

Review

## Beneficial Effects of Temperate Forage Legumes that Contain Condensed Tannins

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**Abstract:** The two temperate forage legumes containing condensed tannins (CT) that promote ruminant production are birdsfoot trefoil (*Lotus corniculatus* L.; BFT) and sainfoin (*Onobrychis viciifolia* Scop.; SF). Both are well-adapted to the cool-temperate climate and alkaline soils of the Mountain West USA. Condensed tannins comprise a diverse family of bioactive chemicals with multiple beneficial functions for ruminants, including suppression of internal parasites and enteric methane. Birdsfoot trefoil contains 10 to 40 g·CT·kg<sup>-1</sup> dry matter (DM), while SF contains 30 to 80 g·CT·kg<sup>-1</sup> DM. Our studies have focused on these two plant species and have demonstrated consistently elevated rates of gain for beef calves grazing both BFT and SF. Novel results from our BFT research include carcass dressing percentages and consumer sensory evaluations equivalent to feedlot-finished steers and significantly greater than grass-finished steers, but with omega-3 fatty acid concentrations equal to grass-finished beef. We have further demonstrated that ruminants fed BFT or SF will consume more endophyte-infected tall fescue (*Schedonorus arundinaceus* (Schreb.) Dumort.) forage or seed than ruminants fed a non-CT forage legume. There is great potential value for sustainable livestock production in the use of highly digestible, nitrogen-fixing legumes containing tannins demonstrated to improve ruminant productivity.

**Keywords:** proanthocyanidin; birdsfoot trefoil (*Lotus corniculatus* L.); sainfoin (*Onobrychis viciifolia* Scop.)

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## 1. Introduction: Structural Diversity and Function of Condensed Tannins:

Condensed tannins (CT) are a heterogeneous family of highly-reactive, carbon-based secondary compounds of high molecular weight [1] that bind to proteins with great affinity [2,3], precipitating them from solution [4]. These biomolecules, also known as polyphenolics or proanthocyanidins, cause responses in herbivores that vary with the diversity of their chemical structures [5,6]. Such diversity is in part due to the fact that CT are polymers of flavan-3-ol subunits, which offer the possibility of a wide array of molecular weights [7,8], ranging from dimers and trimers to oligomers with multiple subunits [9]. The structure of CT also depends on the degree of polymerization of these subunits, stereochemistry, the hydroxylation pattern on the “A” and “B” rings of the flavan-3-ol subunits and the presence or absence of the 3-hydroxyl group in the molecule [6,8]. In addition, CT are amphipathic molecules with aromatic (hydrophobic) rings and hydroxyl (hydrophilic) groups, allowing for bonds with different molecules, from proteins and minerals to polysaccharides and other plant secondary compounds [10].

The abundance of CT in the leaves of forest trees and early findings on the negative relationship between CT concentration and levels of insect herbivory led to the proposal that CT evolved as a quantitative chemical defense against insect herbivory [11]. This early view was reinforced by the fact that there are no compelling findings suggesting that CT have a fundamental role in plant physiological processes [12,13]. Nevertheless, several recent studies have failed to show a consistent protective role for CT against herbivory (*i.e.*, [14,15]), and thus, the role of CT as a defensive chemical has been challenged. For instance, it has been noted that the vision of CT as toxins is at odds with the fact that humans have enjoyed CT in drinks and foods for thousands of years [4]. Moreover, recent evidence suggests that at appropriate doses, CT may enhance the nutrition and health of consumers, as well as the quality of milk and meat products [16–18].

In ruminants, the binding and precipitation of dietary proteins by CT shifts the site of protein digestion from the rumen to the intestines and nitrogen excretion from urine to feces [19]. Such shifts can improve the nutrition of ruminants [20] in feeds that have a greater concentration of soluble protein than is required for carbohydrate utilization by rumen microbes, which is the case with most well-managed forage legumes. Moreover, improving the protein nutrition of ruminants enhances immune responses [21,22], which may increase resistance to gastrointestinal nematodes [23]; increasing the essential and branched-chain amino acids reaching the small intestine also improves reproductive efficiency in ruminants [24]. By consuming CT-containing forages, herbivores alleviate bloat [25], reduce methane emissions [26,27] and reduce internal parasites [21]. For instance, CT-containing legumes, like sainfoin (SF; *Onobrychis viciifolia* Scop.), have antiparasitic activity against helminth nematodes [28], and sheep appear to recognize this benefit of SF during grazing by increasing their selection of this forage when challenged by parasitic burdens [29]. Further, when herbivores consume feeds containing CT, their meat is lighter in color, with a greater concentration of

antioxidants and omega-3 compared with omega-6 fatty acids, reduced “pastoral” flavor [30] and is generally more desirable for human consumption [16,17,31,32].

For this review, we will focus on the beneficial effects of CT and CT-containing temperate legumes in ruminant diets and the potential interactions that can enhance such effects. Both birdsfoot trefoil (BFT; *Lotus corniculatus* L.) and SF perform well under irrigation in the high pH soils and cool-temperate climate of the Mountain West USA, and both are beneficial for ruminant productivity [4,18].

## 2. Condensed Tannins in Temperate Forage Legumes

The CT synthesized in forage plant species differ in molecular weight and the type and proportion of subunit (see the comprehensive appendix of [4]). The most commonly-cultivated temperate forage legumes are alfalfa (*Medicago sativa* L.) and white clover (*Trifolium repens* L.). Alfalfa expresses CT in its seed coat, and white clover expresses CT in its flowers. The selection of white clover for elevated floral CT [33] resulted in white clover shoot CT concentrations as great as 12 g·kg<sup>-1</sup> dry matter (DM). Alfalfa and white clover have recently been genetically engineered to express CT in their leaves [34], but commercial release of CT-containing cultivars is anticipated to require nine years or more [35,36]. Two forage plant species that grow well in the Mountain West USA and that naturally contain significant concentrations of CT in their leaves are BFT, which contains 10 to 40 g·CT·kg<sup>-1</sup> DM, and SF, which contains 30 to 80 g·CT·kg<sup>-1</sup> DM [9].

### 2.1. Grass and Legume Forages

Grazing-based cattle and sheep production is commonly carried out on grass or mixed grass-legume pastures. The rapid digestibility and greater accessibility of proteins in legumes, such as alfalfa and white clover, can result in bloat if these forages constitute more than 25% of a pasture mixture [37] or if they occur in patches that can be selected by ruminants. However, CT concentrations as little as 5 g·kg<sup>-1</sup> DM can prevent bloat [38], so pastures composed of CT-containing legumes can be grazed without restriction. Ruminant intake is negatively correlated with forage fiber concentration, and intake is greater for ruminants fed legumes than grasses [39]; ruminant production on forages is a function of intake, which is typically limited by rumen fill and fiber digestion [40]. At similar stages of forage maturity, legumes have less fiber than grasses (e.g., [41]) and can be digested more readily. The protein content of forage legumes is often greater than the dietary protein requirement of ruminants, and when the available protein exceeds the available carbohydrate (*i.e.*, energy) in the rumen, amino acids will be used for energy [42]. This results in an undesirable generation of ammonia that is excreted in urine or milk [43].

### 2.2. The Beneficial Role of Some Condensed Tannins in Ruminant Digestion

Condensed tannins prevent bloat by binding to and precipitating proteins, which reduces protein concentration in the rumen and increases rumen bypass or “undegradable” protein [44]. The CT expressed by many forages can bind to salivary proteins, reducing palatability and intake; CT can also form indigestible complexes with rumen microbes and cell wall carbohydrates, reducing the rate of rumen digestion and intake [45]. As a result, forages, such as big trefoil (*Lotus pedunculatus* Cav.), can

prevent bloat, but also reduce ruminant productivity [46]. The CT in BFT is present in a relatively low concentration and is not reported to inhibit intake or digestion [47,48]. Birdsfoot trefoil CT precipitates excess plant proteins in the rumen, preventing bloat, but it does not suppress post-ruminal digestion of proteins or absorption in the small intestine [4,49]. This has resulted in consistently better productivity of sheep fed BFT compared with alfalfa [50,51] and cattle fed BFT compared with non-CT legumes [52,53].

### 3. Ruminant Production on CT Legumes in the Western U.S.

#### 3.1. Conventional Beef Production

The conventional North American beef production system consists of a low-input, grazing- and hay-based cow-calf phase lasting 11 months to 12 months and a high-input feedlot phase in which a ration comprised primarily of grain is fed for three to four months, for a total of 14 months to 16 months from birth to slaughter. The resulting grain-finished beef is juicy and tender; the intramuscular fat content of the longissimus muscle of beef graded choice ranges from 4% to 8% [54]. Alternatively, weaned calves that are never fed grain, antibiotics or hormones may be certified as grass-fed beef [55] and typically are slaughtered at 18 months to 24 months [56]. The longissimus intramuscular fat concentration of grass-finished beef is approximately half that of grain-finished beef [57].

#### 3.2. Beef Production on a CT-Containing Forage Legume

Birdsfoot trefoil is productive and persistent in the northern Mountain West [58], typically continuing to increase in DM yield for two years after planting [59]. In production-scale swards, mature BFT stands averaged approximately 7000 kg·ha<sup>-1</sup> per year in the second and third year after planting [60], about two-thirds the DM yield of grazing types of alfalfa [59]. In a study carried out at Utah State University (USU), yearling Angus (*Bos taurus*) steers that were finished for 111 days (3.7 months) gained 0.55 kg·day<sup>-1</sup> on introduced grass pastures, 0.95 kg·day<sup>-1</sup> on BFT pastures or 1.74 kg·day<sup>-1</sup> on a concentrate diet [61]. Steers that averaged 451 kg when treatments were initiated weighed 512 kg, 557 kg and 644 kg at slaughter when finished on grass, BFT and concentrate, respectively. Stocking densities were low; post-grazing pasture DM did not fall below 1700 kg·ha<sup>-1</sup>. Expressed as the number of cattle required to produce one billion pounds of beef (Table 1; adapted from [62]), estimates from USU studies for cattle finished on grass (USU grass-finished (GFD); 3.4 million) were similar to those reported for current model predictions (GFD; 3.6 million) [62]. The estimate of the number of cattle required to produce one billion pounds of beef with BFT (USU BFT), however, was 2.9 million cattle, which compared favorably with Capper's [62] estimate for feedlot finishing in a U.S. conventional system that includes growth-enhancing feed additives (2.7 million) or in a feedlot system that does not include growth-enhancing feed additives (natural; 3.0 million). Age at slaughter ranged from 14.6 months for feedlot-finished beef to 22.6 months for grass-finished beef in Capper's [62] estimate, while the USU cattle were all slaughtered at 18 months. This comparison illustrates the importance of dressing percentage, which was 62% for BFT-finished beef and 64% for feedlot-finished beef. The dressing percentage for grass-finished beef in both reports was similar:

57.5% for GFD and 57% for USU GFD [62]. Time to finishing for all cattle in the USU study was 18 months, while time to finishing varied from 14.6 months for feedlot-finished cattle to 22.6 months for grass-finished cattle in Capper's [62] estimate.

**Table 1.** Capper [62] calculated the number of days to slaughter, final weights, dressing percentage and the number of cattle required to produce 1 billion kg beef for three U.S. beef production systems: CON (feedlot concentrate-finished), NAT (CON without growth-enhancing feed additives) and GFD (grass-finished). Results from Pitcher [61] have been compared in columns labeled USU (Utah State University). Treatments were USU NAT (CON without growth-enhancing feed additives), USU BFT (birdsfoot trefoil-finished) and USU GFD (grass-finished). Output is the number of cattle required to produce 1 billion kg red meat.

	Time in System (day)					
	CON	USU NAT	NAT	USU BFT	GFD	USU GFD
Pre-weaned beef calf	207	215	207	215	207	215
Stocker	123	216	159	216	159	216
Yearling finishing	<u>110</u>	<u>111</u>	<u>110</u>	<u>111</u>	<u>313</u>	<u>111</u>
Total in days	440	542	476	542	679	542
Total in months	14.6	18	15.8	18	22.6	18
	Weight (kg)					
	CON	USU NAT	NAT	USU BFT	GFD	USU GFD
Pre-weaned beef calf	245	289	245	289	226	289
Stocker	122	162	122	162	67	162
Yearling finishing	<u>204</u>	<u>193</u>	<u>163</u>	<u>106</u>	<u>192</u>	<u>61</u>
Total weight	571	644	530	557	486	512
Dressing percentage (%)	63.8	58.1	63.3	62.1	57.5	57.0
Cattle required for $1 \times 10^9$ kg red meat	2,745,005	2,672,625	2,980,715	2,891,034	3,585,836	3,426,535

The underlining signifies that the numbers in the next row are the sums of the first three rows in both the upper and lower halves of the table.

Cattle from the three USU treatments in Table 1 were slaughtered, and steaks from the longissimus muscle were subjected to consumer sensory evaluation. For the characteristics tenderness, juiciness, degree of fattiness and overall preference, steaks from BFT-finished steers were comparable to steaks from grain-finished steers and preferred to steaks from grass-finished steers [63]. The fatty acid composition of steaks from these treatments was also determined, and the meat from grass- and BFT-finished steers had an equivalent ratios of omega-6 (n-6) to omega-3 (n-3) fatty acid concentrations, and both were less than the n-6:n-3 of grain-finished beef, with greater n-3, as well as reduced n-6 in BFT-finished beef [64]. Likewise, beef from cattle fed CT-containing SF had greater marbling scores, quality grades (select *versus* standard) and backfat thicknesses than alfalfa-fed animals. Steaks from cattle finished on CT-containing SF were redder in color than steaks from cattle finished on alfalfa and contained more unsaturated fatty acids [65].

In a 2014 grazing study, the enteric methane emissions of beef cows grazing BFT were half those of cows grazing meadow brome grass (*Bromus riparius* Rehm.) [61]; we believe these are the first data

comparing enteric methane emissions of grazed perennial grasses and CT legumes. Along with the reduction of excess rumen protein due to CT, BFT has a relatively great concentration of non-fibrous carbohydrate [66] that could contribute to the elevated gain and dressing percentage observed for the BFT-finishing treatment.

### 3.3. Dairy Production on a CT-Containing Forage Legume

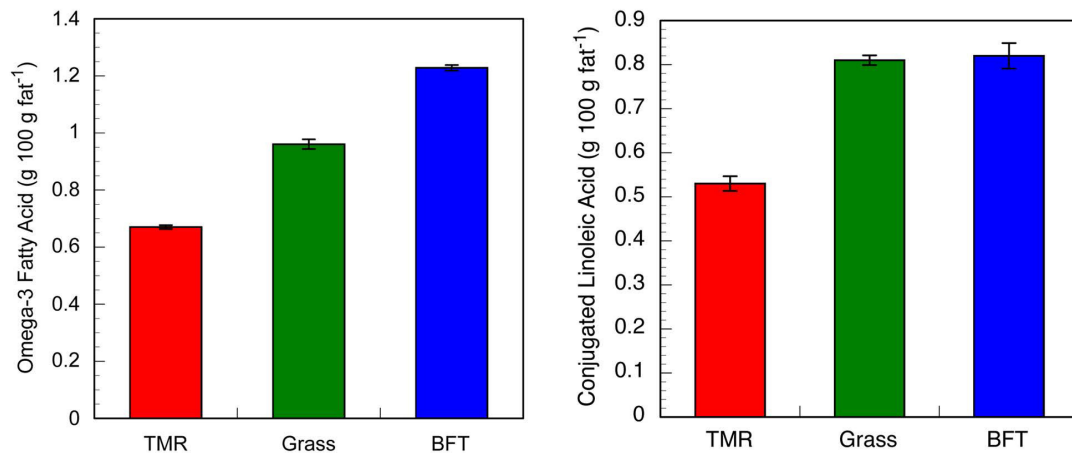
In a study carried out on a commercial organic dairy in southeast Idaho USA, an 8-ha sprinkler-irrigated grass pasture was subdivided, and 4-ha were cultivated and seeded with ‘Norcen’ BFT in late summer of 2011. Data were collected on establishment in autumn of 2011 and spring of 2012 [67], and forage and milk production data were collected in 2012 and 2013. Grass pastures were comprised of *Lolium perenne* L., *Dactylis glomerata* L., *S. arundinaceus*, *Elymus repens* (L.) Gould and *T. repens* L. Nine Holstein dairy cows rotationally grazed either the BFT or the grass pasture. Cows were also fed 2.27 kg of barley each day, which included a vitamin and mineral supplement, and moved to fresh paddocks after each milking (every 12 h). Intake was estimated with a rising plate meter as the difference between pre-grazing and post-grazing DM. Milk production was measured at the beginning of the study and every two weeks by collecting milk from each cow at four successive (two morning and two evening) milkings.

Forage intake and milk production were significantly greater on BFT in 2012 and 2013 (Table 2). A medium cheddar cheese was made from the milk of cows grazing grass and BFT pastures and compared with cheese made at the same time from the milk of non-organic cows fed a total mixed ration (TMR). Cheese made from the milk of pasture-fed cows was significantly greater in omega-3 fatty acids and conjugated linoleic acid than cheese made from the milk of TMR-fed cows. The omega-3 fatty acid concentration of cheese made from the milk of BFT-fed cows was also significantly greater than that of cheese made from the milk of grass-fed cows (Figure 1).

Birdsfoot trefoil is a tap-rooted legume, like alfalfa, giving it an agronomic advantage over grasses [68] even under irrigation in an environment that has low humidity and elevated evapotranspiration, such as the semi-arid Mountain West. The BFT was inoculated with *Mesorhizobium loti*, so it was receiving nitrogen from a symbiotic relationship with soil bacteria. Legumes typically have more crude protein and less neutral detergent fiber than grasses [69], which increases the rate of forage digestion, resulting in greater intake [70]. Dairy intake and production on BFT pastures likely benefitted from the combined effects of plant adaptation, morphology, nutritive value and CT concentration.

**Table 2.** Mean intake and milk production on pastures in 2012 and 2013.

Year	BFT Intake	SEM	Grass Intake	SEM	BFT Milk Production	SEM	Grass Milk Production	SEM
	kg/ha				kg/cow/day			
<b>2012</b>	1603	235	773	149	30	1.4	25	1.6
<b>2013</b>	2183	256	1301	181	35	0.7	30	2.1



**Figure 1.** Omega-3 (left) and conjugated linoleic fatty acid concentrations (right) of cheese made from the milk of organic dairy cows grazing mixed grass pastures or birdsfoot trefoil (BFT) pastures, compared with cheese made from the milk of non-organic cows fed a total mixed ration (TMR).

#### 4. Chemical Interactions of Condensed Tannins within a Dietary Context

The aforementioned analysis describes recent findings on the positive effects of CT and CT-containing legumes on ruminant nutrition and product quality. However, ruminants ingest a diversity of chemicals during grazing, from those present in a single forage to those ingested with a diverse diet. Thus, there is potential for multiple interactions among all of the different chemicals ingested within and between meals; this is particularly true for CT, since as stated above, these biomolecules are highly reactive.

##### 4.1. Interaction with Proteins

The CT-protein interaction has been given considerable attention since the basis for the role of CT in chemical defense has been attributed to their ability to precipitate plant proteins and gastrointestinal enzymes [5,71], despite the fact that the CT-protein bond may be prevented or reversed [71].

The formation of CT complexes involves covalent and non-covalent bonding with other molecules [5]. During oxidative coupling, covalent bonds are formed by the conversion of phenols to quinones or semi-quinones, and these bonds are not reversible [2]; however, the CT-binding mechanism in a dietary context typically involves non-covalent forces (*i.e.*, hydrogen bonds and hydrophobic interactions), which are reversible [10,72]. Condensed tannins that interact predominantly via hydrogen bonds form stronger complexes with dietary proteins than those based on hydrophobic interactions. Therefore, CT that form hydrogen bonds with proteins are more likely to result in ruminal escape proteins, while CT that interact with proteins via hydrophobic bonds form weaker complexes [4]. Condensed tannin-protein complexes formed by hydrogen bonds are stable in the rumen at pH values close to neutrality, but may become unstable in the more acidic (*e.g.*, pH 2.5 to 3.0) abomasum. The protein released from the disrupted complex provides amino acids for digestion and absorption in the small intestine at pH 8.0 to 9.0 [49,73].

Weaker CT-protein bonds may also mean an increased likelihood for interactions of CT with chemical structures present in the broad array of plant species ingested by herbivores, such as in pastures with diverse forage species composition [74]. Such interactions may lead to antagonistic effects that reduce the bioavailability of CT or to synergistic effects that increase their bioactivity [74]. As an example, the negative post-ingestive effects of different CT may be attenuated due to complexation when they are consumed in the same meal. It has been observed that DM intake by sheep is enhanced as the number of CT-containing shrubs in the diet increases relative to single shrub diets [75]. Likewise, phenolic compounds have been shown to have antagonistic interactions, making some of them (e.g., resveratrol) much less bioavailable when other phenols are present in the diet [76]. In contrast, other nutrient or plant chemical interactions may increase the activity or bioavailability of CT. Synergistic effects have been observed between increments in dietary calcium concentration and the bioavailability of resveratrol, a phenolic compound found in grapes and berries [77].

#### 4.2. Interactions with Carbohydrates

It has been reported that greater CT concentrations depress rumen digestion of both readily fermentable and structural carbohydrates [44,46,78]. These effects are likely to be caused by an inactivation of extracellular microbial and mammalian enzymes through the formation of CT-enzyme complexes [79], rather than by a direct CT-carbohydrate interaction. In addition, CT can potentially interfere with the adhesion process of microbial bacteria onto forage cell walls, which can also lead to a depression in structural carbohydrate digestion [79].

#### 4.3. Interactions with Saponins

Steroidal and triterpenoid saponins are a family of chemical compounds consisting of an isoprenoidal-derived aglycone (sapogenin), covalently linked to one or more sugar moieties [80]. Saponins are generally regarded as plant defenses, although several valuable pharmacological properties have recently been identified, such as anti-cancer, immunomodulatory and cholesterol-lowering activities [81]. In addition, saponins have been shown to reduce methane emissions [82] and to control gastrointestinal nematodes in ruminants [83]. The anthelmintic effects of CT and saponins can be explained through their toxic effects on parasites [84].

Consuming a diversity of plant secondary compounds like saponins and CT may reduce the overall toxic effect of the mix, as the formation of gastrointestinal complexes could reduce the absorption and activity of single toxic compounds [85]. In support of this, it has been found that intestinal bonding of CT and saponins results in moderated toxic effects, representing a mechanism that allows herbivores to consume more nutrients when offered diverse foods [86]. Condensed tannins and saponins cross-react and bind in the gastrointestinal tract, nullifying the effects of both compounds [86]. For example, goats increase intake when shrubs contain a combination of CT and saponins relative to when animals are offered single shrubs [75], and sheep offered a choice between saponin- and CT-containing rations ate more feed than animals only offered CT or saponins in single rations [87]. However, the *in vivo* antiparasitic effect of the CT-saponin combination was found to be less than that of the single rations [87]. Thus, a reduction in the negative impacts of CT or saponins on the herbivore (*i.e.*, through inactivation) can be carried over to the endoparasite, resulting in beneficial effects for both the herbivore and the parasite.



In other words, the complexation (and potential inactivation) of CT and saponins can be beneficial to the ruminant relative to nutrient intake, but negative in regard to its effects on parasite loads. This suggests that the value of the interaction between saponins and CT may depend on whether concern is with nutrient intake or antiparasitic activity.

#### 4.4. Interactions with Alkaloids

Condensed tannins are known to complex not only with proteins and saponins, but also with alkaloids [88]. Alkaloids are nitrogen-based secondary compounds, and the strong binding capacity of CT for nitrogen-containing compounds [89] may be responsible for this interaction. Stable complexes between alkaloids and CT made alkaloids less available in the gastrointestinal tract, thus reducing their toxic effects [90]. A CT-containing legume like BFT ingested prior to eating endophyte-infected (E+) tall fescue (*S. arundinaceus* or reed canarygrass (*Phalaris arundinacea* L.)), both alkaloid-containing forage grasses, enabled lambs and calves to consume more tall fescue or reed canarygrass (and therefore more energy and protein) than lambs and calves fed the same grasses without the legumes [91–93]. Likewise, lambs offered CT-containing supplements ingested more alkaloid-containing rations than lambs offered just the alkaloid-containing rations [94,95]. Lambs offered a choice of alfalfa with an elevated saponin concentration, BFT containing CT and E+ tall fescue containing alkaloids preferred alfalfa [96]. However, lambs receiving intraruminal infusions of saponins increased their preference for BFT and E+ tall fescue, and lambs receiving intraruminal infusions of CT increased their preference for E+ tall fescue. Overall, these results support the notion that CT complex with other secondary compounds and attenuate negative post-ingestive effects of individual components of the complex.

Recent evidence further supported the interaction of CT and alkaloids: polyethylene glycol, a polymer that selectively binds to CT, reduced the benefits of SF CT on a basal diet containing E+ tall fescue in sheep [90]. These benefits included an increase in the total amount of nutrients ingested and improvements in some physiological parameters indicative of fescue toxicosis, such as reduced rectal temperatures, increased numbers of leukocytes and lymphocytes and increased plasmatic concentrations of globulin and prolactin compared with control lambs that consumed E+ tall fescue without CT-containing SF. Radial diffusion assays [97] in which tannins with or without ergot alkaloids were precipitated as they diffused through agar containing bovine serum albumin demonstrated that ergotamine, an alkaloid from E+ tall fescue, reduced the protein binding capacity of CT from SF and BFT (B. Goff, personal communication). This *in vitro* evidence supports *in vivo* observations of increased intake of E+ tall fescue seed by lambs consuming SF, but reduced intake by lambs consuming the non-CT forage legume cicer milkvetch (*Astragalus cicer* L.) [98].

#### 4.5. Interactions with Terpenes

Terpenes are a large and diverse class of carbon-based secondary compounds, biosynthetically derived from isoprene subunits [99] and produced by a variety of plants, particularly woody species. Evidence suggests that CT bind to terpenes and reduce their bioavailability. When offered feeds with higher levels of terpenes and CT, sheep consumed more feed containing terpenes if they first consumed feed with CT [100]. Likewise, sheep with a preference for terpene-containing sagebrush

(*Artemisia tridentata* Nutt.) consumed considerably more CT-containing bitterbrush (*Purshia tridentata* (Pursh) DC) than sheep with less preference for sagebrush [101]. These findings are consistent with the hypothesis that terpenes and CT interact in the digestive system of sheep. Finally, lambs offered CT- and terpene-containing feeds consumed more than when they were offered only one feed [102], which again suggests the formation of CT-terpene complexes with reduced toxicity.

## 5. Conclusions

Condensed tannins are a family of plant secondary compounds with diverse structures and multiple impacts on herbivores that can range from detrimental to beneficial. Condensed tannins can form complexes with proteins, as well as with other plant secondary compounds. The temperate forage legumes BFT and SF have CT concentrations ranging from 10 g·kg<sup>-1</sup> to 80 g·kg<sup>-1</sup> and protein concentrations ranging from 12 g·kg<sup>-1</sup> to 25 g·kg<sup>-1</sup>. Their CT are generally beneficial to ruminants by eliminating bloat, suppressing internal parasites, reducing enteric methane emissions and increasing the quantity of protein that is absorbed from the intestines. Our studies have demonstrated greater productivity of beef cattle fattened on BFT compared with other forages and greater milk production of commercial dairy cows grazing BFT compared with cows grazing grass pastures in mid-summer. We have also demonstrated the attenuation of negative tall fescue endophyte effects when CT were ingested along with E+ tall fescue. One of the next challenges in the study of CT-containing forages is to relate CT biochemical structures to CT activities within the ruminant gut, particularly to balance beneficial effects on protein digestion with suppressive effects on parasites and toxic secondary compounds.

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## Author Contributions

The authors contributed equally to the content of this article.

## Conflicts of Interest

The authors declare no conflict of interest.

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