing system, and C sequestration in soils was also assumed to be at equilibrium. Nevertheless, pasture-finishing systems other than grass (e.g., tannin-containing legumes) need to

be included in the discussion about efficiency and contrasted against conventional finishing systems.

In contrast to both cereal grains and perennial grasses, legumes fix their own N (Temperton et al., 2007). Unlike annual grains, perennial legumes are productive for multiple years after establishment without additional cultivation or planting. The ability to depend on biologically fixed N as opposed to industrial N fertilizer that is typically applied to cereal grains and grasses reduces both input costs and N losses to the environment (Muir et al., 2014). Forage legumes are lower in fiber than forage grasses and therefore more nutrient-dense, and are digested more rapidly than grasses by ruminants, so intake and gain are greater than for forage grasses. The tannin-containing legumes such as BFT and SF are non-bloating and can therefore be grazed in pure stands; the grazing of tannin-containing perennial legume pastures for a 3- or 4-mo period is an entirely feasible approach to beef finishing.

In a study where we finished cattle on natural (NAT) and grass-finished (GRASS) diets—comparable to those described by Capper (2012)—as well as on pastures of the perennial legume BFT, the concentration of nonfibrous carbohydrates (NFC) in BFT was found to be similar to that observed in the NAT diet and approximately twice that of the GRASS diet (Table 1; Chail et al., 2016). BFT was also found to have a lower concentration of neutral detergent fiber and a greater concentration of NFC than ALF when grown in the northern Mountain West (MacAdam and Griggs, 2013). In addition, the unique tannins produced by these forage legumes, particularly BFT (Waghorn, 2008), combined with its high fiber digestibility (Hunt et al., 2014a,b; Christensen et al., 2015), further enhance the efficiency of energy and protein use in ruminants compared with grasses and other perennial legumes (Wang et al., 2015). By finishing cattle on perennial tannin-containing legume pastures under management-intensive grazing in regions where these forages are well-adapted, persistent (e.g., 5 to 8 yr), and high-yielding (e.g., 6,000 to 7,600 kg DM/ha; Hunt et al., 2015), ruminant productivity per land unit area can make legume pasture beef finishing competitive with drylot concentrate-based finishing.

Gain, carcass quality, and consumer sensory perception were assessed for cattle entering a finishing study at a mean BW of 451 kg and finished for 111 d on grass pastures (GRASS(U), BFT pastures [BFT(U)], or in a feedlot without growth-enhancing technology [NAT(U); Table 2). All cattle in this study were slaughtered at 18 mo, whereas the cattle

Table 1. Composition of diets offered to cattle in a study that compared the consumer acceptability and chemical properties of conventionally finished and grass-finished beef with the unique properties of bird's-foot trefoil-finished beef (from Chail et al., 2016)

Component, % DM	Finishing diet ¹		
	GRAIN	BFT	GRASS
CP	15.4	24.4	18.2
ADF	16.5	26.8	32.2
NDF	31.0	28.9	50.4
Ash	8.5	7.0	10.8
Crude fat	2.4	2.0	3.4
Lignin	3.2	4.4	3.3
Nonfibrous carbohydrate	42.7	39.8	19.3

ADF = acid detergent fiber; CP = crude protein; NDF = neutral detergent fiber.

¹GRAIN = conventional feedlot; BFT = perennial legume, bird's-foot trefoil (*Lotus corniculatus*); GRASS = meadow brome (*Bromus riparius* Rehmann).

in Capper's life-cycle assessment were slaughtered at 14.6 (CON), 15.8 (NAT), or 22.6 (GRASS) mo of age. The study demonstrated that the number of cattle required to produce 1 billion kg of hot carcass beef when finished on BFT pastures (BFT(U)) was similar to CON- and NAT-finished cattle, whereas the 18-mo-old GRASS(U) cattle were similar to the 22.6-mo-old GRASS cattle in Capper's (2012) calculations. Perennial grasses and legumes were grown on alkaline (pH 7–8) soils under irrigation in the Mountain West and were more productive and retained more NFC than forages produced in low-elevation, humid climates on acidic (pH 5.5–6.5) soils. However, a study of cattle comparing ADG on BFT or endophyte-free tall fescue in Missouri reported even greater gains on BFT pasture (Wen et al., 2002). In a subsequent Utah study (MacAdam et al., 2016), cattle grazing BFT or the non-tannin legume cicer milkvetch (*Astragalus cicer* L.) produced less enteric methane than cattle grazing meadow bromegrass.

The greater nutrient density of tannin-containing forage legumes compared with grasses increases ruminant production efficiency, which substantially reduces land use and increases rate of gain, mitigating the environmental impacts calculated by Capper (2012). Condensed tannins and greater NFC concentrations also reduce methane and urinary N emissions, further reducing the environmental impacts of the legume finishing system compared with a grass-finishing system. Improved ADG and reduced GHG emissions could be further enhanced by offering combinations of PSC-containing legumes that take advantage of

synergies and associative effects among PSC. Thus, the advantages of legumes over grasses regarding finishing systems include 1) perennial legume forages are greater in nutrient content and more rapidly digested in the rumen than grasses, so nutrient intake is greater; 2) greater NFC concentrations in perennial legumes than in grasses combined with condensed tannins that precipitate excess plant proteins, result in a better balance of available protein and carbohydrates in the rumen to support microbial production (Waghorn, 2008); and 3) PSC (i.e., condensed tannins) present in some legume forages provide additional nutritional benefits to ruminants while reducing GHG footprint and N excretion from animals. These benefits point to enhancing animal productivity while reducing costs (e.g., N inputs) and environmental impacts (e.g., GHG emissions), which may increase the likelihood of rancher adoption and represent a diversification option for hay farms.

LIFE-CYCLE ANALYSIS OF PSC-CONTAINING LEGUMES FOR RUMINANT LIVESTOCK PRODUCTION

A life-cycle analysis can be used to assess the net impact of PSC-containing legumes for ruminant livestock on GHG production and the provisioning of ecosystem services (Pogue et al., 2018). A whole-systems approach accounts for all related GHG emissions and removals (sinks), including those associated with pasture growth, C sequestration in soils, feed digestion, urinary and fecal excretion from animals, on-farm use of equipment, and relevant inputs to

Table 2. Three treatments from Capper (2012) (CON [feedlot concentrate-finished], NAT [CON; no growth-enhancing technology], and GRASS [grass finished]) are compared with three Utah State University experimental treatments: BFT(U) (bird's-foot trefoil [*Lotus corniculatus*]-finished), NAT(U) (CON; no growth-enhancing technology), and GRASS(U) (grass-finished; from MacAdam and Villalba, 2015)

	Time in subsystem (d)					
	CON	BFT(U)	NAT	NAT(U)	GRASS	GRASS(U)
Preweaned beef calf	207	215	207	215	207	215
Stocker	123	216	159	216	159	216
Yearling finishing	110	111	110	111	313	111
Total (days)	440	542	476	542	679	542
Total (months)	14.6	18	15.8	18	22.6	18
	Weight (kg)					
	CON	BFT(U)	NAT	NAT(U)	GRASS	GRASS(U)
Preweaned beef calf	245	289	245	289	226	289
Stocker	122	162	122	162	67	162
Yearling finishing	204	106	163	193	192	61
Total	571	557	530	644	486	512
Dressing percentage	63.8	62.1	63.3	58.1	57.5	57.0
Number of cattle required for 1,000,000,000 kg beef	2,745,000	2,890,000	2,981,000	2,673,000	3,586,000	3,427,000

the farming system. The sum of GHG emissions and removals expressed as CO₂ equivalents (which accounts for the warming potential of the individual gases) from the system is expressed relative to a kilogram of beef carcass to calculate emissions intensity (i.e., C footprint). A reduction in enteric methane due to tannin-containing legumes would have a significant impact on total C footprint of beef production, given that enteric methane accounts for >60% of on-farm emissions for beef production (Beauchemin et al., 2010). A shift in the site of N excretion from urine to feces would decrease nitrous oxide emissions, which typically account for about one-quarter of emissions from beef production. An increase in the performance of cattle due to improved forage quality decreases the C footprint despite the increase in feed intake because more product is produced relative to emissions. Finally, pastoral systems can recycle C back to the soil, which improves soil health and lowers atmospheric CO₂. Estimating the net impact of PSC-containing legumes on soil C stocks is complex, but nevertheless would need to be considered in a life-cycle analysis. Over the long term, legumes have greater potential to store soil C than grass based systems (Little et al., 2017), but the effects of PSC-containing legumes on soil C are largely unknown. The impact of PSC-containing legumes for ruminant production on ecosystem services such as water supply and quality, soil quality, and soil nutrient-holding capacity also need to be considered, but few data are available.

PSC-CONTAINING LEGUMES AND MEAT QUALITY

In addition to the benefits of PSC described earlier, tannins can positively influence meat color and quality (Priolo et al., 2005; Vasta et al., 2008). When sheep and goats consume feeds with tannins, their meat is lighter in color, higher in antioxidants, higher in omega-3 (anti-inflammatory in humans) fatty acids compared with omega-6 (pro-inflammatory in humans) fatty acids, lower in “gamey” flavor, and generally more desirable for human consumption (Priolo et al., 2005, 2009; Vasta et al., 2008). The bactericidal properties of tannins influence ruminal biohydrogenation and the production of ruminal indole and skatole (3-methyl-indole) which in turn affects the composition of fatty acids as well as the concentrations of “off-flavors,” respectively, in meat and milk products (Vasta et al., 2008; Priolo et al., 2009). In support of this, lambs grazing on *L. corniculatus* pastures had lower concentrations of ruminal indole and skatole, and lower levels of skatole deposited in the fat than lambs

grazing perennial ryegrass and white clover pastures (Schreurs et al., 2007). In addition to findings in small ruminants, cattle grazing a mix of tall fescue and tannin-containing SF had greater marbling scores, quality grades, and backfat thicknesses than ALF-fed animals. Steaks from cattle finished on tannin-containing SF were redder than steaks from cattle finished on ALF and contained more unsaturated fatty acids (Maughan et al., 2014). Likewise, meat (*longissimus thoracis*) samples from cattle finished on BFT were comparable in sensory quality to grain-finished beef but with reduced ratios of omega-6 to omega-3 fatty acids and concentrations of saturated fatty acids similar to grass-finished beef (Chail et al., 2016). In a study of cheese made from organic milk produced by dairy cows grazing either grass or BFT, the concentration of omega-3 fatty acids was not only higher in both pasture treatments than in cheese made from the milk of total-mixed-ration-fed dairy cows, but the omega-3 fatty acid concentration of the BFT-based cheese was greater than that of the grass-based cheese (MacAdam et al., 2015). Terpenoids may also have a positive effect on meat quality as they reduce cholesterol and reduce lipid oxidation (Potter et al., 1993; Brogna et al., 2014).

PSC-CONTAINING LEGUMES AND SOIL QUALITY

The majority of mineral nutrients in pasture-based systems is returned in excreta and remain in the ecosystem (Temperton et al., 2007; Muir et al., 2014); however, additional N is needed to maintain grass production (Ledgard, 2001). N-fixing bacteria present in the root nodules of legumes can provide all the N needed for pasture plant growth, but nodule N fixation decreases if soil N becomes available, minimizing the creation of excess N in pasture systems (van der Heijden et al., 2008). N applied as fertilizer or returned in excreta can be lost due to volatilization, or leached past the root zone (Follett and Walker 1989; Strebel et al. 1989). The tannins present in tannin-containing legumes can alter N dynamics by shifting N excretion from the urine to the feces, which ultimately slows the release and leaching potential of N in pasture agroecosystems. Increasing the proportion of BFT in perennial ryegrass pastures decreased the N content of urine by as much as 29% and increased the N in feces by as much as 35% (Woodward et al., 2004), and ammonia production from the manure of dairy cows fed BFT silage was 35% lower than that of cows fed ALF (Misselbrook et al., 2005).

Condensed tannins are large polar molecules that, when consumed by grazing animals, remain in the gastrointestinal tract and are excreted with the feces (Waghorn, 2008). In addition to condensed tannins, terpenes (i.e., saponins) are known to affect both C and N cycling in the soil (Smolander et al., 2012), particularly by increasing N immobilization (Bradley et al., 2000). The mechanism underlying this process has been explored in boreal forest systems, and studies suggest that these PSC may bind organic N compounds, representing an increased C resource for soil microbes or by becoming toxic to microbes (Smolander et al., 2012). Consistent with the latter, research in silvicultural soil systems shows that condensed tannins and terpenes influence C and N cycling, decrease decomposition rates, and inhibit soil mesofauna and soil enzymatic activity (Smolander et al., 2012; Madritch and Lindroth, 2015). Phenolic compounds are known to hinder nitrification in soil by inhibiting N-fixing bacteria such as *Nitrosomonas europaea* (AlSaadawi, 1988). Research on the effects of PSC in pastoral agricultural soils is emerging and there is evidence that their effect is similar to that observed in forest systems. A recent study (Clemensen et al., 2018) found greater soil nitrate (NO_3^-) in saponin-containing ALF than in tannin-containing SF plots, yet total N content and biomass of these legumes were very similar. In addition, application of feces from cattle consuming tannin-containing SF or saponin-containing ALF to soils increased N immobilization relative to a control treatment (N fertilizer matching the N content in feces; Clemensen et al., 2018). Thus, PSC-containing forages in pastoral agroecosystems have the potential to increase N immobilization in soils, thus reducing N loss.

DESIGNING PASTURE CHEMOSCAPES TO ENHANCE THE ECOSYSTEM SERVICES OF PASTURELANDS

Incorporation of biochemically rich and diverse legumes into pasturelands enables us to create diverse “chemoscapes” that provide benefits to animals (nutrition, health), their environment (cleaner air and healthy soils), and us (quality of meat). The challenge for managers, however, will entail designing these forages in spatiotemporal arrangements such that these multiple benefits converge in the same farm or arrangements of farms in a particular landscape—grassland (Gregorini et al., 2017; McWilliam and Gregorini, 2018).

New “bioactive-containing forages” in spatiotemporal arrangements will have to either be plastic

enough to grow in the ecoregion of the farm or be bred to increase adaptability, resilience, productivity, competition, and persistence. One key challenge faced by pasture-based feeding systems is that perennial forage crops and cultivars are mainly bred for their productivity as monocultures. Thus, when these forages are used in mixtures, they do not always produce well or even persist in the mix, turning into a pure culture (i.e., the dominant species in the mix) within a short time. Forage breeding programs should consider this variable for the creation of productive and persistent diverse swards. Alternatively, rather than “perfectly intermingled –mixed swards,” forage plantings should enhance functional diversity such that the arrangement of plants in the landscape allows animals of different classes to choose and combine forages in space and time (e.g., the capacity of cattle to select for individual plant species in a perfectly intermingled sward is more restricted than that observed in animals of smaller body size like sheep). Thinking and designing “functional” diverse foodscapes rather than a “mixed salad” will enable grazers to utilize different forages across the landscape as sources of nutrients and medicines at different temporal scales (from days to seasons). Previous reports in the literature help to illustrate this concept. For instance, planting forages in monoculture strips overcomes many difficulties inherent in establishing and maintaining mixed pastures and also mimics what happens naturally as plant species aggregate in response to environmental conditions (Chapman et al., 2007). Moreover, time is lost while animals search for and handle preferred food items in a diverse community. These activities inevitably reduce harvest efficiency (Chapman et al., 2007). Studies offering animals the choice of alternative forage species such as ryegrass and white clover growing side-by-side, rather than sown as a conventional intermingled mixture, have provided evidence that animal performance benefits from having such a spatial choice (Nuthall et al., 2000; Cosgrove et al., 2001). In addition, herbivores satiate on the orosensorial characteristics of single feeds consumed too frequently or in excess (Provenza, 1996), like when animals graze monocultures of single species. Neurons for taste, smell, and sight stop responding to the taste, odor, and sight of a food on which an animal has been fed to satiation, yet they continue to respond to other foods. This is why an animal that stops eating a certain food will often consume another food, leading to an increase in the total number of calories ingested relative to when just one food is available for ingestion (Provenza, 1996; Villalba et al. 2011). In addition,

a diversity of side-by-side patches may contribute to enhance animal welfare as animals exposed to a diverse array of foods display lower levels of stress than those exposed to single rations (Catanese et al., 2013). Alternatively, some tannin-containing legumes may contribute to reduced stress levels in livestock; beef cattle grazing BFT showed the lowest levels of hair cortisol—a biological marker of chronic stress—in a study where animals grazed ALF, BFT, SF, or combinations of these species (S. Lagrange et al., unpublished results).

Herders in the Alps of France design grazing circuits at a meal scale to continuously motivate feeding and diet diversity, avoid grazing weariness, and increase intake of abundant but less palatable forages by sheep and goats (Meuret and Provenza, 2015). Gregorini et al. (2017) adapted this model of French herders to more intensive pasture-based livestock production systems, proposing the concept of foodscape and “menu” (daily arrangements of feeds) designs for multipurpose (environmental protection, animal welfare, and productivity) outcomes. The objective of “designed foodscapes” is to embrace the idea of plant diversity in space and time to create synergies among meals and meal phases (Meuret and Provenza 2014, 2015) and herbivores’ feeding strategies and personalities (Gregorini et al. 2017). As it can be implemented with monoculture paddocks in pasturelands, herders partition the landscape into grazing sectors that are carefully grazed within daily circuits (i.e., daily “menu”). Meals are based on complementarities among plants and patches within and among sectors or paddocks. Herders and farmers identify and allocate sectors or paddocks into phases of a meal or particular meals of the daily menu: appetite stimulator or moderator, first course, booster, second course, and dessert (see Gregorini et al., 2017 for details). The next step to this approach is to create foodscapes where managers provide grazers arrays of forages with a systemic knowledge of all the chemicals and beneficial interactions that occur in each of the grazing sectors of the landscape, i.e., the chemoscape. Such an endeavor pertains not only to grazers, but to a trans- rather than to a multi-multidisciplinary team of researchers, including not only animal and plant scientists, but also landscape ecologists, designers, and architects.

SUMMARY AND CONCLUSIONS

In conclusion, legumes with different types and concentrations of fiber and with high concentrations of cell contents, coupled with different types

and concentrations of PSC can create a “chemoscape” with potential to enhance livestock nutrition, health, and welfare relative to grasses, or pasture monocultures. PSC also contribute to reducing enteric CH₄ emissions and urinary N excretion, while improving meat quality and contributing to soil health. Applications range from legume pasture-based finishing systems that compare favorably in efficiency with concentrate-based drylot finishing systems to grazing circuits with carefully designed chemoscapes, both with benefits to ruminants and the environment compared with conventional production systems. The challenge for grazing managers is to ensure that these forages are strategically available to animals in optimal temporal and spatial scales and sequences to achieve these multiple benefits while maintaining profitable production enterprises, foodscape sustainability, and health of the landscape we all inhabit.

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LITERATURE CITED

- Alsaadawi, I.S. 1988. Biological suppression of nitrification by selected cultivars of *Helianthus annuum* L. *J. Chem. Ecol.* 14:733–741. doi:10.1007/BF01018768
- Barry, T.N., D.M. McNeill, and W.C. McNabb. 2001. Plant secondary compounds: their impact on nutritive value and upon animal production. *Proc. Int. Grass. Conf.* 19:445–452.
- Beauchemin, K.A., H.H. Janzen, S.M. Little, T.A. McAllister, and S.M. McGinn. 2010. Life cycle assessment of greenhouse gas emissions from beef production in western Canada: a case study. *Agr. Syst.* 103:371–379. doi:10.1016/j.agsy.2010.03.008
- Bolinder, M.A., H.H. Janzen, E.G. Gregorich, D.A. Angers, A.J. VandenBygaart. 2007. An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Agr. Ecosyst. Environ.* 118:29–42. doi:10.1016/j.agee.2006.05.013
- Bradley, R.L., B.D. Titus, and C.P. Preston. 2000. Changes to mineral N cycling and microbial communities in black spruce humus after additions of (NH₄)₂SO₄ and condensed tannins extracted from *Kalmia angustifolia* and balsam fir. *Soil Biol. Biochem.* 32:1227–1240. doi:10.1016/S0038-0717(00)00039-0

- Brogna, D.M., R. Tansawat, D. Cornforth, R. Ward, M. Bella, G. Luciano, A. Priolo, and J. Villalba. 2014. The quality of meat from sheep treated with tannin- and saponin-based remedies as a natural strategy for parasite control. *Meat Sci.* 96(2 Pt A):744–749. doi:10.1016/j.meatsci.2013.10.019
- Broom, D.M., F.A. Galindo, and E. Murgueitio. 2013. Sustainable, efficient livestock production with high biodiversity and good welfare for animals. *Proc. Biol. Sci.* 280:20132025. doi:10.1098/rspb.2013.2025
- Capper, J.L. 2012. Is the grass always greener? Comparing the environmental impact of conventional, natural and grass-fed beef production systems. *Animals (Basel)*. 2:127–143. doi:10.3390/ani2020127
- Catanese, F., M. Obelar, J.J. Villalba, and R.A. Distel. 2013. The importance of diet choice on stress-related responses by lambs. *Appl. Anim. Behav. Sci.* 148:37–45. doi:10.1016/j.applanim.2013.07.005
- Catanese, F., R.A. Distel, and J.J. Villalba. 2014. Effects of supplementing endophyte-infected tall fescue with sainfoin and polyethylene glycol on the physiology and ingestive behavior of sheep. *J. Anim. Sci.* 92:744–757. doi:10.2527/jas.2013-6713
- Chail, A., J.F. Legako, L.R. Pitcher, T.C. Griggs, R.E. Ward, S. Martini, and J.W. MacAdam. 2016. Legume finishing provides beef with positive human dietary fatty acid ratios and consumer preference comparable with grain-finished beef. *J. Anim. Sci.* 94:2184–2197. doi:10.2527/jas.2015-0241
- Chapman, D.F., A.J. Parsons, G.P. Cosgrove, D.J. Barker, D.M. Marotti, K.J. Venning, S.M. Rutter, J. Hill, and A.N. Thompson. 2007. Impacts of spatial patterns in pasture on animal grazing behavior, intake, and performance. *Crop. Sci.* 47:399–415. doi:10.2135/cropsci2006.01.0036
- Christensen, R.G., S.Y. Yang, J.S. Eun, A.J. Young, J.O. Hall, and J.W. MacAdam. 2015. Effects of feeding birdsfoot trefoil hay on neutral detergent fiber digestion, nitrogen utilization efficiency, and lactational performance by dairy cows. *J. Dairy Sci.* 98:7982–7992. doi:10.3168/jds.2015-9348
- Clark, M., and D. Tilman. 2017. Comparative analysis of environmental impacts of agricultural production systems, agricultural input efficiency, and food choice. *Environ. Res. Lett.* 12:064016. doi:10.1088/1748-9326/aa6cd5
- Clemensen, A.K., J.J. Villalba, G.E. Rottinghaus, S.T. Lee, F.D. Provenza, and J.R. Reeve. 2018. Can condensed tannins reduce N loss in pasture agroecosystems by reducing N mineralization? *Agric. Ecosyst. Environ.* In Press.
- Conant, R.T., J. Six, and K. Paustian. 2003. Land use effects on soil carbon fractions in the southeastern United States. I. Management-intensive versus extensive grazing. *Biol. Fertil. Soils.* 38:386–392. doi:10.1007/s00374-004-0754-2
- Cosgrove, G.P., A.J. Parsons, D.M. Marotti, S.M. Rutter, and D.F. Chapman. 2001. Opportunities for enhancing the delivery of novel forage attributes. *Proc. N. Z. Soc. Anim. Prod.* 61:16–19.
- Cozier, A., M.N. Clifford, and H. Ashihara, editors. 2006. *Plant secondary metabolites: occurrence, structure and role in the human diet.* Oxford (United Kingdom): Blackwell Publishing; p. 372.
- Crews, T.E., and B.E. Rumsey. 2017. What agriculture can learn from native ecosystems in building soil organic matter: a review. *Sustainability*. 9:578. doi:10.3390/su9040578
- DeLonge, M. S., A. Miles, and L. Carlisle. 2016. Investing in the transition to sustainable agriculture. *Environ. Sci. Pol.* 55:266–273. doi:10.1016/j.envsci.2015.09.013
- Duke, J.A. 1997. *The green pharmacy.* Emmaus (PA): Rodale Press.
- Follett, R.F., and D.J. Walker. 1989. Ground water quality concerns about N. In: Follett, R.F., editor. *Nitrogen management and ground water protection.* New York (NY): Elsevier Science Publishers; p. 1–22.
- Forbey, J.S., A.L. Harvey, M.A. Huffman, F.D. Provenza, R. Sullivan, and D. Tasdemir. 2009. Exploitation of secondary metabolites by animals: a response to homeostatic challenges. *Integr. Comp. Biol.* 49:314–328. doi:10.1093/icb/icp046
- Francisco, A., M.T. Dentinho, S.P. Alves, P.V. Portugal, F. Fernandes, S. Sengo, E. Jerónimo, M.A. Oliveira, P. Costa, A. Sequeira, et al. 2015. Growth performance, carcass and meat quality of lambs supplemented with increasing levels of a tanniferous bush (*Cistus ladanifer* L.) and vegetable oils. *Meat Sci.* 100:275–282. doi:10.1016/j.meatsci.2014.10.014
- Gessner, D.K., R. Ringseis, and K. Eder. 2017. Potential of plant polyphenols to combat oxidative stress and inflammatory processes in farm animals. *J. Anim. Physiol. Anim. Nutr.* 101:605–628. doi:10.1111/jpn.12579
- Gisbert, E., K.B. Andree, J.C. Quintela, J.A. Calduch-Giner, I.R. Ipharraguerre, and J. Pérez-Sánchez. 2017. Olive oil bioactive compounds increase body weight, and improve gut health and integrity in gilthead sea bream (*Sparus aurata*). *Br. J. Nutr.* 117:351–363. doi:10.1017/S0007114517000228
- Gregorini, P., J.J. Villalba, P. Chilibroste, and F.D. Provenza. 2017. Grazing management: setting the table, designing the menu and influencing the diner. *Anim. Prod. Sci.* 57:1248–1268. doi:10.1071/AN16637
- Guo, L.B., and R.M. Gifford. 2002. Soil carbon stocks and land use change: a meta analysis. *Global Change Biol.* 8: 345–360. doi:10.1046/j.1354-1013.2002.00486.x
- Halvorson, J.J., M.A. Schmidt, A.E. Hagerman, J.M. Gonzalez, and M.A. Liebig. 2016. Reduction of soluble N and mobilization of plant nutrients in soils from US northern Great Plains agroecosystems by phenolic compounds. *Soil Biol. Biochem.* 94:211–221. doi:10.1016/j.soilbio.2015.11.022
- Hatew, B., E. Stringano, I. Mueller-Harvey, W.H. Hendriks, C.H. Carbonero, L.M. Smith, and W.F. Pellikka. 2016. Impact of variation in structure of condensed tannins from sainfoin (*Onobrychis viciifolia*) on in vitro ruminal methane production and fermentation characteristics. *J. Anim. Physiol. Anim. Nutr.* 100:348–360. doi:10.1111/jpn.12336
- Heckendorn, F., D.A. Häring, V. Maurer, J. Zinsstag, W. Langhans, and H. Hertzberg. 2006. Effect of sainfoin (*Onobrychis viciifolia*) silage and hay on established populations of *Haemonchus contortus* and *Cooperia curticei* in lambs. *Vet. Parasitol.* 142:293–300. doi:10.1016/j.vetpar.2006.07.014
- van der Heijden, M.G., R.D. Bardgett, and N.M. van Straalen. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11:296–310. doi:10.1111/j.1461-0248.2007.01139.x
- Hernández, I., and F. Van Breusegem. 2010. Opinion on the possible role of flavonoids as energy escape valves: novel tools for nature's Swiss army knife? *Plant Sci.* 179:297–301.

- doi:10.1016/j.plantsci.2010.06.001
- Hocquemiller, R., D. Cortes, G.J. Arango, S.H. Myint, A. Cavé, A. Angelo, V. Muñoz, and A. Fournet. 1991. [Isolation and synthesis of espintanol, a new antiparasitic monoterpene]. *J. Nat. Prod.* 54:445–452. doi:10.1021/np50074a015
- Hoste, H., J.F. Torres-Acosta, C.A. Sandoval-Castro, I. Mueller-Harvey, S. Sotiraki, H. Louvandini, S.M. Thamsborg, and T.H. Terrill. 2015. Tannin containing legumes as a model for nutraceuticals against digestive parasites in livestock. *Vet. Parasitol.* 212:5–17. doi:10.1016/j.vetpar.2015.06.026
- Hu, W.L., J.X. Liu, J.A. Ye, Y.M. Wu, and Y.Q. Guo. 2005. Effect of tea saponin on rumen fermentation in vitro. *Anim. Feed Sci. Technol.* 120:333–339. doi:10.1016/j.anifeedsci.2005.02.029
- Hunt, S.R., J.W. MacAdam, and J.R. Reeve. 2015. Establishment of birdsfoot trefoil (*Lotus corniculatus*) pastures on organic dairy farms in the Mountain West USA. *Org. Agr.* 5:63–77. doi:10.1007/s13165-014-0091-1
- Hunt, S.R., T.C. Griggs, and J.W. MacAdam. 2014a. Change in birdsfoot trefoil (*Lotus corniculatus*) nutritive value with stem elongation, flowering and pod formation. *Proc. European Grassland Fed. Grassland Science in Europe.* 2014:884–886.
- Hunt, S.R., J.W. MacAdam, and T.C. Griggs. 2014b. Lignification and tannin localization during the development of birdsfoot trefoil stems. *Crop Sci.* 54:1876–1886. doi:10.2135/cropsci2013.09.0592
- Koenig, K.M., K.A. Beauchemin, and S.M. McGinn. 2018. Feeding condensed tannins to mitigate ammonia emissions from beef feedlot cattle fed high-protein finishing diets containing distillers grains. *J. Anim. Sci.* 96:4414–4430. doi:10.1093/jas/sky274 In Press.
- Kuzyakov, Y., and G. Domanski. 2000. Carbon input by plants into the soil. *J. Plant Nutr. Soil Sci.* 163:421–431. doi:10.1002/1522-2624(200008)
- Lagrange, S., R. Guevara Ballesteros, K.A. Beauchemin, J.W. MacAdam, and J.J. Villalba. 2018. Methane emissions by cattle grazing tannin-containing legumes. *J. Anim. Sci.* 96(Suppl. 3):223–224. (Abstr.) doi:10.1093/jas/sky404.486.
- Lagrange, S., K.A. Beauchemin, J.W. MacAdam, and J.J. Villalba. 2017. Effects of grazing diverse combinations of sainfoin, birdsfoot trefoil, and alfalfa on beef cow performance and environmental impacts. *J. Anim. Sci.* 95(Suppl. 4):143–144. (Abstr.) doi:10.2527/asasann.2017.290
- Lagrange, S., and J.J. Villalba. 2016. Influence of forage diversity on feeding behavior and diet digestibility in lambs. *J. Anim. Sci.* 94(Suppl. 5):289–289. (Abstr.) doi:10.2527/jam2016-0609
- Lal, R., R.F. Follett, and J.M. Kimble. 2003. Achieving soil carbon sequestration in the United States: a challenge to the policy makers. *Soil Sci.* 168:827–845. doi:10.1097/01.ss.0000106407.84926.6b
- Ledgard, S.F. 2001. Nitrogen cycling in low input legume-based agriculture, with emphasis on legume/grass pastures. *Plant and Soil.* 228:43–59. doi:10.1023/A:1004810620983
- Lipiński, K., M. Mazur, Z. Antoszkiewicz, and C. Purwin. 2017. Polyphenols in monogastric nutrition—a review. *Ann. Anim. Sci.* 17:41–58. doi:10.1515/aoas-2016-0042
- Little, S.M., C. Benchaar, H.H. Janzen, R. Kröbel, E.J. McGeough, and K.A. Beauchemin. 2017. Demonstrating the effect of forage source on the carbon footprint of a Canadian dairy farm using whole-systems analysis and the Holos model: alfalfa silage vs. corn silage. *Climate.* 5:87. doi:10.3390/cli5040087
- Lozano-Mena, G., M. Sánchez-González, M.E. Juan, and J.M. Planas. 2014. Maslinic acid, a natural phytoalexin-type triterpene from olives—a promising nutraceutical? *Molecules.* 19:11538–11559. doi:10.3390/molecules190811538
- Lyman, T.D., F.D. Provenza, J.J. Villalba, and R.D. Wiedmeier. 2011. Cattle preferences differ when endophyte-infected tall fescue, birdsfoot trefoil, and alfalfa are grazed in different sequences. *J. Anim. Sci.* 89:1131–1137. doi:10.2527/jas.2009-2741
- Lyman, T.D., F.D. Provenza, J.J. Villalba, and R.D. Wiedmeier. 2012. Phytochemical complementarities among endophyte-infected tall fescue, reed canarygrass, birdsfoot trefoil and alfalfa affect cattle foraging. *Animal* 6:676–682. doi:10.1017/S1751731111001996
- MacAdam, J.W., K.A. Beauchemin, A.I. Bolletta, and L.R. Pitcher. 2016. Reduced enteric methane emissions on legume vs. grass irrigated pastures. *J. Anim. Sci.* 94(E-Suppl. 5):315. doi:10.2527/jam2016_0660
- MacAdam, J. W., and T. C. Griggs. 2013. Irrigated birdsfoot trefoil variety trial: forage nutritive value. *Electronic Bulletin. AG/Forages/2013-02pr.* Logan (UT): Utah State University Cooperative Extension Service.
- MacAdam, J.W., S.R. Hunt, T.C. Griggs, R. Christensen, J.S. Eun, R.E. Ward, D.J. McMahon. 2015. Enhanced forage intake and milk production on birdsfoot trefoil pastures in the Western US. *Proc. 2015 Organic Agric. Res. Symp.* 2015:25–26.
- MacAdam, J.W., and J.J. Villalba. 2015. Beneficial effects of temperate forage legumes that contain condensed tannins. *Agriculture.* 5:475–491. doi:10.3390/agriculture5030475
- Madritch, M.D., and R.L. Lindroth. 2015. Condensed tannins increase nitrogen recovery by trees following insect defoliation. *New Phytol.* 208:410–420. doi:10.1111/nph.13444
- Makkar, H.P.S., and B. Singh. 1991. Effect of drying conditions on tannin, fibre and lignin levels in mature oak (*Quercus incana*) leaves. *J. Sci. Food Agric.* 54:323–328. doi:10.1002/jsfa.2740540302
- Marais, J.P., I. Mueller-Harvey, E.V. Brandt, and D. Ferreira. 2000. Polyphenols, condensed tannins, and other natural products in *Onobrychis viciifolia* (Sainfoin). *J. Agric. Food Chem.* 48:3440–3447. doi:10.1021/jf000388h
- Maughan, B., F.D. Provenza, R. Tansawat, C. Maughan, S. Martini, R. Ward, A. Clemensen, X. Song, D. Cornforth, and J.J. Villalba. 2014. Importance of grass-legume choices on cattle grazing behavior, performance, and meat characteristics. *J. Anim. Sci.* 92:2309–2324. doi:10.2527/jas.2013-7297
- McWilliam, W., and P. Gregorini. 2018. Re-designing New Zealand's productivist livestock production systems: current strategies and next steps. *Proc. NZ Soc. Anim. Prod.* 78:132–136.
- Meuret, M., and F.D. Provenza. 2014. The art & science of shepherding. Tapping the wisdom of French herders. Austin (TX): ACRES.
- Meuret, M., and F. D. Provenza. 2015. How herders create meal sequences to stimulate intake and optimize use of forage diversity on grazing lands in southern France. *Anim. Prod. Sci.* 55:309–318. doi:10.1071/AN14415
- Mierziak, J., K. Kostyn, and A. Kulma. 2014. Flavonoids

- as important molecules of plant interactions with the environment. *Molecules* 19:16240–16265. doi:10.3390/molecules191016240
- Misselbrook, T.H., J.M. Powell, G.A. Broderick, and J.H. Grabber. 2005. Dietary manipulation in dairy cattle: laboratory experiments to assess the influence on ammonia emissions. *J. Dairy Sci.* 88:1765–1777. doi:10.3168/jds.S0022-0302(05)72851-4
- Mueller-Harvey, I. 2006 Unravelling the conundrum of tannins in animal nutrition and health. *J. Sci. Food Agric.* 86:2010–2037. doi:10.1002/jsfa.2577
- Muir, J.P., J.C.B. Dubeux Jr, J.L. Foster, and W.D. Pitman. 2014. The future of warm-season, tropical, and sub-tropical forage legumes in sustainable pastures and rangelands. *African J. Range Forage Sci.* 31:187–198. doi:10.2989/10220119.2014.884165
- Muir, J.P., L.O. Tedeschi, J.C. Dubeux, M. Peters, and S. Burkart. 2017. Enhancing food security in Latin America with forage legumes. *Arch. Latinoamer. Prod. Anim.* 25:113–131.
- Niezen, J.H., T.S. Waghorn, W.A.G. Charleston, and G.C. Waghorn. 1995. Growth and gastrointestinal nematode parasitism in lambs grazing either lucerne (*Medicago sativa*) or sulla (*Hedysarum coronarium*) which contains condensed tannins. *J. Agric. Sci.* 125:281–289. doi:10.1017/S0021859600084422
- Nuthall, R., S. Rutter, and A. Rook. 2000. Milk production by dairy cows grazing mixed swards or adjacent monocultures of grass and white clover. *Proc. Brit. Grassl. Soc. Research Conf.* 6:117–118.
- Okuda, T., K. Mori, and M. Shiota. 1982. [Effects of the interaction of tannins with coexisting substances. III. Formation and solubilization of precipitates with alkaloids]. *Yakugaku Zasshi* 102:854–858.
- Owens, J., F.D. Provenza, R.D. Wiedmeier, and J.J. Villalba. 2012. Supplementing endophyte-infected tall fescue or reed canarygrass with alfalfa or birdsfoot trefoil increases forage intake and digestibility by sheep. *J. Sci. Food Agric.* 92:987–992. doi:10.1002/jsfa.4681
- Palo, R.T., and Robbins, C.T. 1991. Plant defenses against mammalian herbivory. Boca Raton (FL): CRC Press.
- Pelletier, N., R. Pirog, and R. Rasmussen. 2010. Comparative life cycle environmental impacts of three beef production strategies in the Upper Midwestern United States. *Agric. Syst.* 103: 380–389. doi: 10.1016/j.agsy.2010.03.009
- Piasecka, A., N. Jedrzejczak-Rey, and P. Bednarek. 2015. Secondary metabolites in plant innate immunity: conserved function of divergent chemicals. *New Phytol.* 206:948–964. doi:10.1111/nph.13325
- Pogue, S., R. Kroebel, H. Janzen, K.A. Beauchemin, G. Legesse, D. Maia de Souza, M. Iravani, C. Selin, J. Byrne, and T. McAllister. 2018. Beef production and ecosystem services in Canada's prairie provinces: a review. *Agric. Syst.* 166:152–172. doi:10.1016/j.agsy.2018.06.011
- Poli, C.H.E.C., K.J. Thornton-Kurth, J.F. Legako, C. Bremm, V.S. Hampel, J. Hall, I. R. Ipharraguerre, and J.J. Villalba. 2018. Self-selection of plant bioactive compounds by sheep in response to challenge infection with *Haemonchus contortus*. *Physiol. Behav.* 194:302–310. doi:10.1016/j.physbeh.2018.06.013
- Potter, S.M., R. Jimenez-Flores, J. Pollack, T.A. Lone, and M.D. Berber-Jimenez. 1993. Protein-saponin interaction and its influence on blood lipids. *J. Agric. Food Chem.* 41:1287–1291. doi:10.1021/jf00032a023
- Priolo, A., M. Bella, M. Lanza, V. Galofaro, L. Biondi, D. Barbagallo, H. Ben Salem, and P. Pennisi. 2005. Carcass and meat quality of lambs fed fresh sulla (*Hedysarum coronarium* L.) with or without polyethylene glycol or concentrate. *Small Rum. Res.* 59:281–288. doi:10.1016/j.smallrumres.2005.05.012
- Priolo, A., V. Vasta, V. Fasone, C.M. Lanza, M. Scerra, L. Biondi, M. Bella, and F.M. Whittington. 2009. Meat odour and flavour and indoles concentration in ruminal fluid and adipose tissue of lambs fed green herbage or concentrates with or without tannins. *Animal* 3:454–460. doi:10.1017/S1751731108003662
- Provenza, F.D. 1996. Acquired aversions as the basis for varied diets of ruminants foraging on rangelands. *J. Anim. Sci.* 74:2010–2020. doi:10.2527/1996.7482010x
- Provenza, F.D., J.J. Villalba, J. Haskell, J.W. MacAdam, T.C. Griggs, and R.D. Wiedmeier. 2007. The value to herbivores of plant physical and chemical diversity in time and space. *Crop Sci.* 47:382–398. doi:10.2135/cropsci2006.02.0083
- Rodríguez-Ortega, T., A. Bernués, A.M. Olaizola, and M.T. Brown. 2017. Does intensification result in higher efficiency and sustainability? An energy analysis of Mediterranean sheep-crop farming systems. *J. Clean. Prod.* 144:171–179. Doi:10.1016/j.jclepro.2016.12.089
- Rosenthal, G.A., and D.H. Janzen. 1979. Herbivores: their interaction with secondary plant metabolites. New York (NY): Academic Press.
- Sachs, J. 1873. *Lehrbuch der Botanik*. Leipzig (Germany): W. Engelmann.
- Sanderson, M.A., S.C. Goslee, K.J. Soder, R.H. Skinner, B.F. Tracy, and A. Deak. 2007. Plant species diversity, ecosystem function, and pasture management – A perspective. *Can. J. Plant Sci.* 87:479–487. doi:10.4141/P06-135
- Schreurs, N.M., W.C. McNabb, M.H. Tavendale, G.A. Lane, T.N. Barry, T. Cummings, K. Fraser, N. Lopez-Villalobos, and C.A. Ramirez-Restrepo. 2007. Skatole and indole concentration and the odour of fat from lambs that had grazed perennial ryegrass/white clover pasture or *Lotus corniculatus*. *Anim. Feed. Sci. Technol.* 138:254–271. doi:10.1016/anifeedsci.2006.11.020
- Smolander, A., S. Kanerva, B. Adamczyk, and V. Kitunen. 2012. N transformations in boreal forest soils—does composition of plant secondary compounds give any explanations? *Plant Soil.* 350:1–26. doi:10.1007/s11104-011-0895-7
- Spelman, K., J.A. Duke, and M.J. Bogenschutz-Godwin. 2006. The synergy principle at work with plants, pathogens, insects, herbivores, and humans. In: Kaufman, P.B., L.J. Cseke, S. Warber, J.A. Duke, and H.L. Brielmann, editors. *Natural products from plants*. Boca Raton (FL): CRC Press; p. 475–501.
- Stewart, E.K. 2018. Effect of tannin-containing legume hays on enteric methane emissions and N partitioning in beef cattle [MS thesis]. Logan (UT): Utah State University [Accessed November 22, 2018]. <https://digitalcommons.usu.edu/etd/7170>
- Strebel, O., W.H.M. Duynisveld, and J. Bottcher. 1989. Nitrate pollution of groundwater in western Europe. *Agric. Ecosyst. Environ.* 26:189–214. doi:10.1016/0167-8809(89)90013-3
- Strickland, J.R., J.W. Oliver, and D.L. Cross. 1993. Fescue toxicosis and its impact on animal agriculture. *Vet. Hum. Toxicol.* 35:454–464.

- Teague, W.R., S. Apfelbaum, R. Lal, U.P. Kreuter, J. Rowntree, C.A. Davies, R. Conser, M. Rasmussen, J. Hatfield, T. Wang, et al. 2016. The role of ruminants in reducing agriculture's carbon footprint in North America. *J. Soil Water Conserv.* 71:156–164. doi:10.2489/jswc.71.2.156
- Temperton, V.M., P.N. Mwangi, M. Scherer-Lorenzen, B. Schmid, and N. Buchmann. 2007. Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment. *Oecologia* 151:190–205. doi:10.1007/s00442-006-0576-z
- Tilman, D., and M. Clark. 2014. Global diets link environmental sustainability and human health. *Nature* 515:518–522. doi:10.1038/nature13959
- USDA (United States Department of Agriculture). 2013. *Summary Report: 2010 National Resources Inventory*, Natural Resources Conservation Service, Washington, DC, and Center for Survey Statistics and Methodology, Iowa State University, Ames, Iowa. http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1167354.pdf.
- Van Soest, P.J. 2018. *Nutritional ecology of the ruminant*. Ithaca (NY): Cornell university press.
- Vasta, V., A. Nudda, A. Cannas, M. Lanza, and A. Priolo. 2008. Alternative feed resources and their effects on the quality of meat and milk from small ruminants. *Anim. Feed Sci. Tech.* 147:223–246. doi:10.1016/j.anifeedsci.2007.09.020
- Villalba, J.J., A. Bach, and I.R. Ipharraguerre. 2011. Feeding behavior and performance of lambs are influenced by flavor diversity. *J. Anim. Sci.* 89:2571–2581. doi:10.2527/jas.2010-3435
- Villalba, J.J., C. Spackman, B.M. Goff, J.L. Klotz, T. Griggs, and J.W. MacAdam. 2016. Interaction between a tannin-containing legume and endophyte-infected tall fescue seed on lambs' feeding behavior and physiology. *J. Anim. Sci.* 94:845–857. doi:10.2527/jas.2015-9790
- Waghorn, G. 2008. Beneficial and detrimental effects of dietary condensed tannins for sustainable sheep and goat production—Progress and challenges. *Anim. Feed Sci. Technol.* 147:116–139. doi:10.1016/j.anifeedsci.2007.09.013
- Wang, Y., T.A. McAllister, and S. Acharya. 2015. Condensed tannins in sainfoin: composition, concentration, and effects on nutritive and feeding value of sainfoin forage. *Crop Sci.* 55:13–22. doi:10.2135/cropsci2014.07.0489
- Wen, L., R.L. Kallenbach, J.E. Williams, C.A. Roberts, P.R. Beuselinck, R.K. McGraw, and H.R. Benedict. 2002. Performance of steers grazing rhizomatous and non-rhizomatous birdsfoot trefoil in pure stands and in tall fescue mixtures. *J. Anim. Sci.* 80:1970–1976. doi:10.2527/2002.8071970x
- White, C. 2011. The carbon ranch. *Rangelands*. 33:24–30. doi:10.2111/1551-501X-33.2.24
- Wiesmeier, M., L. Urbanski, E. Hobley, B. Lang, M. von Lützow, E. Marin-Spiotta, B. van Wesemael, E. Rabot, M. Lieb, N. Garcia-Franco, et al. 2019. Soil organic carbon storage as a key function of soils—a review of drivers and indicators at various scales. *Geoderma*. 333:149–162. doi:10.1016/j.geoderma.2018.07.026
- Wilkinson, J.M. 2011. Re-defining efficiency of feed use by livestock. *Animal* 5:1014–1022. doi:10.1017/S175173111100005X
- Wink, M. 2012. Medicinal plants: a source of anti-parasitic secondary metabolites. *Molecules* 17:12771–12791. doi:10.3390/molecules171112771
- Winkler, A., D.K. Gessner, C. Koch, F.J. Romberg, G. Dusel, E. Herzog, E. Most, and K. Eder. 2015. Effects of a plant product consisting of green tea and curcuma extract on milk production and the expression of hepatic genes involved in endoplasmic stress response and inflammation in dairy cows. *Arch. Anim. Nutr.* 69:425–441. doi:10.1080/1745039X.2015.1093873
- Woodward, S.L., G.C. Waghorn, and P.G. Laboyrie. 2004. Condensed tannins in birdsfoot trefoil (*Lotus corniculatus*) reduce methane emissions from dairy cows. *Proc. NZ Soc. Anim. Prod.* 64:160–164.
- Woodward, S.L., G.C. Waghorn, M.J. Ulyatt, and K.R. Lassey. 2001. Early indications that feeding Lotus will reduce methane emissions from ruminants. *Proc. NZ Soc. Anim. Prod.* 61:23–26.
- Wu, V.C., X. Qiu, B.G. de los Reyes, C.S. Lin, and Y. Pan. 2009. Application of cranberry concentrate (*Vaccinium macrocarpon*) to control *Escherichia coli* O157:H7 in ground beef and its antimicrobial mechanism related to the down-regulated *slp*, *hdeA* and *cfa*. *Food Microbiol.* 26:32–38. doi:10.1016/j.fm.2008.07.014